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AN ANALYSIS OF REVERSAL LEARNING IN RELATION
TO THE COMPLEXITY OF TASK IN WHITE RATS

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(Received January 12. 1962)

In the first paper of this series (Dąbrowska 1959a) repeated reversal learning of a complex habit in a serial multiple choice apparatus was described. The apparatus consisted of a platform with four successive partitions, each of them having four doors one of which was unlocked. It has been shown that the number of trials necessary to reach criterion was much smaller in the reversal training than in the original, and it decreased with further reversal trainings until it reached about 1/6 of trials needed in the original learning. Similar results were obtained earlier by Webb (1917), Wiltbank (1919), Hunter (1922), Jackson (1922) and others. However, only one reversal training took place in their experiments. On the other hand, there is considerable evidence to show that under many experimental conditions reversal training is not easier than the original one, but rather more difficult, (Frits 1930, Munn 1932, Konorski and Szwejkowska 1952, 1956, Dąbrowska 1961). In all these experiments the task presented to the animals consisted in a change of a single conditioned reaction, i.e. it was much simpler for the animal than the preceding task.

It should be stressed, however, that experiments showing increased difficulty of reversal training in comparison with the original training were performed by different techniques from those used in our experiments. Therefore the important problem arose as to whether the discrepancy between the two lines of investigation was due to the different techniques, or only due to the complexity of the presented task. In order

to solve this question it was necessary to present tasks of various complexity to the animals in one and the same apparatus, and to see what relation there would be between the rate of the original and the reversal learning. The present paper is concerned with this problem.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were carried out on 20 white rats at the age of 3 months. The apparatus used is shown in Fig. 1. It consisted of a platform with parallel partitions with two one-way doors. In each partition one door was locked and the other was unlocked. Food was placed behind the fourth partition. Starting points

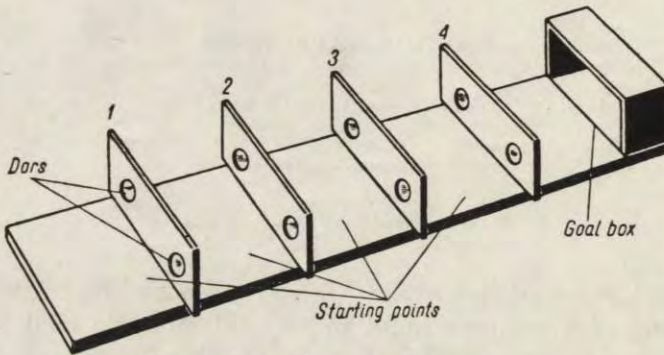


Fig. 1. Experimental apparatus

Table I

Task presented for each group of rats
Unlocked doors

Partitions Groups	Original training				Reversal training			
	I	II	III	IV	I	II	III	IV
1	L	L	R	R	R	R	L	L
2		L	R	L		R	L	R
3			L	R			R	L
4				L				R

L — left door
R — right door

Each experimental session consisted of 6 trials given with 20 second-intervals. The criterion was reached when the animal made 6 successive correct runs.

The animals were divided into 4 groups, each containing five rats. The starting point for the first group was situated before the fourth partition, that is, in

order to reach the goal, the rats had to pass only one door. The rats of the second group started from before the third partition which necessitated crossing two doors. For the third group crossing three partitions was required to reach the goal, and the fourth group had to cross all four partitions.

After the animals had reached the criterion, reversal training was carried out in which all the doors were changed. The tasks presented for each group of rats are shown in Table 1.

RESULTS

The results of our experiments are presented in Table 2 and summarized in Fig. 2.

Table II

Number of runs to criterion in original and reversal learning

Group	1			2			3			4		
	OL	RL	RL/OL	OL	RL	RL/OL	OL	RL	RL/OL	OL	RL	RL/OL
Number of runs for each animal	38	16	0.4	33	17	0.5	19	21	1.1	2	6	3
	37	15	0.4	33	16	0.5	18	24	1.3	6	6	1
	36	17	0.5	35	15	0.4	16	14	0.9	2	7	3.5
	34	16	0.5	32	15	0.4	16	21	1.3	1	9	9
	36	18	0.5	34	13	0.4	11	21	1.9	2	3	1.5
	Mean	36.2	16.4	0.5	33.4	15.2	0.4	16	10.2	1.3	2.6	6.2

CL — original learning

EL — reversal learning

EL/OL — ratio of reversal learning to original learning.

It may be observed that in the original training the number of trials needed to reach criterion depended on the complexity of the task i.e. on the number of partitions the animal had to cross. This dependence, however, is far from being linear, since the one-partition task requires on an average 6 times less trials than the two-partition task, and 13 times less than the three partition-task. On the other hand, the ratio between the number of trials with 4 partitions and those with 3 partitions is not $4/3$ but only $9/8$.

As far as the reversal training is concerned the picture was more complicated. In the two easier tasks (groups 1 and 2) the reversal training required more trials than the original training, while in the two more difficult tasks (groups 3 and 4) the contrary was true (Fig. 2). In consequence, the relation between the rate of reversal training and the com-

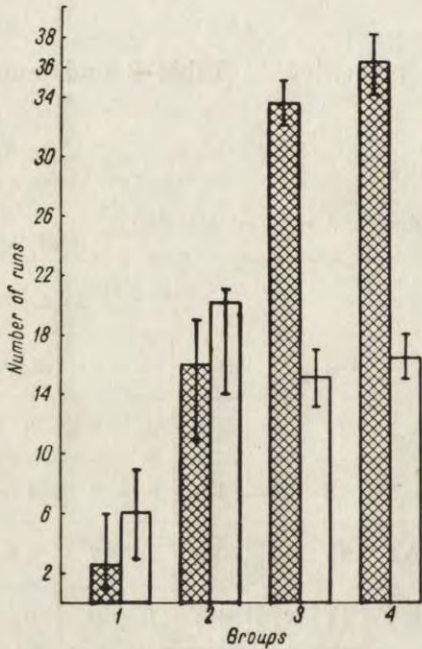


Fig. 2. Number of runs to criterion in original and reversal training

Dark blocks — number of runs in learning, white blocks — number of runs in reversal learning

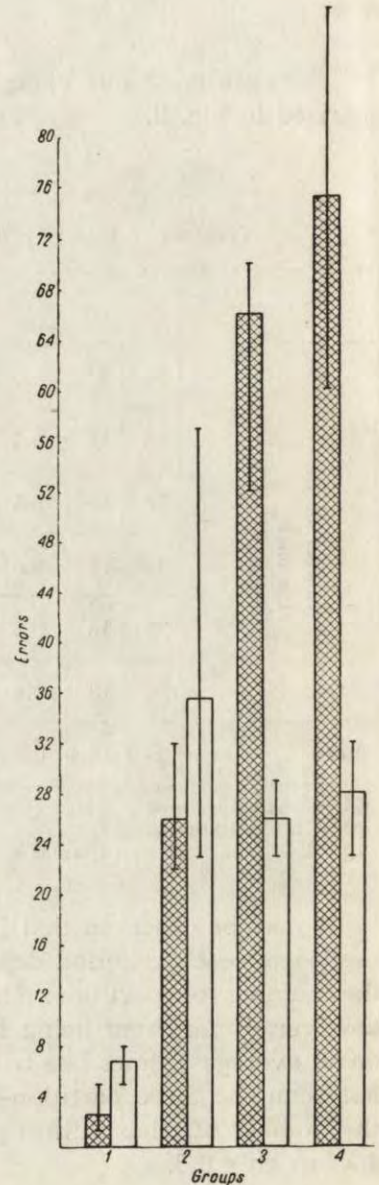


Fig. 3. Number of errors to criterion in original and reversal learning

Dark blocks — number of errors in learning, white blocks — number of errors in reversal learning

plexity of the task was disturbed, the third group of rats requiring more trials to reach criterion than the fourth group.

The same picture is seen when, instead of the numbers of trials, we take into consideration the numbers of errors (Fig. 3). Here, too, we notice that in groups 1 and 2 the number of errors committed in the reversal learning is greater than that in original learning, while in groups 3 and 4 it is smaller.

DISCUSSION

Our results show that by using the same experimental procedure we can obtain either the higher or the lower rate of reversal training in comparison with the original training, and that this depends entirely on the complexity of the task the animal is confronted with. Thus, in the simple tasks reversal training is more difficult than the original training, in the complicated tasks, it is much easier.

How are these results to be explained?

To begin with, let us take into consideration the first group of rats which was confronted with the easiest task, namely with changing only one door. The results of experiments for this group were analogous to those obtained by other authors in experiments with simple tasks (see above). A physiological analysis of such results was given in papers by K o n o r s k i and S z w e j k o w s k a (1952, 1956). In the experiments of these authors the reversal training consisted either in transformation of the excitatory conditioned reflexes into inhibitory ones, and vice versa, or in the transformation of the defensive conditioned reflexes into alimentary ones, and vice versa. The result showed that the original training was much quicker and more complete than the reversal training. On the basis of their findings the authors put forward „the principle of the primacy of first training” according to which the conditioned reflex to a given stimulus is most readily formed when this stimulus has been not engaged in any prior conditioning. According to the authors the explanation of this principle is the following: when conditioned connections have been formed between two centres, they are not annihilated by reversal training. In consequence, if a new conditioned reflex is antagonistic to the old one, the old connections prevent its establishment. K o n o r s k i and S z w e j k o w s k a gave a number of examples from ordinary life to support this view.

The same principle is easily applicable to our experiments with only one partition. As seen in Table 1, the animals almost immediately mastered the first task, while reversal training was more prolonged since they had to suppress the old habit.

When we turn to the more difficult task involving two partitions, we also see that the principle of the primacy of first training is valid, since in 4 animals out of 5 the reversal training was more prolonged than the original one. Therefore, it seems reasonable to believe that this principle is also valid, if we have to do with more complex tasks but, perhaps, in the latter, some other factor intervenes which changes the relation between the original and the reversal training.

In our previous experiments, published elsewhere, (Dąbrowska 1959a, 1959b) a great body of evidence has been collected to show that in the course of mastering the complex four-partition task the rats tend more and more to integrate the whole task instead of splitting it into four separate tasks. This tendency will be even more clearly seen in the next paper of this series when it will be shown that change of the door in one partition destroys the whole habit. Thus, one may assume that with the course of training the whole run through the four-partition apparatus becomes more and more a unitary process and the reversal training is more and more reduced to the substitution of one unitary process by another. And so, the increased rate of reversal learning compared with original learning is due to the fact that the animal, so to speak, acquires a new improved method of learning this habit.

In consequence, the acquisition of a new pathway in a complex learning task is connected, on one hand, with the suppression of the previous habit which tends to prolong the reversal training, but, on the other hand, it involves an increased learning ability which tends to accelerate it. The actual learning curve is a resultant of these two tendencies.

SUMMARY

The present paper deals with the problem of the relation between the rate of reversal and original learning in respect to the varying complexity of the task presented to the animal.

1. It is observed that if the task is composed of only one reaction or two successive reactions, the reversal training requires more trials and is accompanied by more errors than the original training.

2. If the task is composed of three or four successive reactions, the reversal learning is much accelerated in comparison with the original learning.

3. The reason for the difference between these two cases is discussed.

I wish to express my sincere thanks to Professor Jerzy Konorski for his help in the preparation of this paper.

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THE EFFECT OF MEDIAL LEMNISCAL LESIONS
ON THE INSTRUMENTAL CONDITIONED REFLEXES IN CATS

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In the recent papers by Jankowska (1959), and Górska and Jankowska (1959, 1960, 1961) it has been shown that after a complete deafferentation of a limb in dogs and cats the instrumental CRs involving movements of this limb are not abolished. Although the trained movements are much more clumsy and less precise than before operation, they appear already in the first sessions after operation, and their latent period remains more or less the same. The CR is also preserved in the further training in spite of the fact that the feedback from the given limb is absent.

One of the possible explanations of these results is that the performance of the instrumental movement is not necessarily based on the peripheral feedback, but on the feedback provided by connections within the central nervous system.

In a number of papers (Kuypers et al. 1960, Magni et al. 1959, Jabbur and Towe 1961, Towe and Jabbur 1961) it has been shown that ramifications of the pyramidal tract reach neurones of the nucleus gracilis and nucleus cuneatus, and the impulses fired off to this tract by stimulation of the motor cortex produce facilitating or inhibiting effects on these neurones. Thus, it may be supposed that this very kind of shortened feedback may be the cause of the preservation of the instrumental CR when the feedback from the periphery is lacking.

To test this hypothesis it is necessary to cut the afferent pathways above the nucleus gracilis and cuneatus and to see whether the previously established instrumental CRs will be preserved. The aim of this paper is to elucidate this problem.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on 12 cats weighing from 2,8 to 3,2 kg. After the animals had been habituated to the experimental situation, the CR training was begun, the technique of conditioning being the same as in experiments of Jankowska (1959). The cottonwool was put into the right ear of the cat, and whenever he started to perform scratching movements with his right hindleg, a piece of meat (1 cm.³) was immediately presented to him. Already after two or three experimental sessions, each consisting of 30 trials, the instrumental scratching movements without the cottonwool in the ear appeared. After a few more sessions the animal, when brought to the experimental situation, began to scratch instrumentally so that stimulation of the ear was no more used. The instrumental response differed from the natural scratch response in such a way that the animal either performed a few rhythmic movements without touching the skin, or simply lifted his hindleg.

In the subsequent sessions the instrumental reflex was firmly established and was elicited with maximal frequency regulated only by the duration of the act of eating after performance of the movement. A session, which consisted of 30 trials, usually lasted about 3,5 min.

The operation was performed aseptically in nembutal narcosis in the stereotaxis instrument. It was attempted to destroy bilaterally the medial lemnisci by DC of 2.5 mA. The localization of the coagulating electrodes was determined by recording action potentials elicited by electrical stimulation of the right hindleg.

When the animals recovered after operation the experiments with instrumental CRs were resumed.

After the postoperative testing had been completed, the animals were sacrificed, and their brains were perfused with 10% formalin and removed. The loci of lesions were verified on sections cut at 25 μ in the area of coagulation and stained with the Nissl technique.

RESULTS

With regard to the extent of lesion the cats may be divided into two groups. In group I (3 cats) the lesions were small and limited to the partial destruction of the lemniscal structure (Fig. 1). In group II (9 cats) the whole medial lemniscus was destroyed as well as the following structures in the neighbourhood: the substantia reticularis mesencephalica, tractus segmentalis centralis, substantia nigra, the medial part of the corpus geniculatum mediale, and a small part of the nucleus paralemniscalis (Fig. 2).

Since the behaviour of these two animal groups was different, they will be described separately.

Group I. The postoperative disorder in these animals was very slight and short-lasting. It consisted in a transient decrease of reactions to the nociceptive stimuli in the caudal part of the body. The motor activity was not perceptibly affected; only the performance of skillful movements was somewhat awkward. Placing reaction was abolished



Fig. 1. Transverse sections through diencephalon illustrating small lesions in the medial lemniscus

Black areas denote full destruction; hatched areas, degenerative changes

(Fig. 3a). Immediately after operation the act of eating was strongly disturbed. The animals were not able to grasp food properly and displayed some difficulties in biting and swallowing. Sometimes the squint and a slight disorder of the movements of eyeballs were also seen.

As it was said, all these disorders gradually disappeared, and usually after 10 to 15 days the operated animals virtually did not differ from the normal ones.

The CR activity of this group was practically not changed. The character of the instrumental movements remained the same as before the operation (Fig. 4). The only difference was that the frequency of movements was reduced in the initial period of postoperative training, but this was due to the protraction of the act of eating following the presentation of food (Fig. 5).

Group II. The postoperative condition of the cats with extensive lemniscal lesions was usually very severe. During a number of days the animals were neither able to take food nor to move around. They could not perform any, skillful movements, and their motor coordination was totally destroyed. They also displayed distinct visual and auditory disorders.

Such a remarkable postoperative disability usually lasted 2 to 3 weeks.

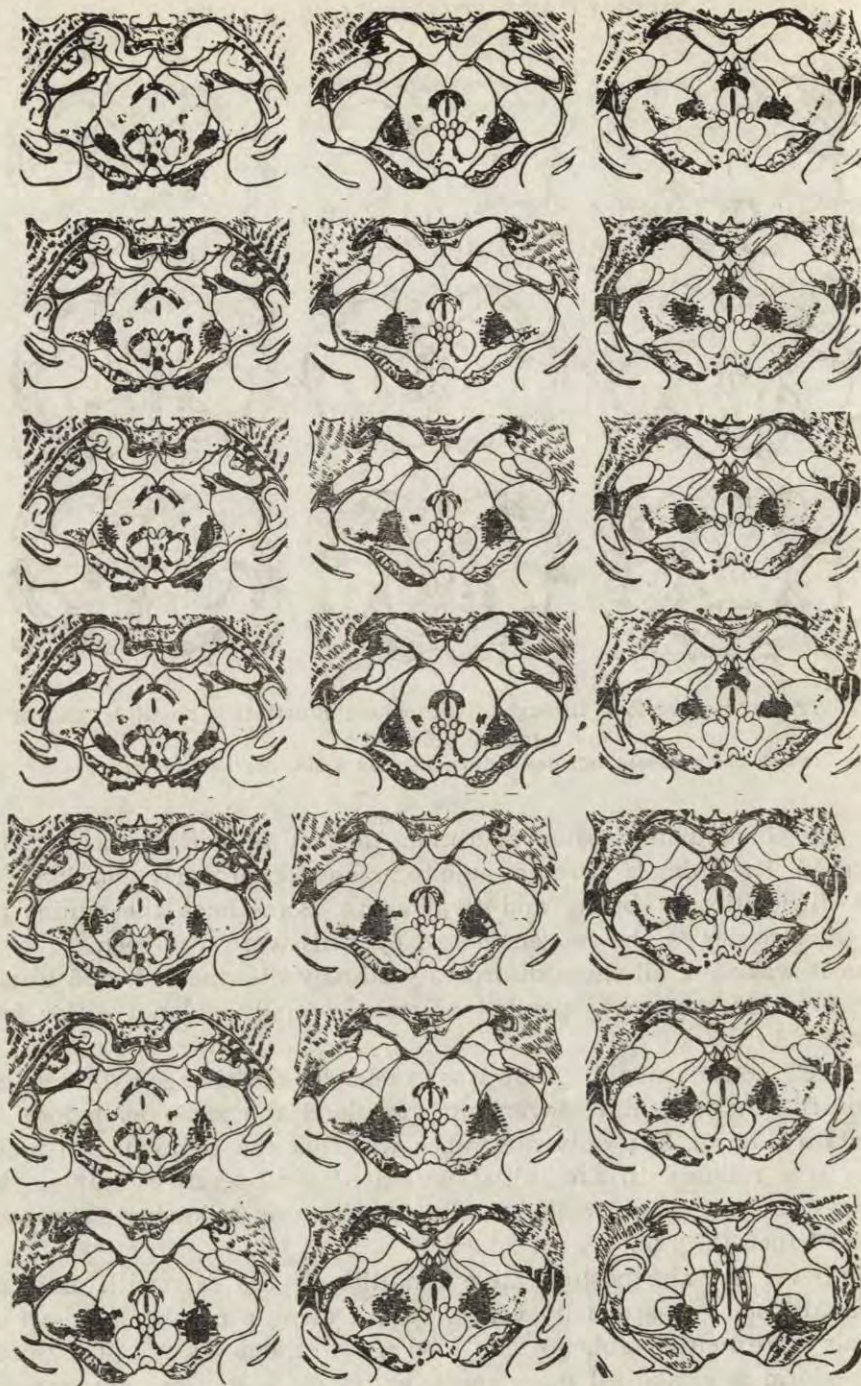


Fig. 2. Transverse sections through diencephalon illustrating large lesions in the medial lemniscus

Black areas denote full destruction; hatched areas, degenerative change

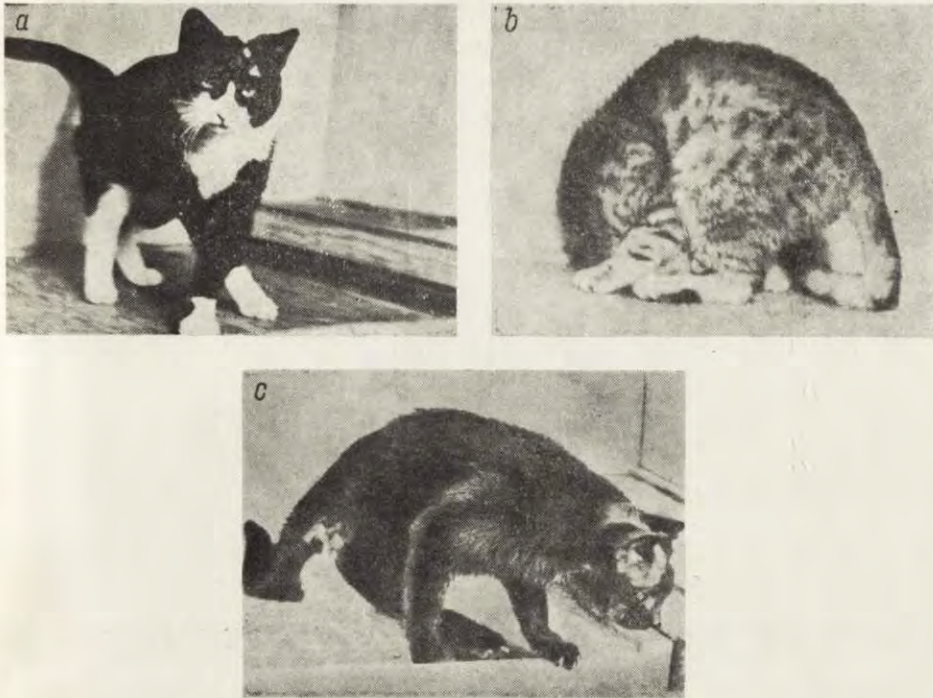


Fig. 3. Disorders of movements caused by lemniscal lesion

a — cat with small lesion, b, c — cats with extensive lesion. Note bizarre postures in cats with large lesions and dirtiness of cat in c

After this period the animals were able to take food spontaneously, and the auditory and (later) visual disorders disappeared. In the majority of animals the spontaneous motor activity such as standing up, lying down, keeping particular postures, etc. was partially restored, but it was far from being perfect. Their walking was clumsy and their legs slid apart. They displayed a prominent ataxia. They often remained for a long period in bizarre positions which they changed very slowly beginning from the forelegs (Fig. 3b and c).

In three cats the ability of spontaneous movements did not recover throughout the period of experimentation (3 to 4 months after operation). These animals were not able to stand up. When set on their legs they fell down, and, if sustained, they performed ambulatory movements.

The reactions to nociceptive stimuli were completely abolished except for the region of the mouth and the upper surface of the neck (and in some animals also of the back), where the pain sensation was apparently not impaired. It was never observed that these cats performed any activities connected with cleaning the fur and skin.

In spite of a considerable impairment of the whole motor activity those cats, in which postural responses and walking in some degree reappeared, were able to perform the trained instrumental movement. This movement, however, was very different from that seen before operation.

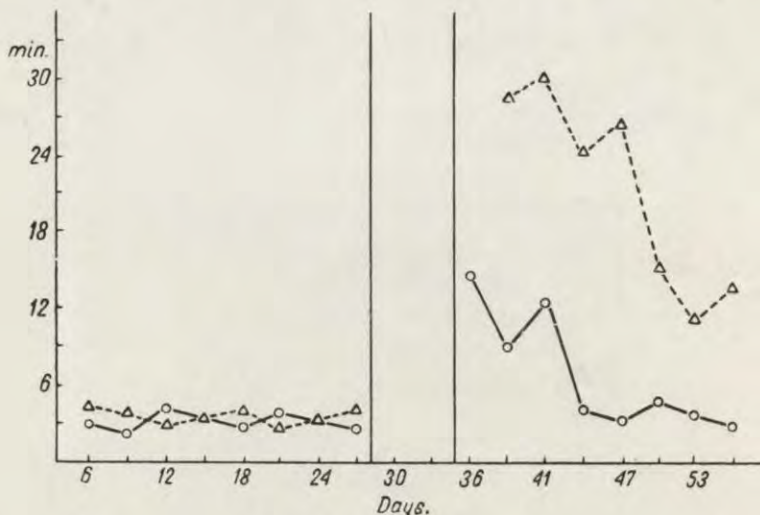


Fig. 4. Duration of experimental sessions (30 trials) before and after lemniscal lesions

Triangles — cats with extensive lesions, circles — cats with small lesions.
Each point denotes mean of three daily sessions

Its most important feature was an utmost irregularity depending on various positions the animal took just before its performance. The amplitudes changed from one trial to another in quite unpredictable manner; instead of high stereotypy of movements observed in normal cats, movements in the lemniscal animals differed one from another and involved various joints. They consisted of some clumsy, uncoordinated flexion without any rhythmical component (Fig. 6a and b). Its frequency was much reduced because of the "technical" difficulties in finding the bodily position being the prerequisite for its performance (Fig. 5).

As mentioned before, in 3 cats the coordinated motor activity did not recover at all, and these cats were not able to maintain the posture enabling them to perform the trained movement. However, if this posture was imposed on them by the experimenter, the animal did perform the trained movement, and since his bodily position remained unchanged, it was even more regular than in less disabled cats (Fig. 6c).

To make sure that the responses observed had a true instrumental character and were not caused by other factors the control experiments



Fig. 5. Changes in instrumental CR after small lemniscal lesion
a, b — before operation; c, d — after operation. Note the normal posture of cats after operation
and slightly reduced amplitude of movements

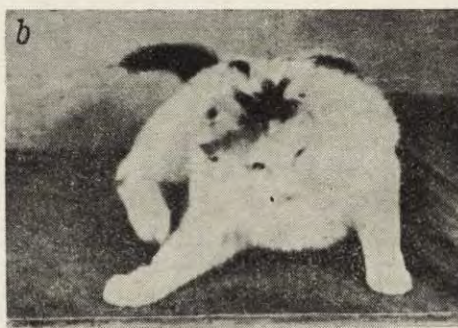
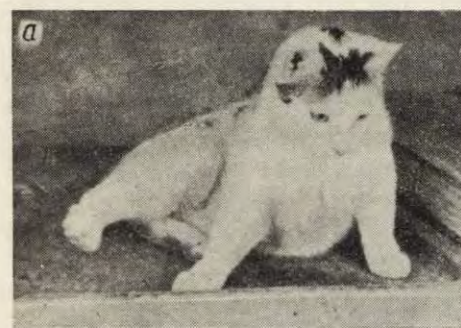


Fig. 6. Changes in instrumental CR after large lemniscal lesions
a, b — cat in which postural reactions partially recovered; c — cat with no postural reactions

were performed in which the same position was imposed on the animal outside the experimental box. In such different situations the cat was lying quietly and never performed any movement of such character.

DISCUSSION

Our data show that the lesions of the medial lemniscus are not followed by the abolition of the instrumental CR established before the operation. When the lemniscal lesion was limited to the region corresponding to the caudal part of the body, the instrumental movement was almost unimpaired. However, even in cats with extensive lemniscal lesions the trained movement was undoubtedly preserved in spite of the very profound impairment of the motor coordination.

These data clearly demonstrate that the hypothesis according to which the instrumental movement depends on the shortened feedback provided by the connection of pyramidal tracts with the nucleus gracilis and cuneatus cannot be held.

Moreover, our results also rule out another hypothesis claiming that the peripheral feedback from the whole body may play a decisive role in preserving instrumental CRs after deafferentation of the limb. The

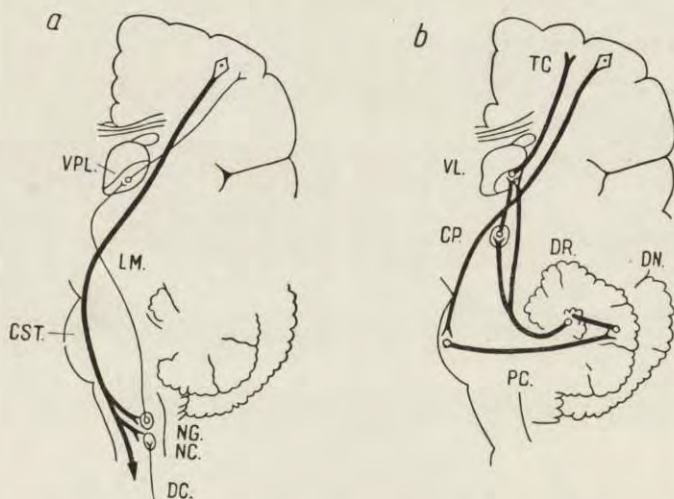


Fig. 7. The diagrams of two loops between the efferent and afferent pathways:

a) pyramido-lemniscal, b) cortico-cerebellar loop

VPL — nucleus ventralis posterolateralis, VL — ventrolateral nucleus, NG — nucleus gracilis, NC — nucleus cuneatus, DN — nucleus dentatus, CST — cortico-spinal tract, TC — thalamo-cortical tract, LM — medial lemniscus, CP — Cortico-pontine tract, PC — ponto-cerebellar tract, DR — dentato-rubral tract, DC — dorsal column

(After Handbook of Physiology — Neurophysiology II. (1959) 819, slightly modified)

extensive lemniscal lesions in group II certainly precluded much of the information from the whole body to the cortex, and yet the trained movement was not abolished.

However, it seems that the hypothesis of shortened feedback being the base of instrumental conditioning cannot be questioned in view of our experiments. We know that a great part of information from muscles reach the motor and premotor cortex through the spino-cerebellar tract, the nucleus interpositus (according to the most recent data of Appelberg 1961), and the nucleus ventrolateralis thalami. On the other hand, as shown first by Adrian (1943), motor cortex sends impulses to the cerebellum through the cortico-pontine tract, thus securing another intercentral feedback which may play a role in instrumental conditioning. It is also possible that any of the two feedbacks described above may be sufficient for the preservation of the instrumental CR and only destruction of both will lead to its abolition (cf. Fig. 7a and b).

These hypotheses should be tested by further experimentation.

SUMMARY

1) The effects of lesions in medial lemniscus on instrumental CR involving the movement of the hindleg were studied in cats.

2) It has been found that the lesions limited to the projection of the caudal part of the body did neither impair the trained movement nor the general motor activity.

3) The more extensive lesions affecting the whole bulk of the lemniscus and adjacent structures produced a remarkable deterioration of the whole motor activity; but the instrumental response was preserved, although it became very irregular and atactic.

4) The significance of these results for the understanding of the mechanism of instrumental CRs is discussed.

I wish to express my thanks to Professor Jerzy Konorski for his kind help in the preparation of this paper.

Also special appreciation is due to Mrs. Cecylia Borkowska for technical assistance.

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CONDITIONED INHIBITION OF THE AVOIDANCE REFLEX

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According to a concept put forward by Konorski and Miller (1933, 1936) and Konorski (1948), later verified experimentally by Sołtysik (1959, 1960a,b,c) and Sołtysik and Kowalska (1960), a firmly established avoidance conditioned reflex (CR) consists of a chain of three acquired reactions:

1° the first is a conditioned fear response (CR_f) elicited by a positive conditioned stimulus (CS);

2° the second, an instrumental motor response (M_{av}) terminating the action of the CS and thus protecting the animal from the nociceptive unconditioned stimulus (US);

3° the third is the inhibitory effect of the afferent feed-back of the instrumental response cutting short the CR_f .

This latter effect is necessary for stabilizing the emotogenic role of the warning CS, because in well established avoidance reflex no US is applied (cf. Sołtysik 1960a,b,c).

The fact that the US is not used in a firmly established avoidance reflex makes the normal procedures of extinction and other inhibitory procedures impossible. Several other procedures of extinction were proposed instead. They consisted in either repetitive presentation of the CS without US and the simultaneous prevention of the performance of the avoidant movement (Solomon, Kamin, and Wynne 1953, Page 1953, 1955, Black 1956, 1958), or in punishing the avoidant response with shock (Solomon et al. 1953, Sołtysik and Zieliński 1961), or else in delaying the termination of the CS beyond the moment of performance of the M_{av} (Bregadze 1953, Bregadze and Akhmeteli 1953, Fonberg 1952, 1960, Sołtysik and Zieliński 1961).

The same method of Bregadze and Fonberg was effective in the differentiation training (Bregadze 1953, Fonberg 1960, Zbrożyna- pers. comm., Sołtysik 1960a,b).

The question arises whether the other form of inhibitory training, namely the "conditioned inhibition" could be obtained by using the same method. This form of inhibitory conditioning consists in some new stimulus (to be "conditioned inhibitor") being presented together or just before the CS and this compound not being reinforced, while the CS alone is reinforced regularly. After some time the conditioned inhibitor (CI) inhibits the CR so that no response is elicited by the CS presented in compound (simultaneous or successive) with the CI, though the same CS evokes a full CR when the CI is absent.

The problem of whether or not this form of inhibitory conditioning could be effective in avoidance CRs seems to be important for further elucidation of inhibitory mechanisms involved in regulation of instrumental behaviour.

MATERIAL AND METHOD

8 adult male cats were used in this study. Experiments were carried out in a cage 65 cm. \times 55 cm. \times 40 cm. with a floor-grid enabling us to apply electric shock to the paws of the animal. In the middle of the rear wall of the cage there was a bar 10 cm. \times 2 cm. This bar was constructed so that it could be easily removed (through a slit in the wall) by pulling a nylon thread. Its automatic return was secured by means of a spring.

This cage was placed in a sound-proof CR-chamber.

An alternating current of 50 c.p.s. and about 20 to 30 volts from a transformer was used as unconditioned stimulus (US). The conditioned stimulus (CS) was a mild tone of about 60 db. and 1000 hz, applied through a loud-speaker from the tone-generator. The bar-pressing reaction served as an avoidance (and/or escape) response (M_{av}). The duration of the CS in a positive trial was 5 sec., then the US was switched on and both stimuli lasted until the animal responded. Pressing the bar automatically terminated the CS or CS-US.

Some cats remained sitting with the paw still on the bar after the CS (or CS-US) had ceased; in those cases the bar was removed for a while and only replaced when the animal removed its paw away from the slit.

Similarly as in our previous work (Sołtysik and Zieliński 1961) cats were first taught either to escape from the shock (no CS was used during this kind of pre-training), or the classical defensive conditioning procedure (CS-US without bar) was applied. After three sessions of this pretraining (i.e. escape learning or classical conditioning) the normal avoidance procedure was introduced during which the cats were trained to avoid the shock and to stop the CS by pressing the bar. Each daily session consisted of 10 trials. After meeting the criterion of 90 correct responses in 100 consecutive trials the avoidance CR was extinguished during 10 sessions (cf. Sołtysik and Zieliński 1961). Then the CR was retrained and beginning from the 11th session of this retraining the inhibitory conditioning was started. As a so-called "conditioned inhibitor" (CI)

we used a rhythmic click, 5 per sec., delivered by an electromagnetic relay placed on the wall of the cage. This stimulus was rather strong and produced a definite orienting reaction in all cats. However, no avoidance responses, due to generalization were elicited by this stimulus. This CI was presented in compound with CS in three different combinations.

(1) the trial started with the CI and 5 sec. later the CS was added for another 10 sec.; thus the CS was presented for 10 sec. and was overlapped by the CI which had started 5 sec. earlier.

(2) Both the CI and CS were presented for 10 sec. in such a way that the CI overlapped the CS for only 5 sec., i.e. the CI was given first and after 5 sec. the CS was added; they acted together for 5 sec. and then the CI was stopped while the CS continued for a further 5 sec.

(3) Both the CI and CS were presented, for 5 sec. each, successively, so that the CS was applied at the exact moment of termination of the CI.

All these combinations are also seen in Fig. 1.

In all these cases the duration of stimuli was fixed independently of how the animal behaved. All animals were trained by using the first combination of CI-CS and then the two other combinations were tried.

There were 10 positive (CS alone) and 10 inhibitory (CI-CS) trials in each daily session. The order of positive and inhibitory trials was irregular, changing from day to day. The schedule for each daily session was prepared by the use of tables of random numbers of Fisher and Yates (1948).

As a criterion of the conditioned inhibition we took 4 consecutive sessions (i.e. 40 positive and 40 inhibitory trials) during which both the avoidance reflex

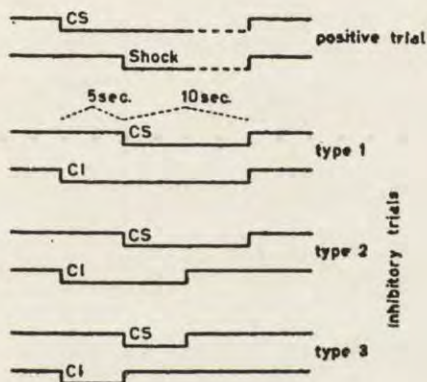


Fig. 1. Time relations between stimuli in the positive and inhibitory trials

and its inhibition reached a 90 per cent level. In other words, 36 correct responses in 40 consecutive trials, both positive and inhibitory, were required. By a criterion number we mean the number of inhibitory trials (from the very beginning of the inhibitory training) necessary to meet the criterion excluding, however, the 40 trials during which the 90 per cent level was reached; the latter trials we call criterion trials (cf. Sołtysik and Zieliński 1961).

RESULTS

1. Inhibitory training with the compound 1
(5-sec. CS—10-sec. CI-CS)

The course of the inhibitory conditioning using the first combination of the CI and CS is shown in 7 cats in Fig. 2. It is seen that the conditioned inhibition was trained quite easily and the criterion number ranged from 41 to 137 (of inhibitory trials). In the first period of this training considerable fluctuations in the percentage of responses to the

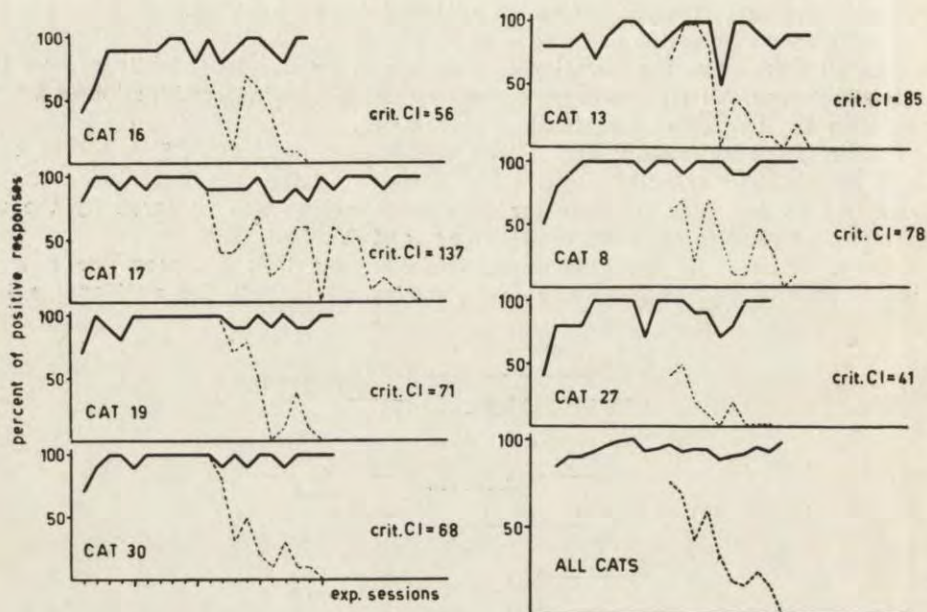


Fig. 2. Training of conditioned inhibition of the avoidance reflex; inhibitory compound 1

Ordinates: percent of positive avoidance responses. Abscissae: experimental sessions. The solid line: performance level to the CS. The broken line: performance level to the compound CI-CS

inhibitory compound were observed from day to day, whereas the percentages of responses to the CS alone remained practically unchanged. There were also no changes in general behaviour of the cats.

It should be mentioned that the form of M_{av} was different in different cats. Some of them responded by a simple local foreleg response; it was, in some cats, pressing the bar always with the same (right or left) forepaw, while other animals used both forepaws simultaneously or alternately. In one cat (cat 27) it was a locomotor reaction during which the animal

stepped with both right extremities on the bar. Some animals performed only a "phasic" shortlasting pushing or pressing movement and immediately took the paw away; others responded "tonically" with prolonged pressing, so that it was necessary to take the bar away for a moment and replace it only after the animal withdrew its paw from the slit. Practically all the cats used to sit near the bar in a position enabling them to press the bar without any locomotor reaction; they remained in this position throughout the whole session.

Also the behaviour during the CI-CS trials was different in different cats, even during the criterion sessions when all the cats inhibited their responses perfectly. Some cats did not respond at all and sat quietly. Some others turned the head listening, apparently, to the CI or even walked to another part in the cage. Cat 27, the one that responded with the locomotor reaction, caught the floor-grid with its claws and remained in such a tense position throughout the 15 sec. of CI-CS compound.

No statistically significant correlation was found between the speed of this inhibitory learning and the speed of acquisition or extinction of avoidance response in the earlier training.

2. Inhibitory training with the compound 2 (5-sec. CI—5-sec. CI-CS—5-sec. CS)

After the criterion of conditioned inhibition, using the inhibitory compound 1, was reached, we started in one cat (cat 8) inhibitory training with the compound 2. During the first 7 days there was about 80 per cent of positive responses in the inhibitory trials. No improvement was observed and while in the beginning the responses were seen mainly during the third phase of the CI-CS compound when the CS acted alone, afterwards the motor responses appeared in the second phase (CI and CS acting together) and even during the first 5 seconds of the CI acting alone. When, however, in the 8th session we returned to the inhibitory compound 1, the inhibition of M_{av} was again perfect. Hence, we concluded, that the CI preserved its inhibitory character but the inhibition of response in the compound 2 was too difficult a task for our animals. No other experiments with this compound were performed.

3. Inhibitory training with the compound 3 (5-sec. CI—5-sec. CS)

This form of inhibitory compound was used in 3 cats just after they had reached the criterion of the inhibition in compound 1 and in cat 8 after terminating the training of compound 2. This task was much

more difficult but all 4 cats reached the criterion (Fig. 3). During the training there were considerable changes observed in the percentages of responses both to the CS and to the CI-CS compound; no correlation between them was stated.

It is worth mentioning, that despite a high proportion of inhibitory trials in each session, no changes in the performance level of responses

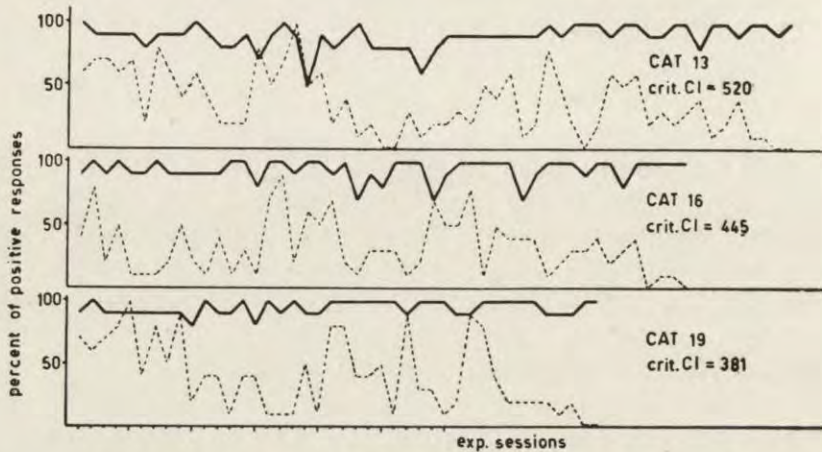


Fig. 3. Training of conditioned inhibition of the avoidance reflex; inhibitory compound 3
Explanations as in Fig. 2

to the CS were observed. Also no falling asleep was seen and the phenomenon of the inhibitory after-effect was only very rarely observed, even after a series of inhibitory trials. There were no apparent changes in general behaviour during the training. During the CI-CS trials no other motor reactions were seen and if there was no bar-pressing response the animal remained quiet.

DISCUSSION

Our experiments have shown that the conditioned inhibition of the avoidance reflex is easily obtainable in cats by using the procedure proposed originally by Bregadze and Fonberg for extinction and differentiation, i.e., by prolonging the action of the CS beyond the response. In all our cats the additional stimulus (clicker) quickly acquired the property of inhibitory stimulus, and the CS applied in compound with it failed to elicit the avoidance response. When the action of the CI terminated before the onset of the CS the inhibitory reflex required a much longer training.

What is the probable mechanism of this inhibitory effect of the CI? Keeping in mind the complex structure of the avoidance CR we may suppose at least three mechanisms of the conditioned inhibition of the avoidance CR. They are exemplified in a sketchy form in Fig. 4.

Scheme 1 represents the reflex-arc of the already established avoidance CR constructed on the basis of our earlier studies (Sołtysik 1960a,b,c, Sołtysik and Kowalska 1960). It is assumed that the CS through pathway *a* elicits a fear reaction (classical CR) and the excitation of the fear centre through the pathway *b* elicits in its turn the motor response M_{av} (instrumental CR). In addition this response is

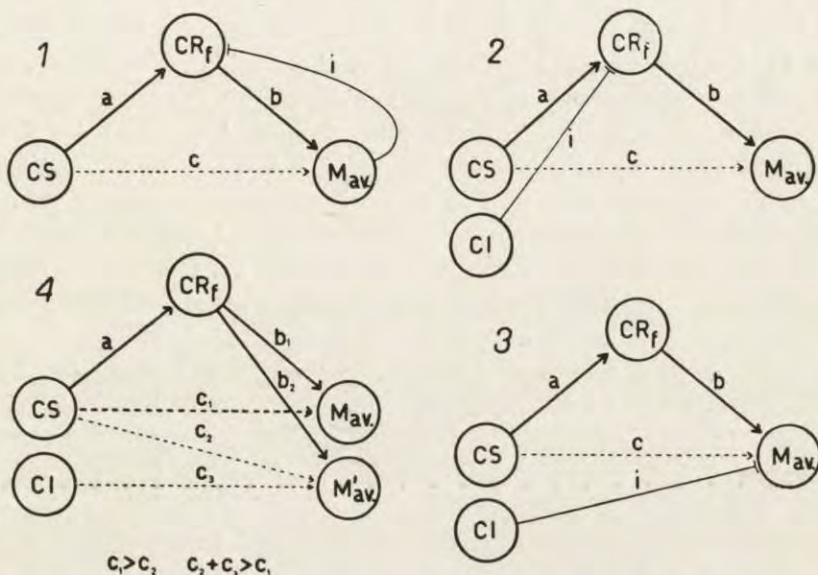


Fig. 4. Schematic representation of hypothetical intercentral relations in positive and inhibitory avoidance reflexes

CS — centre of the positive conditioned stimulus; CI — centre of the inhibitory conditioned stimulus, CR — centre of the reaction of fear, M_{av} — centre of the avoidant movement, \rightarrow denotes: elicits (or excitatory connection), $-|$ denotes: inhibits (or inhibitory connection); (The term „centre” is used here in its functional meaning; it may well be replaced by the term „central excitation”). *a* — conditioned connection through which the CS induces the fear reaction, *b* — conditioned connection through which the avoidant movement is instigated by fear, *c* — conditioned facilitatory connection through which the CS lowers the threshold in the centre of M_{av} , *i* — inhibitory conditioned connection.

Scheme 1: positive avoidance reflex; Scheme 2: inhibitory reflex in which the CI inhibits the fear reaction preventing the performance of the motor response. This may be designated by the term: „classical conditioned inhibition of the avoidance response”. Scheme 3: inhibitory reflex in which the CI inhibits the motor reaction. This may be designated by the term: „instrumental conditioned inhibition of the avoidance response”. Scheme 4: double avoidance reflex in which one response M_{av} is elicited by the CS alone, and the second response M'_{av} is elicited by the compound of two stimuli CS—CI. It is shown how such a behaviour may be explained without considering special inhibitory connections; note the relations between the strength of the 3 facilitatory connections c_1 , c_2 , and c_3 . In schemes 2, 3 and 4 the inhibitory feed-back from the response M_{av} is omitted as not essential in the inhibitory response.

facilitated by the direct connections c between the centres of CS and M_{av} . Since the instrumental response terminates the CS and prevents the shock, its feed-back becomes an inhibitory stimulus suppressing the fear state (pathway i). Two important consequences of this conditioned recurrent self-inhibition of the CR_f should be stressed. First, it is an additional source of instrumental reinforcement of the M_{av} ; this inhibitory feed-back supplements the passive drive reduction resulting from the cessation of the warning CS by the addition of the active drive inhibition. The second consequence of this inhibition is a protection of the fear-CR against extinction, which otherwise would develop since the CS in the established avoidance reflex is not reinforced by the noxious US.

Taking this scheme into account it may be asked why the CI added to the CS suppresses the performance of the avoidance response.

In scheme 2, the first possible mechanism of this suppression is shown. According to this mechanism the CI produces inhibition in the fear centre so preventing its activation by the CS. It may be added that such a mechanism was in operation in the original experiments of Konorski and Miller (1936), in which differential inhibition was trained before the establishment of the avoidance reflex. Afterwards, when the animals were taught to perform an avoidant response, the inhibitory stimulus did not elicit either fear or the instrumental movement.

It is clear that this mechanism is not directly responsible for the establishment of the inhibitory reflex to the compound CI-CS in our cats, since in this case both the CS and CI-CS were not reinforced by shock. However, the unsuccessful (in terminating the CS) response was quickly eliminated, probably through the mechanisms discussed below (Schemes 3 and 4). In this case the CS presented in compound with the CI is deprived of the inhibitory feed-back delivered by M_{av} , and therefore is exposed to extinction. Since, however, at the same time the CS presented alone (in positive trials) is reinforced by shock whenever the animal fails to respond, discrimination between the two modes of presentation of the CS should be acquired: in consequence the CS elicits the full avoidance reflex, while the CI-CS compound does not, because the CI neutralizes the CS in its emotogenic function. Thus scheme 2 may be assumed as the final result of our procedure, but not as its direct consequence. We may designate this form of inhibitory reflex as a "classical conditioned inhibition of the avoidance reflex"; the adjective "classical" stresses the fact that the classically conditioned component of the avoidance reflex, i.e., CR_f , is inhibited.

Scheme 3 represents the hypothetical S-R inhibitory mechanism which in this context may be called "instrumental conditioned inhibition of the avoidance reflex". The CS applied in compound with the CI is

not terminated by the M_{av} , so this response is not reinforced (or at least not immediately reinforced) by the reduction of fear. In consequence it becomes inhibited. It should be remembered that similar ideas were put forwards by Thorndike (1911), Troland (1928), Miller and Konorski (1928) and others, especially in explaining the effects of punishment.

However, it is clear that this form of inhibitory response could exist only temporarily. If the animal fails to perform the M_{av} the extinction of the CR_f should occur because the CI-CS compound is neither reinforced by US nor protected from extinction by the inhibitory feed-back of the M_{av} . So, the final result should be that the CI would inhibit both the CR_f and the M_{av} .

Scheme 4 shows another possibility of explaining the "inhibitory avoidance reflex" without assuming the formation of any new inhibitory connections. When the CS and the corresponding fear state continue in spite of the performance of the M_{av} the animal resorts to other movements of his defensive repertory such as grasping, locomotion, crouching etc. Since some of these movements may happen to coincide with the termination of the CS they may be instrumentally conditioned and replace the original movement of bar-pressing. This is probable, especially in the case where the new avoidant response is of tonic character lasting thus up to the termination of the CI-CS compound. The possibility of the formation of two different avoidant responses based on the same reinforcement was shown by Kowalska (unpublished experiment). In order to explain such a behaviour we may assume different direct facilitatory connections c_1 and $c_3 + c_3$. However, also in this case, the extinction of the CR_f (Scheme 2) might occur after some training because failure to respond with this "private" avoidance movement is not punished by shock; thus the CS presented in compound with the CI gradually loses its emoto-genic value.

An analogous mechanism of extinction of the avoidance response was proposed by Page (1955) who found that some new responses appear as a result of prevention of the original response.

Which of these mechanisms might account for the behaviour of our cats? Certainly, the data at present are far from complete and as the fear is not measured along with the motor responses, all the mechanisms remained highly conjectural. The impression, however, we got from analysing our data, supported by observation of the animals, is that all three above mentioned mechanisms of inhibitory avoidance reflex are not so much alternative but rather represent different phases or components of one complex reaction. In the beginning of the inhibitory training there occurred an elimination of the M_{av} while the CR_f still was

present. In this stage of training some cats performed different movements and when one of those movements was fixated (as in the cat 27) the scheme 4 might be suitable. In other cats which remained motionless, though seemed to be in fear, the scheme 3 was more fitting. But the final result was that all our animals seemed to be quiet in the presence of the CI-CS compound; here the inhibitory reflex of scheme 2 might come into play.

SUMMARY

Conditioned inhibition of the avoidance response was studied in 8 cats. The avoidance response consisted in pressing the bar in response to the presentation of a 5-sec. conditioned stimulus (a tone), thus terminating the tone and preventing the shock which followed the failure to respond within the 5-sec. interval. The conditioned inhibitor was a clicker, which acted before and during the CS; this compound was neither reinforced by shock nor terminated by pressing the bar. Such procedure was effective in making the clicker a conditioned inhibitor i.e., this stimulus inhibited the avoidant response to the CS presented together with it.

It was also possible to obtain the trace conditioned inhibition of the avoidance response, but this required a much longer training.

The probable neural mechanisms of this inhibitory reflex are discussed.

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PROPERTIES OF TRANSFORMED CONDITIONED STIMULI
I. DEFENSIVE CONDITIONED STIMULUS TRANSFORMED
INTO FOOD CONDITIONED STIMULUS

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It has been shown (Vatsuro 1948, Rikman 1949, Konorski and Szwejkowska 1952, 1956) that a food conditioned stimulus (CS), which has been transformed from a defensive CS, clearly differs from the regular CS which has been associated with food reinforcement throughout the entire training.

First, it has been found that a food conditioned reflex (CR) to a previously defensive CS generally does not attain the level of the reflex elicited to the regular CS (RCS). Secondly, if the transformed CS (TCS) is again followed by the nociceptive unconditioned stimulus (UCS), its defensive conditioned significance is immediately restored. Moreover, when the TCS is used against its previous experimental background, it elicits a defensive response even after a prolonged food training.

All these data indicate that the TCS preserves in a latent form its previous defensive character which is revealed if the defensive excitability is increased. However, in the course of our experiments we have observed that the defensive response to such a stimulus may also be displayed under certain food conditions. The aim of the present paper is to deal with this problem.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were carried out on four male dogs in a semisoundproof CR chamber. At first, an instrumental food CR to intermittent light in dogs Nos. 1 and 2, and to a soft buzzer in dogs Nos. 3 and 4 was trained. The CR consisted of placing the right foreleg on the foodtray, whenever the CS was applied. The response was immediately followed by the presentation of food.

After about 30 experimental sessions with food reinforcement an avoidance CR to intermittent light in dogs Nos. 3 and 4, and to a soft buzzer in dogs Nos. 1 and 2, was trained in the same experimental situation. In order to avoid an electric shock delivered to the right hindleg, dog No. 2 was trained to bark in response to the CS, whereas dogs Nos. 1, 3, and 4 were required to flex this leg. The barking CR was established in such a way that whenever the animal barked during the application of the CS, the stimulus was discontinued and the electric shock was not given. Within about 40 experimental sessions the avoidance CR was well established.

Following the avoidance training, the food CR was retrained in about 60 sessions. Next, the defensive CS was introduced, but from then on, it was always reinforced by food, independently of whether or not the response was performed. Both CSi were applied in random order in 8 trials a day.

In two dogs (Nos. 3 and 4) the defensive CS was very easily transformed into the food CS. Already after one presentation of food the animals stopped performing the avoidance response and, instead, they performed the food response to light. However, in two other dogs (Nos. 1 and 2), in which the defensive CS was a buzzer, the transformation of the stimulus was more difficult and it was necessary to return to the passive movement training.

In the end, however, the transformation of the defensive CS into the food CS was quite successful in all four dogs, and to all presentations of the stimulus the dogs displayed a pure food reaction, not contaminated with any signs of a defensive one.

RESULTS

A. Acute extinction of CRs. In intervals of about 3 weeks, special experiments were performed in which CSi were applied without reinforcement. Experiments were conducted in 2 ways. Either the stimulus was presented for a period of one minute ("continuous extinction"), or it was repeatedly applied for 6 sec. in intervals of about one minute ("intermittent extinction"). In the latter form of extinction, both the RCS and the TCS were applied in various sequence. In some sessions the RCSi were presented first, and after a number of trials, the TCSi were given; in others, TCSi were applied from the very beginning. Typical trials of the first type of extinction are presented in Fig. 1. It is seen that whereas the RCS elicits only the food instrumental response which disappears after some time, the TCS evokes first the food response which is then replaced by the instrumental defensive response.

Similar results were obtained when intermittent extinction was carried out. When a session began with repeated application of the RCS, a regular food instrumental response was elicited which tended to disappear (Fig. 2a,b). Only in some dogs after many repetitions of this stimulus was the defensive response occasionally observed (Fig. 2b). On the other hand, when the session began with application of the TCS, it first evoked the food response, but after its disappearance always the

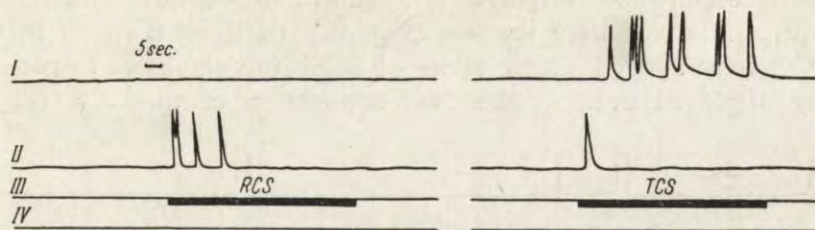


Fig. 1. Acute continuous extinction of food CR in dog No. 4.

RCS — regular food CS; TCS — transformed food CS; I — instrumental defensive response (movement of the right hindleg); II — instrumental food response (movement of the right foreleg); III — conditioned stimulus (1 minute); IV — food reinforcement (no food was presented). The RCS elicits food instrumental responses which tends to decrease. The TCS evokes the food response which is subsequently replaced by a strong instrumental response

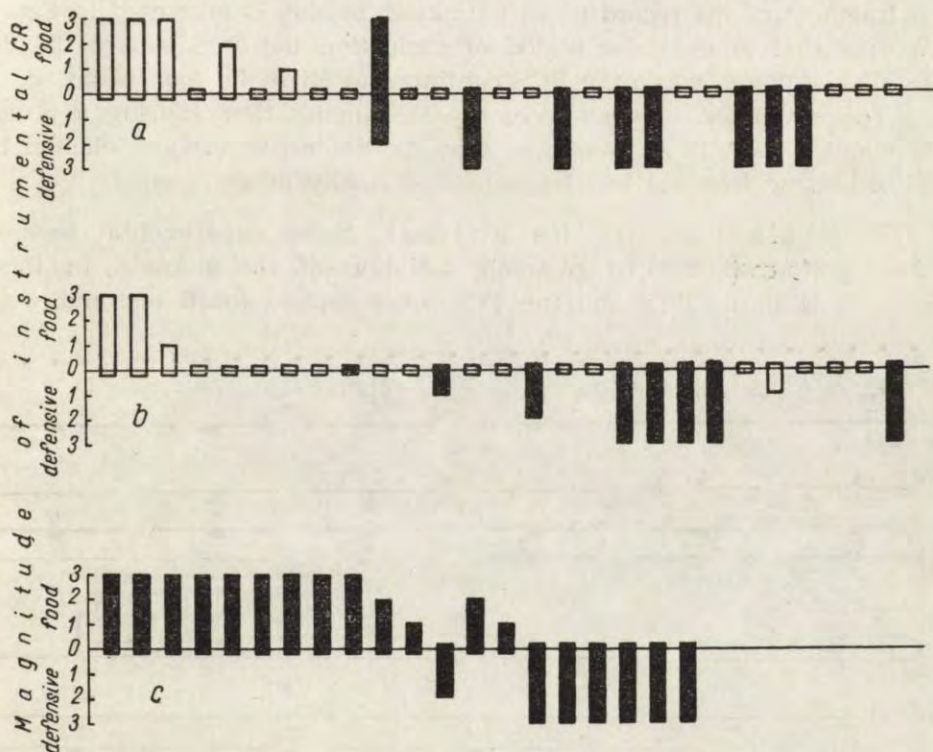


Fig. 2. Acute intermittent extinction of food CR (a — dog No. 2; b, c — dog No. 3) White columns — instrumental responses to RCS; black columns — instrumental responses to TCS; up — food response; down — defensive response. The height of each column denotes the strength of the instrumental response; 3 — full response (placing the leg on the foodtray), 2 — high lifting of the leg, 1 — abortive movement; a, b — experimental sessions which begin with application of the RCS; c — experimental sessions which begin with application of the TCS. It is seen that the RCS elicits the food response which tends to disappear, whereas TCS evokes the defensive response

defensive response was displayed (Fig. 2c). In some trials the TCS evoked both responses one after another (Fig. 2a). In those sessions in which the TCSi were applied after a series of RCSi, the defensive response was usually displayed even at the first application of the TCS (Fig. 2a).

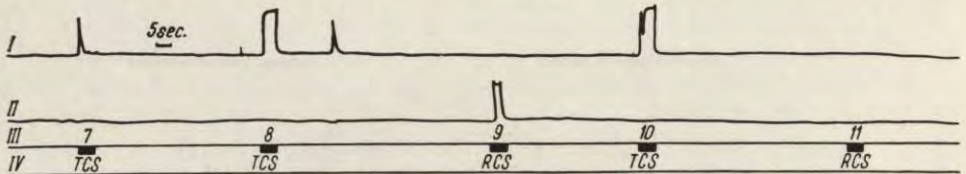


Fig. 3. Acute intermittent extinction in dog No. 1 (part of the record). Numbers 7, 8, 9... denote successive trials. Other explanations as in Fig. 1. Note that the TCS elicits a defensive response, whereas the RCS continues to elicit the food response.

A fragment of the record of an extinction session is presented in Fig. 3. We see that in the later period of extinction the TCS evokes the defensive response, while the RCS continues to elicit the food response.

The extinction sessions were repeated many times during a period of about a year. It was observed that the defensive response elicited by TCSi became less and less frequent and finally disappeared.

B. Satiation of the animal. Some experimental sessions were performed after a complete satiation of the animals. In these sessions both the RCS and the TCS were applied for 6 sec. and were

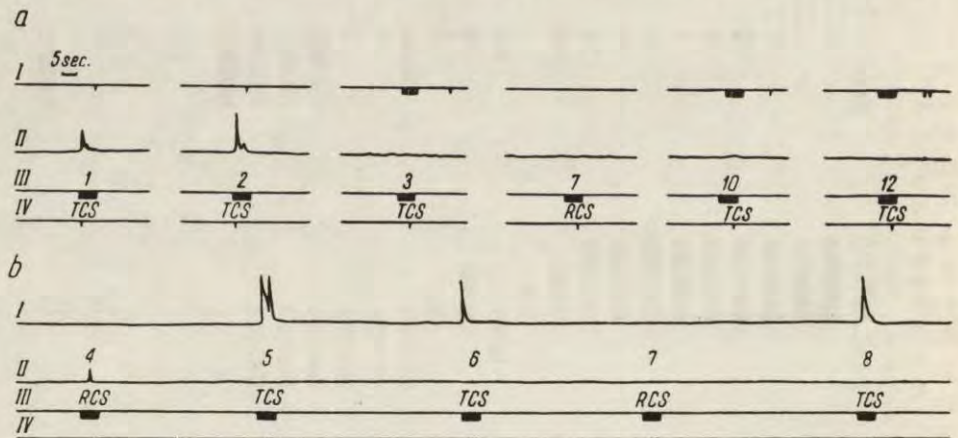


Fig. 4. Instrumental responses to TCS and RCS during satiation (a — dog No. 2, b — dog No. 3)

Numbers denote successive trials; I — instrumental defensive reaction (barking in dog No. 2, movement of the right hindleg in dog No. 3), II — instrumental food response (movement of the right foreleg). Other explanations as in Fig. 1. It is seen that the RCS evokes neither the alimentary nor the defensive instrumental response, whereas the TCS elicits the defensive instrumental response which in dog No. 2 tends to increase

followed by food, regardless of whether or not the food movement was performed and the food in the preceding trial was taken. Typical protocols of experiments with satiation are presented in Fig. 4a, b. It is seen that

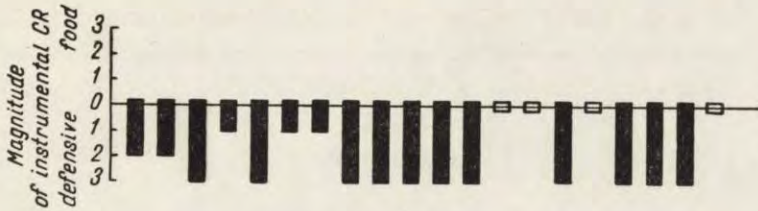


Fig. 5. A typical session after satiation in dog No. 3
 Explanation as in Fig. 2. Note that the instrumental defensive reaction is a response to the TCS, whereas the RCS evokes neither food nor defensive response

while the RCS elicits neither the food nor the defensive instrumental response, the TCS regularly evokes the defensive instrumental response (see also Fig. 5).

C. Application of CSi during the act of eating.
 In some trials food was presented without being preceded by any CS, in which case either the RCS or the TCS was applied during the act of eating. The RCS applied under these conditions sometimes evoked the instrumental food response although the dog did not interrupt the

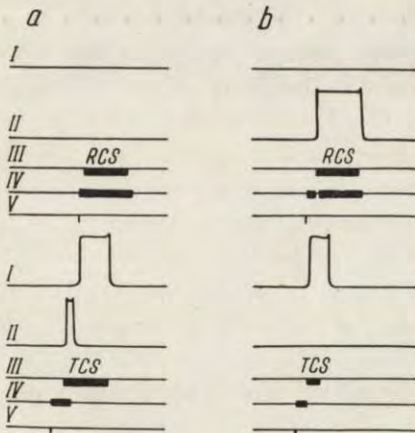


Fig. 6. Application of CSi during the act of eating in dog No. 1
 I — instrumental defensive response (movement of the right hindleg), II — instrumental food response (movement of the right foreleg), III — conditioned stimulus, IV — duration of the act of eating, V — food reinforcement. Note that the RCS evokes either the instrumental food response (b), or no response (a); the TCS elicits either the food response which is immediately followed by the instrumental defensive response (a), or it evokes only the defensive instrumental response (b)

act of eating. The TCS in dogs Nos. 1 and 2 also occasionally evoked the instrumental food response but then the animal stopped eating and performed the avoidance response (Fig. 6a, b).

The appearance of the defensive instrumental response to the TCS applied during the act of eating was not observed in dogs Nos. 3 and 4. In dogs Nos. 1 and 2 it was transient and after 6 trials was no longer observed.

DISCUSSION

The above results indicate that a food CS, which had been transformed from a defensive CS elicits an instrumental defensive response instead of a food response in the following experimental situations:

- a) during extinction,
- b) after satiation of the animal,
- c) if the TCS is applied during the act of eating.

Under the first two conditions, the occurrence of the defensive instrumental response may be explained on the basis of earlier data concerning the structure of the TCR. It has been shown by Konorski and Szejmowska (1952, 1956) that when the food CR is transformed from the defensive CR, the conditioned connections between the "centre" of the CS and the defensive "centre" are preserved, and connections between the CS-centre and the feeding-centre are additionally formed. It follows from this assumption that, whenever the connections between the CS-centre and the feeding-centre are blocked, the connections with the defensive centre may take the upper hand and become manifested. According to the data obtained by Konorski (1939), Wyrwicka et al. (1959, 1960), and Sołtysik and Kowalska (1960), the given instrumental response is "guided" by the appropriate unconditioned centre, i.e. the excitation of the defensive centre elicits the earlier established instrumental defensive response (avoidance movement), while the excitation of the feeding centre elicits the instrumental food response. Now, both the satiation of the animal, and the non-reinforcement of the CS leads to a temporary blocking of the food CR. While with the RCS this blocking is manifested simply by the disappearance of the instrumental food response, application of the TCS is followed additionally by the performance of the defensive response.

We have seen that, with repetition of the extinction sessions, the defensive instrumental response tends gradually to disappear. This effect may be easily understood in the light of the results obtained by Föberg (1958) and Bregadze (1953). These authors have shown that if a defensive CS is not discontinued immediately after the performance

of the avoidance movement, the movement gradually disappears. Since in our extinction experiments the CS always lasted for 6 sec., the conditions leading to disappearance of the avoidance movement were present. An explanation for the appearance of the defensive movement to TCS applied during the act of eating is less obvious.

The possibility of elicitation of quite different responses to CS applied before the presentation of food from that applied during the act of eating was demonstrated by Zbrożyna (1953). The author has shown that when the food CS is presented during the act of eating and signals the withdrawal of food, the animal stops eating in response to the CS, while the CR to the same CS is preserved when it precedes the presentation of food.

The problem arises, why is it that under our experimental conditions the act of eating released the defensive response to the TCS which had not occurred when this stimulus preceded the presentation of food. According to our previous consideration the defensive response to the TCS is manifested when the excitation of the hunger centre is decreased, which would mean that the excitation of this centre is lower during the act of eating than in the intervals. Now, according to an assumption of Sołtysik (unpublished) it is possible that antagonistic relations exist between the "hunger centre" and the "consumption centre". In consequence, during the act of eating the "hunger centre" would be inhibited and thus the defensive aspect of the TCS could be again revealed. Such an explanation may be either corroborated or disproved if additional evidence concerning the validity of Sołtysik's hypothesis is brought forth.

SUMMARY

1. The present paper is concerned with the properties of the instrumental food CS which has been transformed from the instrumental defensive CS.

2. It has been found that the transformed CS elicits the defensive instrumental response instead of the food response under the following conditions:

- a) during extinction of the food CR,
- b) after satiation of the animal,
- c) during the act of eating.

3. When the regular food CS is used under the same conditions, the defensive response does not occur.

4. A tentative mechanism of these findings is discussed.

I wish to express my thanks to Professor Jerzy Konorski for his help in the preparation of this paper.

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PROPERTIES OF TRANSFORMED CONDITIONED STIMULI
II. FOOD CONDITIONED STIMULUS TRANSFORMED
INTO DEFENSIVE CONDITIONED STIMULUS

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In the previous paper of this series (Wojtczak-Jaroskowa, 1962) it has been shown that a food conditioned stimulus (CS) transformed from a defensive CS produces again the defensive response when it is subjected to acute extinction.

The present paper deals with the question of what happens when the defensive CS, which was transformed from the alimentary CS, is subjected to acute extinction.

MATERIAL AND EXPERIMENTAL PROCEDURE

Experiments were performed on three dogs in a semisoundproof CR chamber. In the first experimental series an instrumental food CR was trained to one of the following CSi: a tactile stimulation of the animal's side in dog No. 1, an intermittent light in dog No. 2 and a buzzer in dog No. 3. The animal was taught to place his right foreleg on the foodtray, whenever the CS was presented. The second series consisted of the establishment of an instrumental defensive (avoidance-type) conditioned reflex (CR) to a buzzer in dogs Nos. 1 and 2 and to a bell in dog No. 3. The animal's task was to bark (dogs Nos. 1 and 3) or to flex the right hindleg (dog No. 2) to avoid an electric shock applied to the leg.

After both kinds of instrumental reflexes had firmly been established, a new series of experiments began in which both CSi were applied and the food CSi was transformed into the defensive CS. The transformation was carried out in the following way. When the animal placed his foreleg on the foodtray in response to the food CS, an electric shock was delivered. If however, the animal performed the avoidance movement, which had been trained to the defensive CS, the food CS was discontinued and no shock was applied. Using this procedure, the animal started to perform the avoidance movement in response to the food CS, and did it as regularly as to the original defensive CS.

Extinction sessions, carried out once every two weeks were of two types. In some, "continuous extinction" was used, that is, the CS lasted for many minutes till the defensive instrumental movement totally disappeared. In others, "intermittent extinction" was conducted. This procedure was as follows. The CS was used for a period of 6 sec. at intervals of about 30 sec. instead of discontinuing it immediately after the performance of the trained movement. In both methods only the transformed CS was subjected to extinction.

RESULTS

When the transformed defensive CS was continuously used, extinction of the avoidance response took place after 15 to 45 minutes, while intermittent extinction lasted from 30 minutes to 1.5 hours. But despite the difference in time, the course of both extinction sessions was identical. Initially, the CS elicited a marked avoidance response which was associated with general restlessness. Only from time to time did the

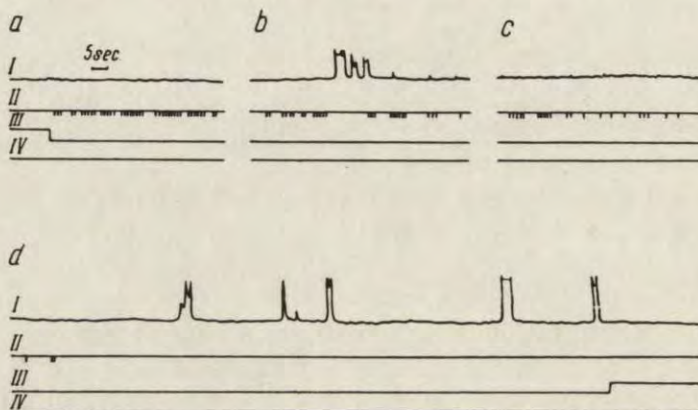


Fig. 1. Acute continuous extinction of the defensive CR to the transformed CS in dog No 1

a — the beginning of the experimental session; b — after 2 minutes; c — after 20 minutes; d — 42 minutes after the beginning of the experimental session; I — movement of the right foreleg (food CR type II), II — barking (defensive CR type II), III — Conditioned stimulus, IV — food reinforcement (no food was presented)

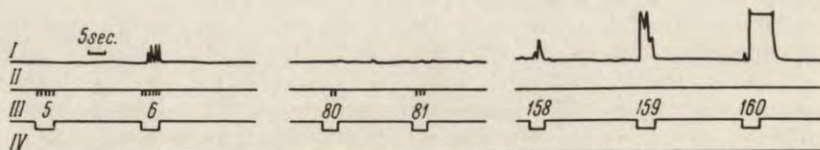


Fig. 2. Acute intermittent extinction of defensive CR to the transformed CS in dog No. 1

Numbers: 5, 6, 80..., denote successive trials. Others explanations as in Fig. 1

food response occur as well in a rather abortive form (Fig. 2 trial 6, Fig. 1b). While continuing extinction, the avoidance response diminished, and, finally, it was abolished. However, the animal was still very excited and irritated. Towards the end of the extinction period the restlessness subsided and was followed by a remarkable food behaviour: the animal looked into the dish and, after a while, a noticeable instrumental food response was elicited (Fig. 1). This response was not displayed to every presentation of the transformed defensive CS, and usually after a few trials tended to decline.

With repetition of the extinction sessions the instrumental food response occurred irregularly and finally ceased to appear.

DISCUSSION

The above results show that if a defensive CS, which was primarily associated with food reinforcement, is submitted to extinction, it elicits again the instrumental food response. The explanation of this finding may be the same as that put forward in connection with a reverse situation in which a food conditioned stimulus transformed from a defensive CS elicited a food response during extinction (Wojtczak-Jaroszowa 1962). According to Konorski and Szwejkowska (1956) it may be assumed that the centre of the transformed CS is connected with both the food and defensive unconditioned centres. While blocking the connections with the defensive (fear) centre during extinction of the transformed defensive CS, the connections with the food centre prevail. Behaviourally, this results in abolition of the defensive CR and elicitation of the food CR.

It is interesting to note the difference between the character of the food CR during the extinction of the defensive CR, and that of the defensive CR while extinguishing the food CR. It was found that extinction of the transformed food CS was followed by an immediate performance of the instrumental defensive response (Wojtczak-Jaroszowa, 1962). On the other hand, after extinction of the defensive response the animal continued to be excited and irritated. Only when irritation subsided did the food response occur but it was never regular and rapidly tended to decline. It is likely that the very late elicitation of the food response during extinction of the transformed defensive CR is due to the preservation of certain classical components of the defensive CR which is manifested by irritation and restlessness. Only when the latter symptoms are depressed, may the food response occur. The irregularity and transient character of the reoccurred food response might be supposed to be due to the absence of food reinforcement during extinction sessions.

SUMMARY

1. The transformed defensive CS, which had originally been reinforced by food presentation, was subjected to acute extinction. It has been shown that after extinction of the defensive (avoidance-type) CR and suppression of defensive excitation the transformed defensive CS elicited the food CR instead of the defensive CR.

2. The difference between the character of food CR during extinction of the transformed defensive CR and that of defensive CR during extinction of the transformed food CR is discussed.

I wish to express my thanks to Professor Jerzy Konorski for his help in the preparation of this paper.

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STUDIES ON THE AVERSIVE CLASSICAL CONDITIONING.
2. ON THE REINFORCING ROLE OF SHOCK IN THE CLASSICAL
LEG FLEXION CONDITIONING

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The term "reinforcement" introduced into behavioural sciences by Pavlov (1951-1954) is now used in two different meanings. One of them, applied originally by Pavlov himself, is used in classical conditioning. Here, we understand by reinforcement a stimulus eliciting a definite response applied in association with another stimulus originally neutral in respect to this response. As is well known, after repeated application of such a combination the latter stimulus elicits the same response as that produced by the reinforcing agent (substitution principle). We shall denote this type of reinforcement: "classical reinforcement".

The second meaning of reinforcement stemming from an early work of Thorndike (1911) was later developed by Konorski and Miller (1928, 1933, 1936), Troland (1928), Hull (1943) and others. Here the reinforcer is any agent or event which influences the S-R connection (or the probability that S will elicit R), where S is any stimulus (or sensory situation) and R is a skeletal muscle reaction. The reinforcement is called positive when, after its application, the S-R "action potential" ("strength of connection") is increased, and negative, when the tendency of S to elicit R is diminished. In contrast to the classical reinforcement, this reinforcer (let us call it "instrumental") is used for reinforcing the required motor response, but does not elicit it by itself.

Although a number of authors based all learning processes on a single principle (e.g. Pavlov 1951-1954, Guthrie 1952, Hull 1943, 1952,

Miller N. E. 1948 and others), the general opinion is that certain types of learning are based on the first kind of reinforcement ("conditioning type I" of Konorski and Miller 1928, Konorski 1948, or "classical conditioning" of Hilgard and Marquis 1940) while in others the Thorndikian "law of effect" is in operation ("conditioning type II" or "instrumental conditioning").

Most authors agree that autonomic and emotional responses are classically conditioned, while learning of motor acts is governed by the laws of instrumental conditioning (Miller and Konorski 1928, Skinner 1935, Schlossberg 1937, Razran 1939, Maier and Schneirla 1942, Tuttle 1946, Mowrer 1947, and many others).

There are, however, such forms of conditioning in which the exact nature of reinforcement is not clear. For instance, the leg flexion conditioning based on shock reinforcement is a case in which different authors found either classical (e.g. Beritoff 1927, Asratian 1941, and others) or instrumental (Bregadze 1953, Gibson 1952) or both classical and instrumental (Schlossberg 1937, Brogden 1939) conditionings involved.

It was the aim of this work to establish the exact character of the conditioned flexion response in dogs. Therefore in a group of animals the classical conditioning procedure was applied and after establishing a stable conditioned flexion response, two alternative hypotheses were tested.

The first hypothesis was that the flexion is a classical defensive conditioned reflex (CR) which was developed and is maintained due to shock reinforcement.

The second hypothesis was that the flexion is an instrumental response; it might be reinforced by cessation of fear and/or pain; it seemed also quite probable that the conditioned flexion is performed because the shock is somehow more tolerable when applied to the flexed leg than when applied to the extended leg. The suggestion that the flexion response obtained in classical defensive training might be an instrumental CR was recently supported by Pakovich (1961) who observed an immediate increase and fixation of a particular form of flexion when shock was withdrawn.

To verify the above presented hypotheses the shock was omitted or prolonged in a single trial; The changes of latency of the CR in the two consecutive trials (normally reinforced) were measured and compared with some standard. Lengthening of latency of the flexion response was interpreted as a weakening of the CR, while shortening was considered as an increase of the CR.

MATERIAL AND METHOD

14 dogs were used in this study and conditioned defensive reflexes were trained in all (cf. Jaworska et al. 1962, Jaworska and Sołtysik 1962). Experiments were performed in the CR-chamber. The CS was a buzzer operating for 3 sec. and regularly reinforced by a single shock from the condenser; the wet silver electrodes were fixed between the toes of the right hindleg. The shock was applied at the moment of termination of the CS. Much attention was paid to secure a stable contact between the electrodes and the skin to avoid the possibility of any, even partial, escape from the shock. Therefore the resistance between electrodes was frequently controlled during each session; no changes in this resistance during the movements of the animal were observed.

Two polygraphs were used for observing the behaviour of the animals. The high speed one was used for recording latencies of the motor CR, the heart rate and respiratory movements, while on the low speed polygraph the course of the motor response was registered.

Each session consisted of 10 to 12 trials. In two of them, henceforth denoted as test-trials, certain modifications of CS-US relations were introduced. Four kinds of such modifications were used: 1° applications of the CS for 3 sec. without shock; 2° application of the CS for 6 sec. without shock; 3° application of the CS and discontinuing it without reinforcement after the performance of the motor act (i.e. the duration of the CS was equal to the latency of the flexion response as in avoidance training), and 4° application of the CS for 3 sec. and reinforcing it by multiple shock (5 shocks in 0.2 sec. intervals). The two test trials were randomly distributed among 10 normal trials, however, they were interspaced by at least 3 normal trials.

The effect of modification introduced in a given test-trial was observed in the two succeeding trials; we shall denote them as post-test-trials.

The latencies of the motor CRs in the test-trials did not differ from the mean latency in the other training sessions or in the pre-test-trials (i.e. trials just preceding the test-trials), and we took the latencies in the test-trials as control for comparison with the latencies in the post-test-trials. Two procedures of this comparison will be described later.

The cardiac CRs were also compared in the test-trials and post-test-trials. As a measure of cardiac CR we took the pulse rate in the 2nd sec. of the CS as compared with the pre-stimulus heart rate (in 10 sec. before the onset of the CS).

RESULTS

Two groups of 7 dogs each with newly established CRs were tested. In one group the tests 1 and 2 were applied while the second group served for tests 3 and 4. Also the first group was used for tests 3 and 4, but only after a long period of training (6 months); this was done in order to find out whether or not the overtrained reflexes differ from the newly established ones. As the effects of tests 3 and 4 were the same in both groups of dogs we shall consider them as a single group.

Table 1 shows the results of our experiments. It is seen in the first

row, that in the first 3 tests, in which no shock was used, an increase of mean latency was found, while in the 4th test with the prolonged noxious stimulus there was a small shortening of latency. Plus and minus refer to the increase or decrease of mean latency; results are expressed in seconds. The second row shows the statistical reliabilities of these changes in latencies: the lengthening of the latency in all tests without shock is statistically significant, while the effect of the prolonged shock did not reach a 0.05 level of confidence.

Table I

Changes of motor and cardiac CRs in the post-test trials

T E S T	Test 1	Test 2	Test 3	Test 4
	without shock			multiple shock
Duration of CS	3 sec.	6 sec.	latency of flexion	3 sec. 3 sec.
Change of latency (comparison of arithm. means)	+ 0.163	+ 0.252	+ 0.255	- 0.084
Risk level by t-test	0.024	0.0006	0.00001	0.11
Change of latency (frequency analysis)	+17.1%	+16.4%	+14.3%	-15.3%
Risk level by X^2 -test	0.005	0.001	0.005	0.001
Change of cardiac response (frequency analysis)	- 4.6%	- 8.1%	1.4%	+ 4.7%
Risk level by X^2 -test	0.5	0.2	0.8	0.3

Unfortunately, the application of the t-test to our data was not fully justified because the assumption of normality was not fulfilled. However, a very high level of confidence in tests 2 and 3 allows us to assume that these results would remain reliable also after some normalizing transformation.

Nevertheless we used another measure of changes in the CRs, which enabled us to apply Chi Square Test.

We calculated the frequencies of increased, decreased and unchanged latencies in post-test-trials as compared with the latencies in the preceding test-trial. In other words we measured what is the probability of

increased, decreased or unchanged latency of the CR, compared with the latency in the preceding trial. The frequencies of increased and decreased latencies were nearly equal both in the test-trials (compared with the pre-test-trials) and in trials taken from those sessions in which no tests were applied. The number of unchanged latencies was negligible since the accuracy of our method was up to 0.05 sec.

Then a comparison was made between the test-trials (compared with pre-test-trials) and the post-test-trials (compared with the test-trials). The third row in Table 1 shows changes in proportions (expressed in percent) of the CRs with increased latency. It is clear that there was a considerable rise in the tendency to respond with a longer latency after a single non-reinforcement and a definite drop in this tendency after a single trial with the multiple shock. In all cases the confidence level of these changes is very high (fourth row in Table 1).

We also tried to establish whether the changes in latency, as well as in frequency of response with longer latencies, were the same in the first and second post-test-trials. It was found that the mean latency was more influenced in the first than in the second post-test-trial, but in neither case was this difference significant. In the frequency analysis of lengthened and shortened latencies, on the other hand, no such difference was found. This means that in the second post-test-trial the tendency to respond with a longer (or shorter) latency remained the same as in the first post-test-trial, but the latencies were less changed in the second than in the first.

As far as cardiac responses are concerned, no change in their amplitude was found in post-test-trials. However, the changes of frequencies of increased and decreased responses, though statistically insignificant, were in agreement with those observed in motor responses: omitting the shock produced a slight decrease in the number of responses with larger amplitude, while the application of a repeated shock produced the reverse effect (row 5 and 6).

It should be stressed here that the changes of CRs in post-test-trials were more or less similar in all our dogs, though in some of them they were quite negligible.

DISCUSSION

The first point to be emphasized in discussing our results is the procedure we adopted for securing the formation of the pure classical CRs without any admixture of an instrumental response. With this aim, the hindleg was chosen for conditioning as being probably much less "instrumentalized" during the life of animals than the foreleg. Then, a shortlast-

ing discharge of a condenser was used as an US so that the animal could not try to escape from and to "stamp-in" some accidental response which might coincide with the termination of shock. Furthermore, the accurate fixation of electrodes eliminated the possibility of reducing the strength of the shock by displacement of electrodes caused by the movements of the animal. No blind trials (i.e. without shock) were ever given during the preliminary training of the CR, which might enable the animals to develop some avoidance responses. And finally, by keeping the dogs during the sessions in the Pavlovian frame, we restricted their locomotor and other responses, which might, otherwise, replace or mask the flexion CRs.

However, the possibility was not excluded that the shock delivered to the flexed leg was less painful or discomforting than that to the extended leg. In consequence, the flexion of the leg could play the role of an instrumental response attenuating the annoying character of the shock. In such a case one should expect an increase of the strength of the response (i.e. a shortening of latency) in all tests in which the shock was omitted. This increase should be most conspicuous in test 3 in which the CS was terminated at the very moment of performing the flexion, and weaker in "3-sec." and "6-sec." tests.

On the other hand, if the motor conditioned response is not instrumental but purely classical, then the nonreinforced trials should cause the decrease of the conditioned responses manifested by prolongation of latency.

As seen in Table 1 our results unequivocally support the latter conclusion. Thus, we may infer that in our experiments we had to do with purely classical conditioning not only of the autonomic but also somatic responses. This view is further supported by our test 4, in which an increase in the amount of noxious stimulation caused strengthening of the conditioned response in post-test-trials.

The cardiac CR showed no significant changes in the post-test-trials. This finding is in agreement with our earlier observation (Jaworska et al. 1962) showing that the motor and cardiac CRs are relatively independent, the motor CR being more plastic in both acquisition and extinction.

The problem arises as to what are the reasons for the conflicting opinions of various authors concerning the character of the CR in question. The first possibility is that the methods used by these authors differed slightly from ours so that they could obtain both classical and instrumental CRs.

That the classical flexion may be transformed into the instrumental avoidance response was illustrated a long time ago by Petropav-

lovskii (1927). However, this author did not recognize the non-classical nature of his procedure, which consisted in omitting the shock whenever the flexion CR was performed. From his results it is clear that he had, in the beginning to do with the classically conditioned flexion, which was later transformed and fixed as an instrumental act. More recently a similar method was used by Bregadze (1953), Bregadze and Akhmeteli (1953), Shirkova (1956), Vasil'eva (1957), Markarian (1960) and others. The general feature of these methods is that the noxious agent used for punishing the incorrect responses, itself elicits a reaction identical or similar to that required for avoiding the shock. We criticized this method elsewhere (Sol'tysik 1960a) since it does not show for certain when the flexion CR ceases to be a classical and becomes an instrumental CR. It is possible that both components, classical and instrumental are always present in such a reflex, since any incorrect response and the subsequent application of shock should restore the classical flexion CR*.

This mixed character of the flexion CR should also appear in the classical defensive CRs if no special attention is paid to exclude the instrumental conditioning. Thus, such minor differences in training procedure as using the foreleg response, application of the prolonged shock, leaving the animal unrestrained, using the blind trials (without shock), and inaccurate fixation of electrodes, might be favorable factors for changing the character of the motor CR.

Our results have shown that it is possible to establish the purely classical motor response and that this response may preserve its classical character even in a much overtrained CR. We did not observe any definite changes in the form of the flexion throughout the training. Therefore we cannot agree with either of the opinions expressed by Culler (1938) and Gibson (1952) concerning the classical defensive conditioning. Culler's view was that "the CR begins as a copy of the UR and then grows into something different" (Culler 1938). Gibson on the other hand stated the reverse: "... the greatest resemblance between the CR and the UR comes in the late stages of training when singlelimb flexion develops. The early reactions to the signal take the form of rapid backing or running and are not copies of the UR" (Gibson 1952). When we study the differences in their training procedures

* On the contrary, the method used by Konorski and Miller (1933, 1936) consisting in that the dog avoids, by the flexion movement, the noxious stimulus applied to the mouth (acid) or ear (jet of air), similarly as the modification of the Petropavlovskii's method so that the animal avoids, by the flexion of one leg, the shock applied to the other one, both these methods seem to be proper for establishing the pure instrumental CRs (cf. Skipin etc.).

it becomes clear that in Culler's experiments some form of instrumental response has replaced the classical flexion CR ("CR differentiates into a specific preparation for the oncoming US" stated the author), while in the experiments of Gibson the animals were unrestricted and responded to the shock with "the repertory of emergency reactions", i.e., with some natural instrumental escape and avoidance reactions; Gibson observed at least 10 different reactions which gradually disappeared (as unsuccessful in protecting from shock) and the flexion response developed. Probably the conditions of free movement in the experimental room facilitated the transfer of all motor defensive instrumental CRs, already established during life, so masking the classical flexion response. We do not agree either with Gibson's final con-

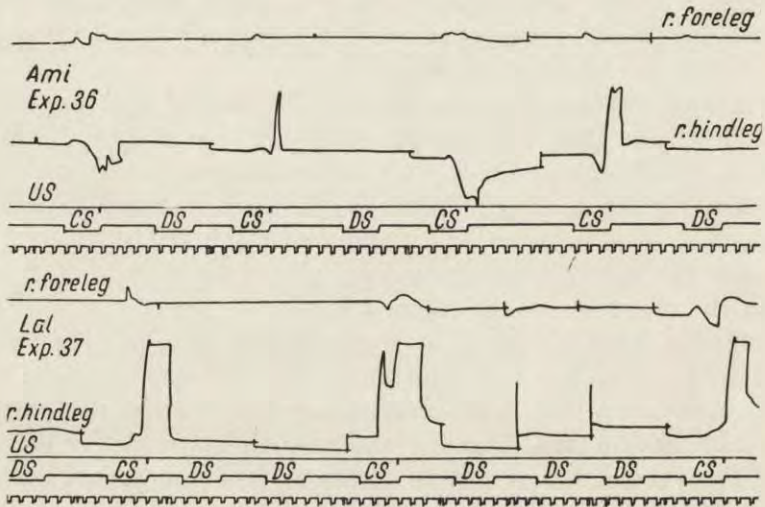


Fig. 1. Motor defensive conditioned responses in dog

Two kymograms of defensive CRs are presented. From top to bottom: movements of the right foreleg, movements of the right (shocked) hindleg, shock, conditioned (CS) and differential (DS) stimulus, time (1 sec.). Upper record: dog Ami; lower record: dog Lal. Note the tonic slow responses preceding the flexions

clusion that the electric shock "does not act to reinforce a withdrawal movement"; even in her experiments, the flexion movement was obtained after eliminating the other "emergency reaction". Our results have shown that the shock is a real reinforcer of the classically conditioned flexion movement.

There is, however, another point which needs some comment. We observed practically in all our dogs, both by simple inspection and by

analysing the records, that besides the flexion response there were also other motor responses in our dogs. This was a slow "tonic" adjustment of the body so that the right hindleg was relieved from supporting the trunk. This is seen on the kymogram as a small deflexion of the tracing just preceding the flexion responses (see 1st and 3rd response of dog Lal in Fig. 1). Sometimes the flexion was performed at once without any visible preparation (see 2nd response in dog Lal) and very rarely we observed an opposite reaction, i.e. the dog pressed the leg to the stand thus hindering the flexion movement (see kymogram of dog Ami in Fig. 1: upper record). Against this background of an increased extensor tonus the shock produced either flexion (2nd and 4th responses in Fig. 1) or merely a jerk without lifting the leg (1st and 3rd responses).

The origin of this tonic CR accompanying the flexion response seems to be the following. The flexion produces the postural tonic readjustment for securing the equilibrium of the body. This is not a defensive response but a reflex to labyrinthine and proprioceptive stimuli generated by flexion. After a number of CS—US trials this postural response becomes a classical CR to the CS and could appear even before the flexion CR, though it comes after the flexion when the shock alone is applied. This means that these two reactions are conditioned independently. Such binary CRs, in which one CS is reinforced by two different USs (simultaneously) were thoroughly investigated by Khodorov (1955) and more recently in Asratian's laboratory Asratian 1961 — personal communication), who also stressed their relative independence from one another.

Such conditioned "secondary reflexes" (not "secondarily conditioned" which implies using the CS as a classical reinforcer of some new neutral stimulus) may influence the form of the flexion response. It was often argued that the response to the CS, not being the exact copy of the UR, needs some other explanatory principles (e.g. "expectancy"), the substitution principle being not sufficient for explaining it. In our experiments, however, we did not find this necessary.

SUMMARY

The effect of an increase or a decrease in the amount of noxious reinforcement was studied in 14 dogs, in which classical defensive flexion CR was established.

It was found that omitting the shock in one trial produced the lengthening of the latency of the flexion response in the following trials, whereas the prolongation of shock had the reverse effect. The

accompanied cardiac CRs were not changed significantly. The results obtained are considered as an evidence for the classical conditioned character of the flexion CR. The problem of binary flexion-postural CR and resulting dissimilarities of the motor UR and CR were also discussed.

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STUDIES ON THE AVERSIVE CLASSICAL CONDITIONING
3. CARDIAC RESPONSES TO CONDITIONED AND UNCONDITIONED
DEFENSIVE (AVERSIVE) STIMULI

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In this paper we present some data concerning the form of the cardiac response to conditioned (CS), differential (DS), and unconditioned (US) stimuli in classical defensive conditioning situation. The need for a more exact knowledge of autonomic ("diffuse" or "unspecific") responses to noxious stimuli and their conditioned substitutes arises from the notion that these responses represent a peripheral counterpart of the central emotional processes which, in turn, are closely related to the hypothetical motivational variables ("drives"), influencing behaviour in both performance (i.e. vigor of responding) and learning. In fact the view that emotional discharge is not merely a by-product of "instincts", but a peripheral effect of central activity which impels and directly influences behaviour, is shared by an increasing number of contemporary authors (e.g. Leeper 1948, Mowrer 1950, 1960, Hebb 1949, Wenger 1950, McClelland 1955 and others).

However, there are only a few papers presenting systematic investigations on the autonomically mediated responses accompanying the simple behavioural acts. An extensive program of research on the measurements of autonomic functions in human beings has been carried out in Wenger's laboratory (Wenger et al. 1957). On dogs, however, traditionally used as subjects in experimental studies on the nervous mechanisms of behaviour, there are no papers showing the time course of cardiac responses; also the statistical method is present only in a few papers dealing with the amplitude of cardiac responses (Ehrlich and

Fronkova 1959, some recent papers from Gantt's laboratory, see Gantt 1960).

In this paper we intend to analyse the pulse curves of classical defensive CR. The results obtained are hoped to be a step in studying the role of emotional responses in relatively complex situations of instrumental learning (cf. Sołtysik 1959, 1960a, b, Sołtysik and Kowalska 1960).

MATERIAL AND METHOD

Experiments were performed on 16 adult, male mongrel dogs. All the dogs were well habituated to the experimental situation and recording devices. In each dog a carotid loop was prepared for the registration of heart beats. Experiments were carried out in a CR-chamber (for details see Sołtysik et al. 1961, and Jaworska et al. 1962).

The US used was a single shock from a condenser 1—2 μ F fed from a battery of 70—120 volts. Stimulating electrodes were placed between the toes of the right hindleg.

The CS and DS were the same buzzer-like tones of 60 db. and 3-sec. duration delivered from two loud-speakers. A tone from the loud-speaker placed in front of the animal was regularly reinforced by shock and became a positive CS, while the same tone from the loud-speaker placed aside the dog was not reinforced and became a DS.

The heart rate was recorded on a high-speed polygraph by a piezoelectric transducer connected with an a.c. amplifier and the EEG ink writer. The movements of both right extremities and respiratory movements were recorded on a slow kymograph.

The animals were taken every day for experiment. Each daily session consisted of 10 trials. The intertrial intervals varied from 1—2 min. When both the positive and inhibitory conditioned stimuli (CS and DS) were used, each of them was presented 5 times in the session in random order.

In every trial the pulse rate was measured in one-second intervals (second-by-second method) including 10 secs. before and 10 secs. after presentation of conditioned, unconditioned or differential stimuli. The regular pulse curves were obtained by the superposition and averaging a number of records; each point in the obtained curve was an arithmetic mean of at least 125 measurements. This method seems to be very effective in eliminating some accidental deflections which are found in individual records and result from respiratory activity and other uncontrolled factors. Next, by the use of analysis of variance, the smallest significant difference (at the risk level of 0.05 and sometimes even at 0.001) was calculated to enable a comparison of: (1) any two points on the curve, and (2) any point during the stimulus and after its termination with the pre-stimulus level of pulse rate (see, for instance, Fig. 2).

The method gives maximum information in a simple graphic form, thus saving the need to study the numerical data collected in tables.

Since some doubts might arise as to the normality, we must add that in our subjects, taken both individually or collectively, the distribution curve had a single peak, but suffered from some skewness. This, however, was never as extreme as to rule out applying the normal tests.

RESULTS

1. Cardiac responses to buzzer prior to conditioning

Fig. 1a shows the cardiac reaction to the buzzer of 60 decibels and 3 sec. duration applied through the loudspeaker placed in front of the animal. Data obtained on 16 dogs are presented. In each dog this stimulus was applied 10 times in one session, the intervals between successive presentations ranging from 1—2 min. The dogs were divided at random into two groups of 8 dogs. In the first group the buzzer was presented soon after the animals were well accustomed to the experimental situation*. This group is referred to as "experimentally naive" and the cardiac responses of these dogs are presented in Fig. 1a by a thin continuous line. The dogs of the second group were given 150 shocks to the right hindpaw in 15 daily sessions (10 trials in each session), and only then was the buzzer applied 10 times in the 16th session. This was done for two reasons. First, we wanted to know the shape and amplitude of the pulse curve representing the response to the shock (the future US reinforcing the buzzer) and its possible modifications during this series of shock sessions. Secondly, we wanted to know whether or not the cardiac responses to the buzzer depend somehow upon the character of the experimental situation. In the first, that is in the "naive" animal group, the situation was neutral, while in the second group the experimental situation became aversive, due to the repeated application of shock.

The response to the buzzer in the shock-group (a thin broken line in Fig. 1a) did not differ from the response in the naive group. This means that no sensitization of cardiac response to the buzzer was produced by the repetitive application of shock. It is worth mentioning, however, that the dogs of the shocked group were markedly excited only in the first shock sessions; the dogs performed the flexion of the shocked leg in the intertrial intervals, barked and frequently tried to escape from the Pavlovian frame. Also the pre-stimulus heart rate was high. These symptoms of generalised excitement diminished gradually and at the end of this series of shock-sessions the animals were almost as quiet as the dogs of the "naive" group. They performed the flexions only in response to the shock, except for dog Car, which performed this movement also during intertrial intervals. In the 16th session, in which the buzzer was 10 times applied, the dogs responded to its presentation with

* In addition, this group of dogs was used in a 10-day study on cardiac responses to the presentation of acoustic stimuli (see: Sołtysik et al. 1961) without, however, any conditioning.

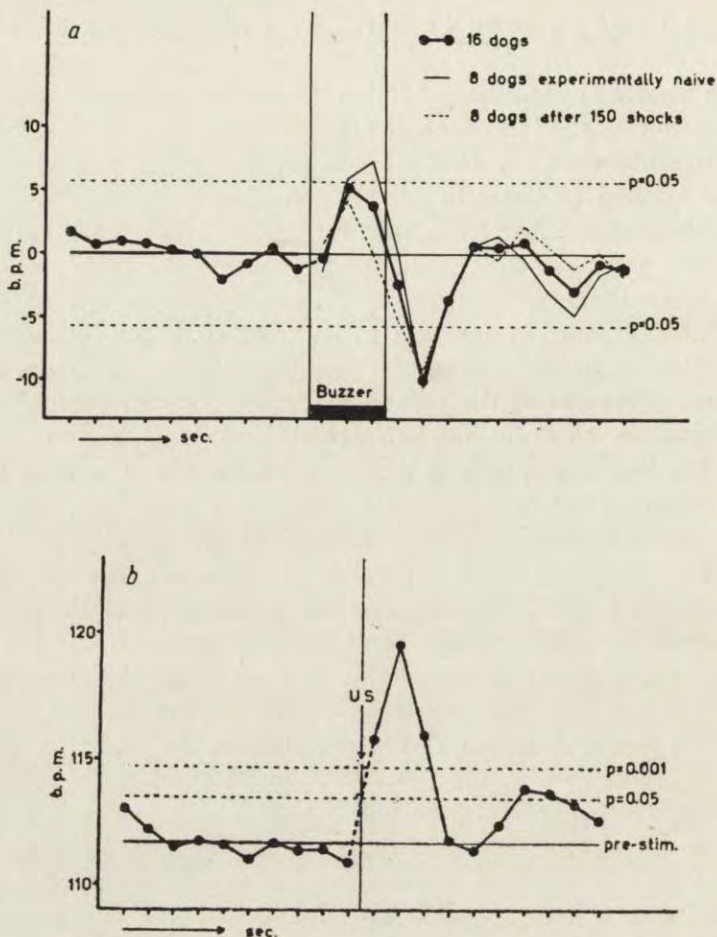


Fig. 1. Cardiac response to a buzzer and to a shock

a) Cardiac response to a 3-sec. buzzer of 60 decibels in 16 dogs is shown (a solid dotted curve). A thin continuous line shows the response in 8 experimentally naive dogs. A thin broken line represents the cardiac response in 8 dogs which had previously been given a series of 150 shocks to the right hindleg. No differences between these curves are seen, that of naive dogs showing a slightly higher acceleration during the action of the stimulus.

The pre-stimulus level of heart rate is taken as zero level, but it should be mentioned that the shock group of dogs had a much higher pre-stimulus pulse rate (120 b.p.m.) than the naive group (96 b.p.m.). Ordinates: heart rate in beats per minute; the pre-stimulus pulse rate is taken as zero. Abscissae: time in seconds.

b) Cardiac response to a single shock from the condenser (1 or 2 μ F, 70–120 volts) applied through the electrodes placed between the toes of the right hindleg. The shock was so adjusted as to produce a definite jerk and flexion of the leg. 8 dogs were used. In each dog the shock was presented 150 times in 15 daily sessions. Ordinates: pulse rate in beats per minute. Abscissae: time in seconds.

a moderately pronounced orienting reflex. No flexion was seen during the 3 sec. of buzzing, except for the dog Car, which performed this movement in three (out of 10) trials with the buzzer.

The cardiac responses to the buzzer in all 16 dogs is shown in Fig. 1a as a solid dotted line. It is seen that during the action of this stimulus there is a small but definite increase of heart rate, amounting to about 5 beats per minute (later denoted as b.p.m.), statistically, however, not significant. Just after the termination of stimulus the pulse rate dropped to about 10 b.p.m. below the initial level; this decrease is significant at the 0.001 level.

2. Cardiac responses to the shock

Quite a different picture is seen in Fig. 1b, in which the cardiac response to a single electric shock is presented. We see an immediate increase of pulse rate which is statistically significant already in the first second and still accelerates in the 2nd sec. However, it should be noticed that the amplitude of the response amounts only to about 8 b.p.m.; The high statistical significance of this increase in pulse rate is due to a great number of measurements: each point of the curve is an arithmetic mean of 1,200 measurements (8 dogs \times 150 trials), and the pre-stimulus level (observed during 10 secs.) is an average of 12,000 measurements).

After reaching its maximum, the curve drops to the prestimulus level and subsequently in the 7th or 8th seconds it rises again significantly. This second "wave" is a stable component of cardiac response to shock and is seen in nearly all our dogs (cf. Figs. 3 and 5).

The most striking difference between the responses to buzzer and shock is that the curve representing the response to the shock does not decrease below the pre-stimulus level.

3. Cardiac response to the buzzer transformed into the conditioned defensive (aversive) stimulus

In Fig. 2 we present the cardiac conditioned responses to the buzzer. The data are taken from 7 dogs belonging to the "naive" group; the 8th dog was not tested as it was too excited and aggressive. The pulse curves represent the responses in the first 15 conditioning sessions, i.e. each curve is calculated from 150 records. The 8th curve (the last curve) is the averaged curve from all 7 dogs.

Let us consider at first the averaged curve and compare it with the curves in Fig. 1. It is quite evident that the response (pulse rate) during the CS is much increased compared with the response to the buzzer

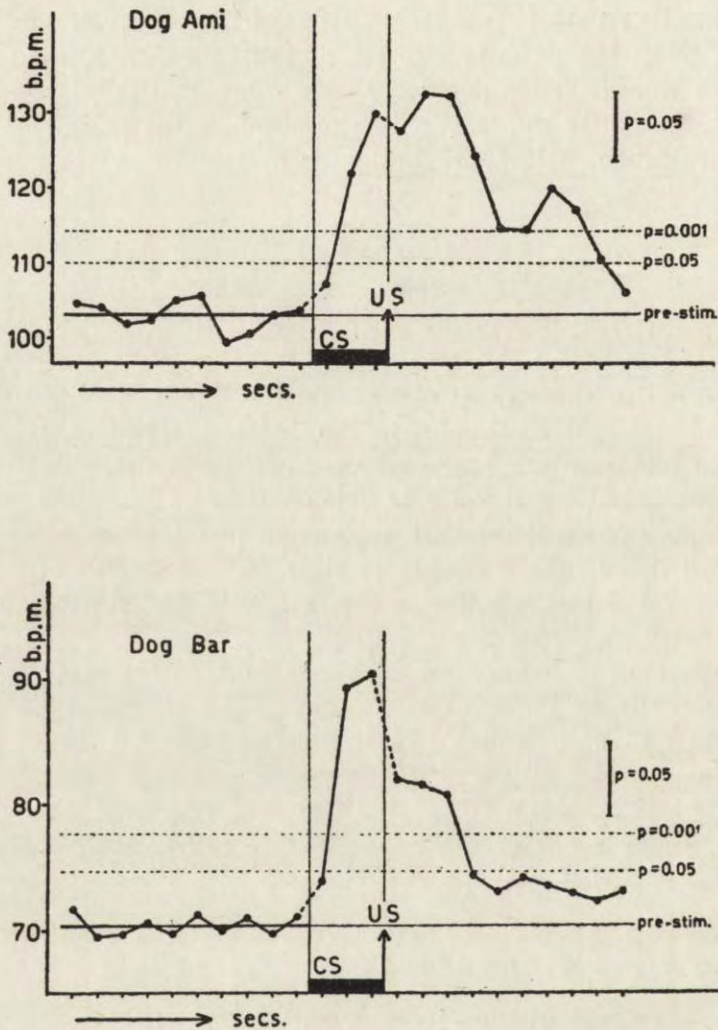


Fig. 2. Cardiac conditioned response to the buzzer signalling the shock. Individual curves of 7 dogs are shown. The 8th curve represents the average cardiac curve of all 7 dogs. In order to show the reliability of the obtained results, the minimal significant difference between any two points of the curve was calculated by analysis of variance (vertical line on the right side of each picture), and also the minimal significant difference between any of the points during and after the CS and the pre-stimulus level (horizontal broken lines) are shown at the two levels of risk: 0.05 and 0.001. Note the considerable differences in the form of curves in individual dogs. Ordinates: pulse rate in beats per minute. Abscissae: time in seconds

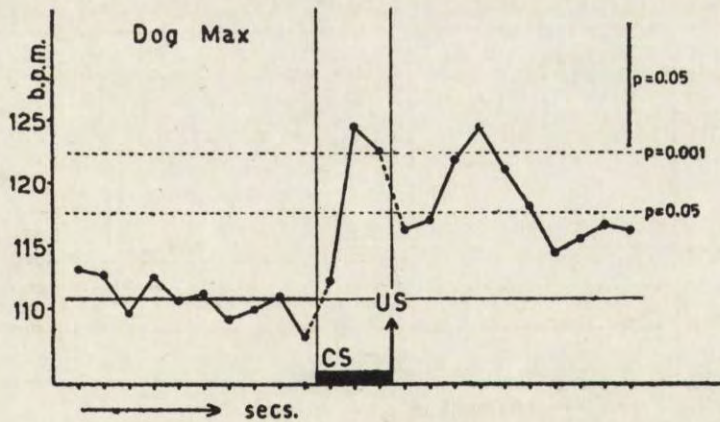
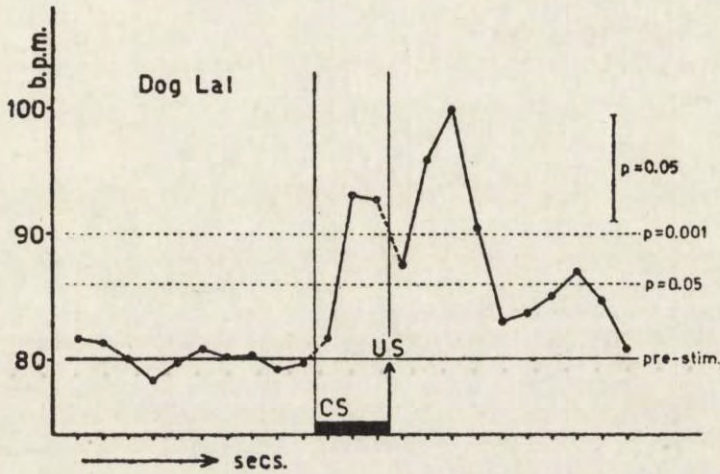
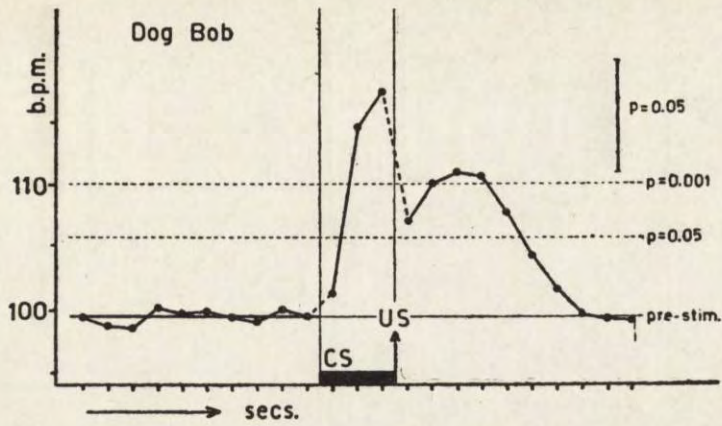


Fig. 2. — continued

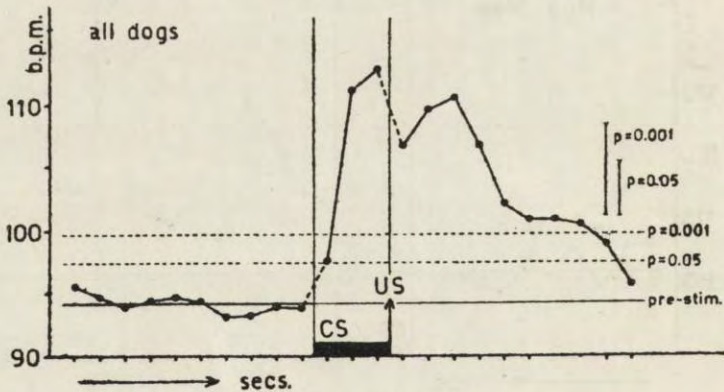
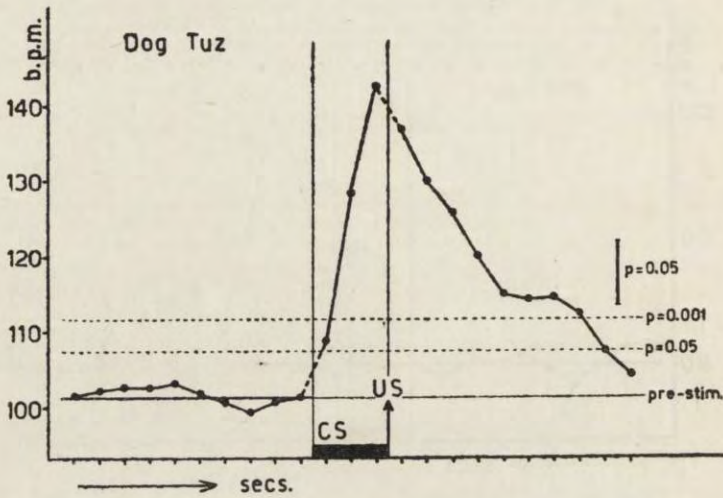
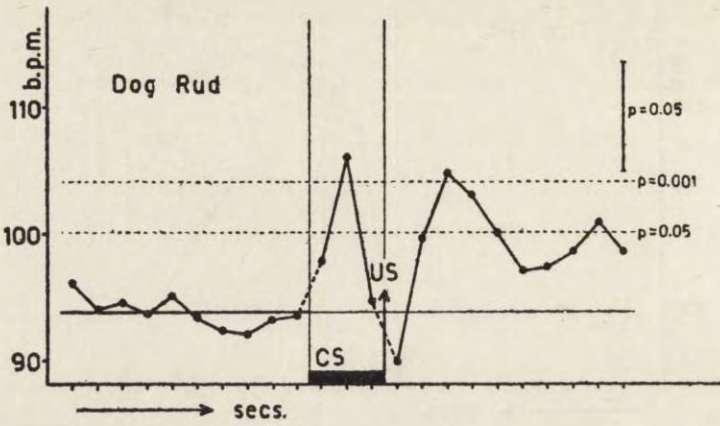


Fig. 2. — continued

prior to conditioning (Fig. 1a) but its general character is unchanged. On the other hand, the form of the curve after the termination of the CS (and after application of the US which coincided with the cessation of the CS) is a resultant of the aftereffects from the response to buzzer (Fig. 1a) and the response to the shock (Fig. 1b). First of all, there is an immediate drop in the pulse rate in the first second after termination of the CS (and application of the US). However, in the next two seconds the pulse rate again increases. Then the pulse rate decreases, but in the 6th, 7th and 8th secs. a secondary wave of cardio-acceleration is seen. Thus the over-all picture of the pulse curve following the CS—US trial resembles the response to the shock, except that the pulse rate drops in the 1st second and the peak of the curve is shifted to the 3rd sec.

If, however, the responses of individual animals are taken into account, considerable differences are seen. In fact every dog possesses its own curve which differs from those of other dogs. Analysing similarities and differences of all 7 curves, we see that the reactions during the first 2 secs. of the CS are in all the dogs quite similar: there is a small increase in the pulse rate in the first second and a remarkable increase in the 2nd sec. The response during the 3rd sec. is not so uniform: in 3 dogs (Ami, Bob, Tuz) a further increase of pulse rate was observed, whereas in 3 other dogs (Bar, Lal, Max) there was no change of pulse rate and in one dog (Rud) a steep drop was seen.

In the first second after the termination of the CS and the shock a drop in pulse rate was seen in all dogs. Afterwards, the curve ascended for 2 to 3 secs. except for two dogs (Tuz and Bar). The secondary wave was seen in the 7th to 9th sec. in all the dogs except one (Bob).

The relations between the amplitude of the cardiac CR and Ur are also different in different dogs. In three dogs the amplitude of the UR is definitely smaller than that of the CR (Bar, Bob, Tuz), in three others no difference is seen (Ami, Max, Rud), and only in one (Lal) does the UR evidently exceed the CR.

4. Cardiac response to the buzzer transformed into differential stimulus (DS)

After the CR to the buzzer had firmly been established, the training of differentiation was started. The DS used was the same buzzer presented from another place. In the first session this "to be DS" was presented 25 times without reinforcement. The cardiac response did not decrease during this session (in spite of non-reinforcement of the stimulus) so the average pulse response from all the 25 trials is exactly the same as the pulse rate response to the positive CS (Fig. 3a).

Fig. 3b shows the response to the CS (full circles) and DS (open

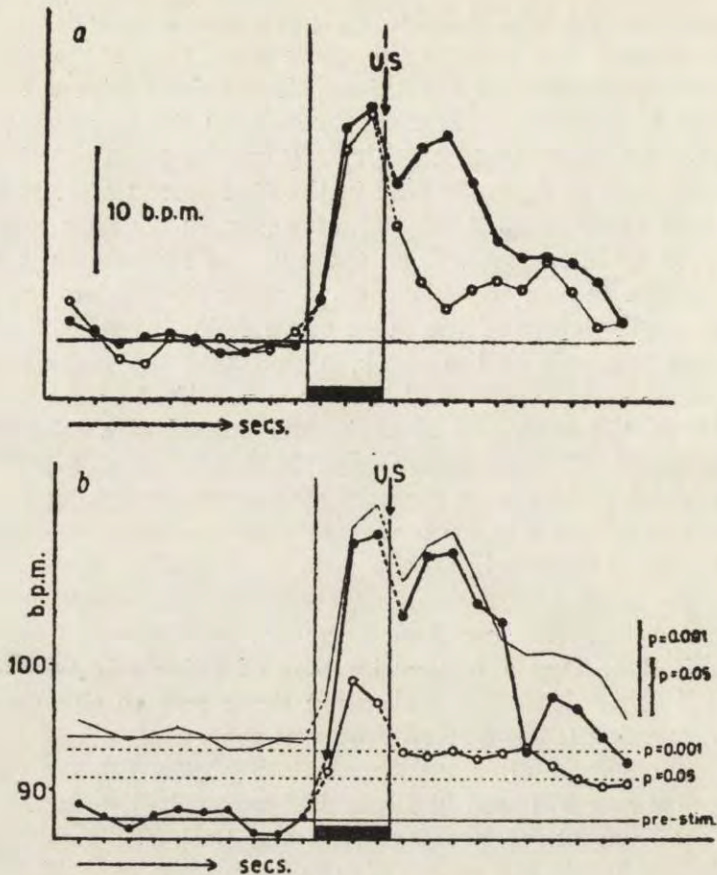


Fig. 3. Differentiation of the cardiac defensive conditioned reflex

a) Cardiac response to the CS, i.e. a buzzer acting in front of the animal (full circles) and cardiac response to the same stimulus applied in another place (aside the dog) without reinforcement (open circles). Data concerning the non-reinforced buzzer are taken from 7 dogs. The curve represents the average of 25 consecutive trials.

Both curves are presented in such a way that the pre-stimulus level of each lies on the same horizontal line, so that the amplitudes of both curves are easily comparable. It is seen that the non-reinforced buzzer (the future differential stimulus) produced at the beginning the same cardiac response, both in form and amplitude, as did the positive CS. It is also clear that the drop in heart rate in the first second after termination of the CS is not caused by the shock, as this drop is even greater in the case of the non-reinforced stimulus; on the contrary, it seems that the rise in the heart rate seen in the 2nd and 3rd secs. after the application of the shock (applied at the moment of cessation of the CS) is the response to this US.

b) Cardiac response to the CS (full circles) and to the DS (open circles) after establishing the differentiation of the motor reaction. Data are taken from the sessions 16th—40th (each session consisted of 5 positive and 5 inhibitory trials randomly scheduled), counting from the session when the DS was introduced. The third curve (thin line) represents the cardiac CR in the first 15 sessions (cf. Fig. 2) i.e. 6 months earlier. It is seen, first, that the response to the CS remained exactly the same (cf. form of the black dotted curve with the thin line curve) though the pre-stimulus level fell significantly.

Cardiac response to the DS is much smaller than to the CS or to the DS in the first 25 trials (see A). It also differs from the original response to the buzzer (cf. Fig. 1A) and may be described as a partially extinguished conditioned response.

circles) following the 15 sessions of differentiation training in which all the dogs reached a high level of differentiation of the motor response. It is seen that the cardiac response to the DS differs markedly from both the response to the CS and the original reaction to the buzzer before conditioning (cf. Fig. 1a). It differs from the cardiac CR in amplitude and from the original response to the buzzer by the lack of deceleratory after-effect. Thus the cardiac response to the DS may be characterized as a strongly diminished response to CS.

A similar picture is obtained when the pulse curves of individual animals are surveyed. In all cases except one (Tuz) the response

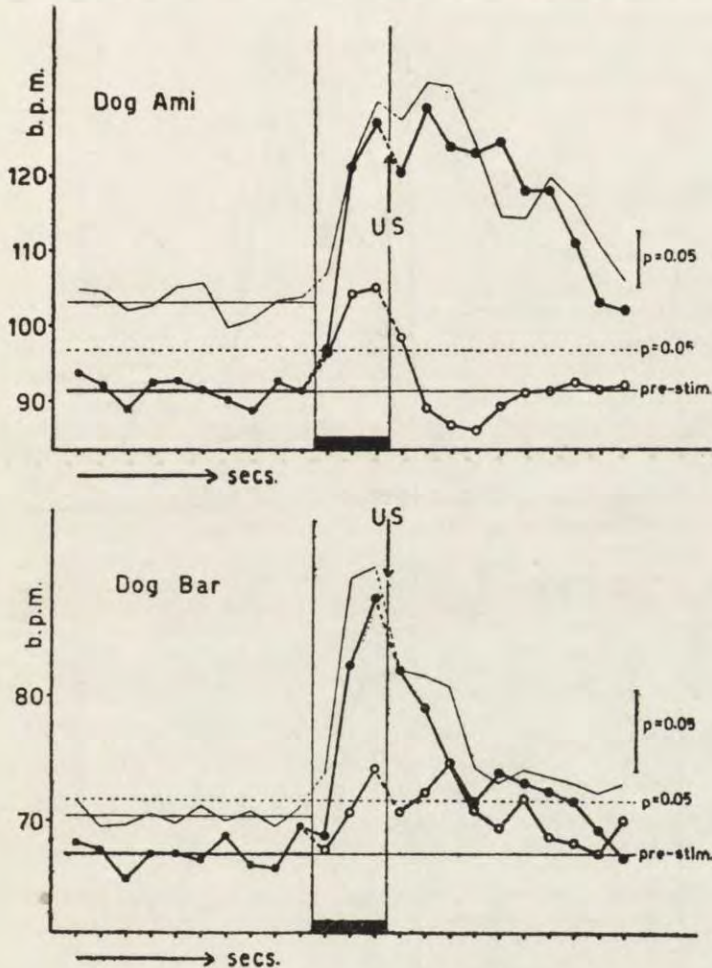


Fig. 4. Cardiac responses to the conditioned and differential stimuli in 7 dogs. The results presented in Fig. 3b are here shown separately for each dog. Note the smaller amplitude of responses to the DS and the persistence of the form of cardiac CRs

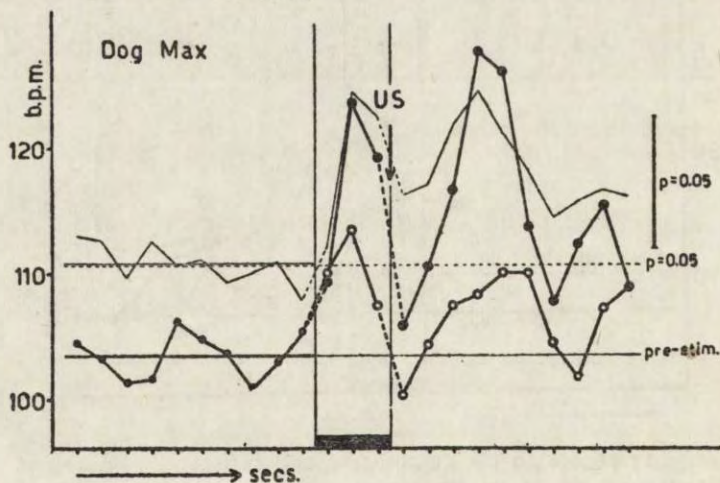
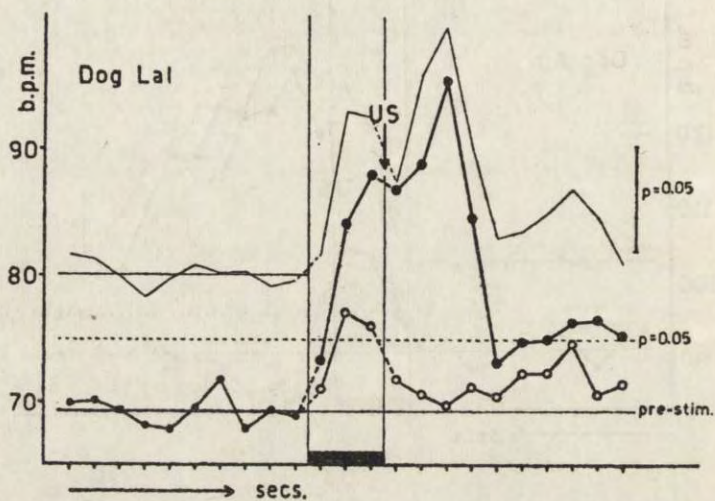
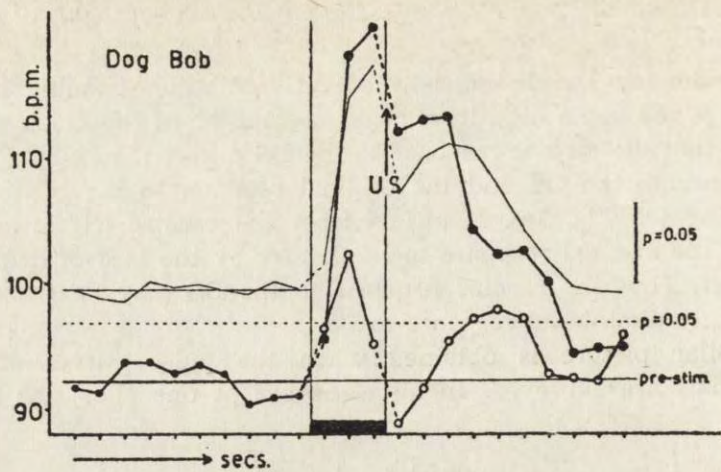


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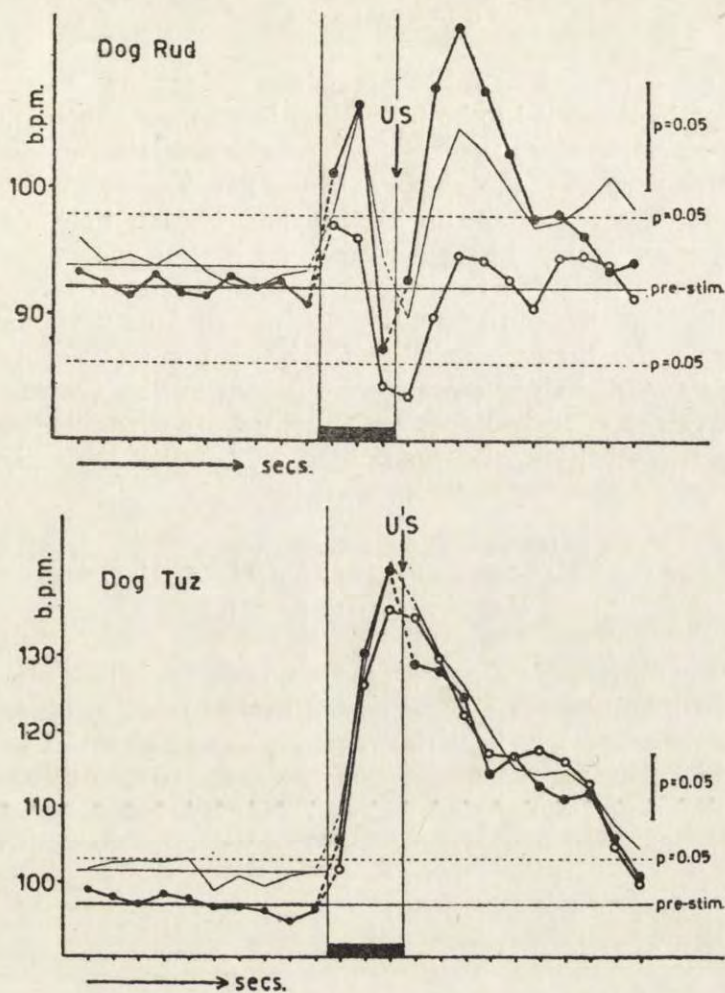


Fig. 4. — continued

to the DS is much smaller than that to the CS, but its form remains roughly the same. It is worth mentioning that the one dog (Tuz), in which the response to the DS remained the same, as that to the CS, was exceptionally fearful in comparison with the others and never established friendly relations with experimenters. The general emotional hyper-reactivity observed in Tuz was thus reflected in the cardiac responses to the CS and DS.

5. Persistence of the shape of pulse curves in cardiac CRs

Since our experimental animals remained under the CR training more than 6 months it seemed to be interesting to compare the amplitude and the form of the cardiac responses in the early and late periods of training. For this purpose the pulse curve of the newly established CR, taken from Fig. 2, was reproduced in Figs. 3b and 4 (thin line). As seen in Fig. 3b the curves representing a new and a well overtrained cardiac CR are exactly the same in shape. The only difference is seen in the absolute level of the pre-stimulus pulse rate and in the amplitude of the response; the firmly established CR has a lower pre-stimulus level and higher amplitude. The same picture is seen in Fig. 4 where the cardiac responses of individual dogs are presented. By examining each curve we see that in every dog the same difference between the early and the late stage of conditioning is observed.

6. Cardiac response accompanying the intertrial flexion movement

While the previous data concern the responses to definite stimuli, now we wish to show the pulse curve of the cardiac reaction observed during the "spontaneous" or intertrial response. It was observed in one dog (Rud), which during the acquisition training, frequently performed flexion movements of the shocked leg. The curve calculated from 100 records, including 10 secs. before and 10 secs. after the movement is

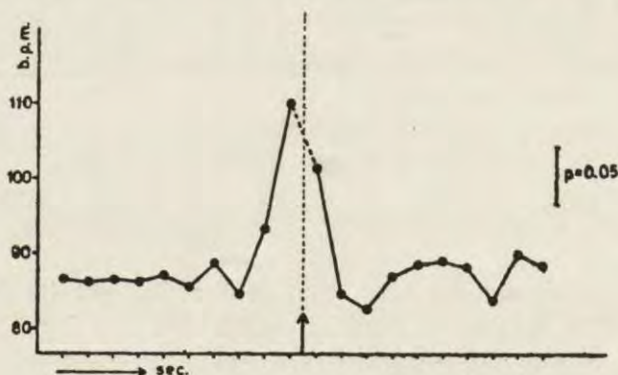


Fig. 5. Cardiac responses accompanying the spontaneous (intertrial) movements. The motor defensive response (flexion of the hindleg) occurring spontaneously during intertrial intervals is here considered. The cardiac curve is obtained from 100 records. It is seen that cardioacceleration preceded the movement and that an immediate suppression of this cardiac response occurred after the movement was displayed.

shown in Fig. 5. Two main features of the curve should be stressed. The first one is the increase of the heart rate resembling the cardiac CR both in amplitude and shape (cf. Fig. 2, dog Rud) which precedes the movement, and the second one is the steep drop of pulse rate observed immediately after the performance of the movement.

DISCUSSION

A thorough analysis of the pulse curves, such as presented in this paper, has never before been performed in dogs. In human beings, Chuchmarév (1926) found the specificity of the pulse curves in different emotions and highly appreciated this method in experimental analysis of emotional reactions.

More recently a group of American authors used the pulse curves for analysis of the mechanism of learning (Zeaman, Dean and Wegner 1954, Zeaman and Wegner 1954, 1957). Since, however, these authors used a different technique from that of ours (trace conditioning and beat-by-beat method of reconstruction of the curves), it is not possible to make any reasonable comparison between their results and ours.

To begin with, let us discuss some general properties of the cardiac response.

First of all the promptness of this response and the apparent lack of inertia, so unusual in autonomic reactions, should be emphasized. The explanation of this fact is that the cardioacceleratory reaction is effectuated by the "release" of spontaneously beating pacemaker from the tonic vagal inhibition (cf. Hunt 1899, Rosenblueth and Simeone 1934, Beebe-Center and Stevens 1937, Bond 1943, Rohse and Randall 1955, and others). All these authors stress the role of diminution of the tonic activity of the vagi as a chief factor in acceleratory response. Sympathetic nerves are said to control rather the strength of cardiac contractions (Rohse and Randall 1955, Murphy 1942), while their acceleratory action is extremely slow — the peak of acceleration occurring only after about 20 sec. (Rosenblueth and Simeone 1934). Also the effect of adrenaline is much delayed — here the peak comes after about 12 secs. (Bond 1943).

It is supposed, therefore, that most of the cardiac responses to external stimuli (except for strong emotional reactions with adrenalinemia) are mediated by inhibition of the vagus centres (Wiggers 1949).

According to our view this sensitivity and promptness of the cardiac response justify its utilisation as a proper indicator of central processes like emotional states and drives. There are, however, some factors which argue against the uncritical approach to this problem.

The main objection is that the pulse rate is an unspecific response and one could never be certain what kind of central state is actually represented by it. Indeed, inhibition of the vagus centre seems to be involved in any alerting responses, such as orienting reflexes, conditioned food reflexes, and many others. If, however, we do not train several kinds of CRs simultaneously in the same situation, the question of unspecificity is not so important. On the contrary, the fact that the cardiac response is unspecific may help in a comparison of quite different CRs (cf. *Soltysik 1960c*).

Another objection is that cardiac response may be a "secondary" reflex from reacting organs, especially muscles. If this were true, the value of cardiac response as an index of central processes would be doubtful. However, there are data indicating that the cardiac response is by no means a mere effect of proprioceptive stimulation. This is best proved by the fact that epileptic seizures may occur without concomitant cardiac acceleration (*Erickson 1939*); *Fuller and Christie (1959)* observed conditioned motor responses without concomitant cardiac reactions; we also found that there is no parallelism between classical motor and cardiac CRs in dogs (*Jaworska et al. 1962*). On the other hand, curarisation does not eliminate the cardiac CR in dogs, although their muscles are paralysed (*Black 1956*). *Peters and Gantt (1948)* concluded that "an increased heart rate... is much more a result of central excitation than of any accompanying peripheral muscular tension". Of course, only such simple and effortless motor activities are here implied which do not produce "oxygen deficit", hypercapnia, or other shifts in the internal milieu.

Yet, another objection is that cardiac response is so much influenced by the self-regulatory mechanisms through the aortic, carotid sinus, and other moderator nerves, that the resultant pulse rate is by no means a direct index of central activities (cf. *Darrow 1943*). However, it should be remembered that if the cardioacceleration is caused by the suppression of vagal centres, the compensatory deceleration initiated by the possible rise in blood pressure is also suppressed. Thus, at the time of the cardiac acceleratory response, the deceleratory reflexes are certainly blocked, or at least partially suppressed.

All these considerations compel us to think that, at least in dogs, the cardiac response is a very profitable method for physiological and psychological research. It is difficult, however, to be sure whether the same applies to other animals, in which, unlike dogs, cardiodeceleratory (e.g. cats; *Jaworska 1958*, *Santibanez 1961*) or complex acceleratory — deceleratory (human beings; *Zeeman et al. 1954, 1957*) responses were found in aversive conditioning.

Let us now proceed to a more detailed discussion of some of our results.

First, the difference in the form of the cardiac response to the buzzer and to shock needs some comment. Present results concerning the cardiac response to the buzzer confirm our earlier findings (Jaworska and Soltyzik 1960, Soltyzik et al. 1961), in which we have shown that the deceleratory aftereffect (called by us "off-response") was seen even after very short auditory stimuli. In contrast, the response to shock is characterized by the lack of negative phase and the pulse rate after the initial peak in the 2nd sec. and secondary wave in 6th to 8th sec. returns to the initial level. This fact may serve as evidence to show that the bi-phasic form of the cardiac response to the acoustic stimulus is not an inherent property of this response as such, but depends somehow on the modality of stimulus. Auditory analyser is well provided with inhibitory mechanisms moderating both the initiation (Galambos 1956) and conduction (Jouvet and Desmedt 1956) of afferent impulses, so that a sharp cutting off or even inhibitory aftereffect in the afferent pathway might be considered as a result of cessation of the stimulus. The pain stimulation, in contrast, is characterized by long afterdischarge in peripheral fibers C (Adrian 1928) which may last well up to 20 secs.

These well known functional differences between the acoustic and nociceptive analysers may be responsible for the observed differences in cardiac responses to corresponding stimuli.

The next problem for discussion is the nature of the conditioned cardiac response to the buzzer. Its true CR character and not just a mere sensitization of acoustic-cardiac reflex (see Soltyzik et al. 1961) is proven by the following fact. First, the response to the CS differs markedly from the original response to a buzzer (cf. Figs. 1 and 2). Secondly, the hypothesis of potentiated startle response is disproved by the fact that there was no enhancement of the cardiac response to the buzzer in 8 dogs which had been given a series of 150 shocks*. Thirdly, the DS elicited much smaller cardiac responses, despite its physical identity with the CS. Since no difference in the vigor of orienting reflexes (movement of eyes, ears, and head) elicited by these two stimuli was observed, the increase of the cardiac response to the positive CS cannot be attributed to increased attentiveness to it.

Let us pass now to the shape of pulse curves representing cardiac CR in individual dogs.

* It should be noticed that this result is in disagreement with the observation made by Brown et al. 1951, that the practicing of the painful stimulation in rats increased startle response to clicks.

While the shape of the CR pulse-curve is more or less similar in all our dogs, small differences occurring only in the third second (except the unusual drop of the curve in dog Rud) the pulse curve to the shock following the buzzer exhibits much more variations in different dogs. Since, however, the cardiac responses in particular dogs are strikingly persistent even during the long period of training (cf. Figs. 2 and 4) they certainly represent definite central processes characteristic for each animal.

According to the general belief concerning the ratio between the amplitude of conditioned and unconditioned classical response (based mainly on the salivary reflexes) we should expect that: 1° the conditioned response will smoothly pass into the unconditioned response, and 2° the response to the shock will be always larger than, or at least the same as, that to the CS. What actually happened was quite the reverse: immediately after the termination of the CS accompanied by shock there was a distinct and statistically significant drop of the pulse curve which in some animals (Rud, Bar, Bob, Max) was quite considerable. Then in most of our dogs (except Tuz and Bar) the curve rose again, but the second peak was usually lower than, or sometimes equal to, the CR peak; only in one dog (Lal) did it definitely surpass the CR peak.

How is this to be explained?

The depression in the curve immediately following the termination of the buzzer may be a reflexion of a much deeper depression observed in the same moment when the buzzer was an indifferent stimulus (cf. Fig. 1A). Thus the rather shallow drop in the pulse curves of Figs. 2 and 4 may be considered as a resultant of that depression and the rise of the curve produced by the shock. The correctness of this explanation may be tested by using, instead of an auditory stimulus as a CS, a visual stimulus which does not give such a depression.

But then one may ask why the succeeding rise of the curve is so small and in some dogs does not exist at all (Tuz, Bar). This question cannot be answered without many control experiments which are now in progress. However, a tentative explanation which is a point of departure for further experimentation is the following. It should be noticed that in our experiments the noxious reinforcement consists of a simple condenser shock. In consequence the three events, namely the termination of the CS, the shock accompanying it, and the flexion of the leg beginning usually one second earlier (as a conditioned response) and terminating just after the shock, signal the cessation of fear produced by the buzzer, and cause the quieting down of the animal for at least one minute. It should be remembered that the inhibitory character of the stimuli closely preceding the termination of either the conditioned

(Sołtysik and Kowalska 1960, Sołtysik 1960a, b) or unconditioned (Konorski 1960, Zbrożyna 1957, Segundo et al. 1961, Aslanova 1960, Sołtysik and Zieliński 1961) stimulus, was shown by several authors. And so, all specified agents acting in common, or may be some of them in particular, might become inhibitory stimuli suppressing the fear reaction and thus reducing the amplitude of the cardiac response to shock. The special observation made on dog Rud showing the immediate drop of the pulse curve after the animal has performed the intertrial defensive movement (cf. Fig. 5) seems to indicate that this inhibitory role is played, at least in part, by the performance of the movement. So, in this respect the inhibitory character of the motor response may be similar to that shown in avoidance conditioning (Sołtysik and Kowalska 1960, Sołtysik 1960 a,b). However, it may appear that the same role is played also by the termination of the CR, or even by the application of the US, which in such a case would play a double role, namely that of eliciting the defensive reaction and that of terminating the state of fear.

The last point to be stressed is the persistency of shapes of the pulse curves in individual dogs. This finding is, as we believe, of great importance. The cardiac response is usually thought of as very feeble and unstable; and this is true, indeed, when individual trials or records are taken into consideration. Our experience with the pulse rate in dogs is the following. The variability in individual records is due to a high "noise level" in the baseline of pulse rate, so that the relatively small reactions are masked and distorted by concurrent accidental reactions. According to our impression, this noise does not result from some spontaneous oscillations in the nervous stabilizing system, but is due chiefly to the lack of "screening" from the internal environment; therefore, even in a perfectly isolated experimental situation, there is a lot of uncontrolled excitations from respiratory movements, labyrinthine and interoceptive stimuli, which all influence the pulse. The fortunate circumstance is, that these uncontrolled agents are not related to the "controlled" external stimuli presented by experimenter. In consequence it is possible to diminish the effects of this "noise" simply by averaging a sufficient number of records. Under the latter conditions the regular and perfectly reproducible in shape pulse curves may be obtained.

SUMMARY

Four types of cardiac responses were analysed in this study:

1. the response to buzzer prior to conditioning,
2. the response to shock,
3. the response to buzzer transformed into the conditioned stimulus signalling the shock, and
4. the response to a buzzer sounding from a different place transformed into the differential stimulus.

It has been found that the cardiac response to a neutral acoustic stimulus (a buzzer of 60 db.) of 3 secs. duration consisted in a small cardio-acceleration during the action of stimulus and in a profound deceleratory off-response which occurred in the first 3 secs. after the termination of this stimulus.

The electric shock (a single discharge of condenser) to the hindleg produced a shortlasting increase of the pulse rate with the peak in the 2nd sec., without, however any deceleratory aftereffect.

After repeated pairing of the buzzer with the shock (the latter having been applied at the moment of termination of the buzzer), the buzzer elicited a cardiac response characterized by a higher amplitude than that obtained both to the buzzer acting alone and to the shock, and by the much diminished deceleratory aftereffect.

The differential stimulus elicited a response similar in form to that produced by the CS, but of much smaller amplitude. The cardiac responses of each experimental animal exhibited their own particular characteristics, which remained stable throughout the period of experimentation.

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ON THE PECULIAR PROPERTIES
OF THE INSTRUMENTAL CONDITIONED REFLEXES
TO "SPECIFIC TACTILE STIMULI"

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In early papers by Konorski and Miller (1933, 1936) it was shown that the type II (instrumental) conditioned reflexes (CRs) obeyed the Pavlovian rule of "strength of conditioned stimuli" (CS) in the same way as did the type I (classical) CRs. According to this rule, the CRs established to different CSi and reinforced by the same US may differ in strength, depending on the character of the CS applied. Thus, auditory CSi generally produce a stronger effect than tactile and visual stimuli, rhythmic stimuli have a stronger effect than continuous stimuli, and the stronger the intensity of the CS, the stronger, up to a certain limit, is its effect (cf. Pavlov 1927, Konorski 1948, chapt. II).

However, according to the observation made by Konorski and Wyrwicka (1950), under certain conditions stimuli of the same strength (i.e. eliciting the same classical conditioned response) may produce instrumental responses of different strength, as measured by their latent periods and/or amplitudes of movement. This used to occur when different stimuli were used in different training procedures. When the instrumental CR was trained to a given stimulus from the very beginning of its application, the motor response to it was strong, but if the instrumental CR had been transformed from the classical CR, the motor response to the CS was weak. On the basis of these findings the authors concluded that various instrumental CSi might possess various motogenic properties depending on the previous training.

The supposition was put forward that the motogenic properties of the stimuli might also depend on their intrinsic character; in particular,

it was suggested that the tactile stimulus applied to the distal part of the leg involved in the performance of the trained movement might appear to be more motogenic than other CSi.

The aim of this paper is to compare the motogenic properties of the tactile stimulus applied to the leg involved in the trained movement (henceforth called "specific tactile stimulus") with ordinary stimuli applied in instrumental conditioning.

METHODS

Experiments were carried out in a regular sound-proof CR chamber. Instrumental food CRs were trained to tactile and auditory stimuli. Tactile stimuli consisted of the rhythmic touching of the skin, applied once per second and delivered by a device attached to the skin (Fig. 1, Podkopaev 1952). The

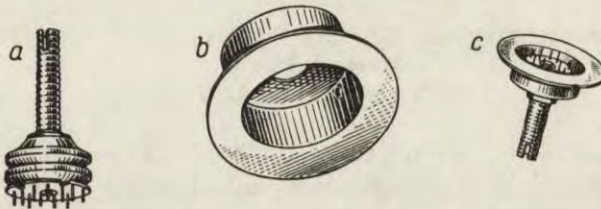


Fig. 1. The apparatus used for tactile stimulation
 a — the rubber capsule extended by pressing the rubber bulb by the experimenter; each pressing contacts the blunt pins with the skin of the animal, b — the metal frame of the capsule attached to the skin, c — the whole apparatus

Instrumental response consisted of placing the right foreleg on the foodtray situated in front of the animal. The presentation of food (pieces of bread or minced biscuits with broth) was accomplished by moving the bowls into position one by one by an electric device controlled by the experimenter. In some animals salivation from the parotid gland through a fistula with a shortened duct (Sołtysik and Zbrożyna 1957) was recorded by Kozak's method (1950).

In the experiments in which the salivary-motor method was used the CS action was followed after 10 seconds by the presentation of food; the intertrial intervals were 3—4 minutes. In purely motor experiments the performance of the trained movement was immediately followed by food reinforcement and the intertrial intervals were about 1 min. Usually 9 trials were given in every daily session.

The first instrumental CR was trained by the Konorski and Miller's method (1933, 1936). According to this method food reinforcement followed the compound composed of a given stimulus and the passive placing the animal's leg on the foodtray, whereas the stimulus applied separately was not reinforced. In order to establish the instrumental CR to subsequent stimuli the method described by Wyrwicka was used. Wyrwicka (1952a, b) found that if an instrumental CR has been firmly established to a given stimulus, and a new stimulus is applied with immediate food reinforcement, the transfer of the instrumental response to this new stimulus occurs after a few trials.

RESULTS

1. Comparison of the formation of instrumental CRs
to specific tactile stimulus
and to other stimuli

In the first series of experiments, carried out on 6 dogs, the first instrumental CR was trained to the tactile stimulus applied to the anterior surface of the wrist of the right foreleg. As seen in Table I, the instrumental CR was formed after a few trials. When the CR was firmly

Table I

Speed of formation of instrumental CR to specific tactile stimulus
and of its transfer to buzzer

Nos. of dogs	1	2	3	4	5	6
First training to specific tact. stim.	16	6	11	6	15	14
Transfer to buzzer	(56)	(66)	(61)	(22)*	(51)	25

Figures denote the numbers of trials necessary to establish the CR. Figures in brackets show that instrumental CR was not established after a given number of trials.

*) Experiments were discontinued because of severe neurosis.

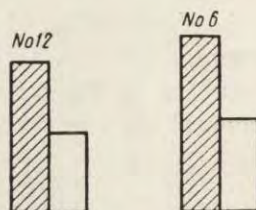
established, an auditory stimulus, the buzzer, was introduced and reinforced by food. It was applied 2 or 3 times in every session among the tactile CSi. In 5 dogs out of 6 the instrumental response failed to appear to this stimulus in spite of more than 50 applications of it with random changing the moment of reinforcement from 2 to 10 seconds or longer. The buzzer elicited merely a direct food reaction toward the food-tray and salivation. Only in one dog (No. 6) did the instrumental response occur to the buzzer after 25 trials, but its latent period was longer than to the tactile stimulus, and from time to time it failed to appear. However, no matter whether the instrumental CR to the buzzer was delayed or absent the salivary response to it was much more conspicuous than that to the specific tactile stimulus, as seen in Fig. 2.

In view of these results, in the second series of experiments, which was performed on 3 other dogs, the procedure was reversed, namely, the instrumental CR to the buzzer was established at first, and there-

after the specific tactile stimulus was introduced. As seen in Table II, the transfer of the instrumental response from the buzzer to the tactile stimulus occurred in all dogs very rapidly.

In order to see whether the lack of transfer of the instrumental CR from the touch of the leg to the buzzer is dependent on the specificity

Fig. 2. The mean salivary conditioned responses in two dogs to buzzer (hatched columns) and to specific tactile stimulus (white columns)
Note that salivation to tactile stimulus is much smaller than that to buzzer



of the leg stimulation, the third series of experiments was performed on 2 dogs in which the first training of the CR was carried out to the tactile stimulus applied not to the leg but to the side of the body, and then the auditory stimulus was introduced. In this case the transfer of the CR from the first to the second stimulus occurred again quite easily (Table II).

Table II

Speed of formation of the instrumental CR to buzzer and tactile stimulus to the body and of its transfer to the specific tactile stimulus to buzzer respectively

Nos. of dogs	7	8	9		10	11
First training to buzzer	21	*)	*)	First training to tact. stim. of the body	24	31
Transfer to specific tactile stimulus	11	5	8	transfer to buzzer	6	4

Figures denote the numbers of trials necessary to establish the CR.

*) Since the first training was accomplished not by reinforcing the passive movements, but by active manipulative movements (method not described here), the numbers of trials are not presented.

To summarize, we have found that if an instrumental CR to the specific tactile stimulus is established in the first training, it prevents a transfer of the instrumental response to other stimuli. Such a transfer is readily obtained if other stimuli (buzzer or touching the body) are used in the first CR training.

2. Comparison of chronic extinction and restoration of instrumental CRs to specific tactile and auditory stimuli

Experiments of this kind were performed on 4 animals. In one, the chronic extinction and restoration of CRs was carried out twice, in the others, once. The experimental procedure was the same in all series and ran as follows:

In all the dogs the instrumental CR was established to the metronome, the buzzer, and touching of the right wrist. The number of applications of the buzzer and touch was equal, and amounted up to 400. Then in the extinction series the metronome was applied with reinforcement

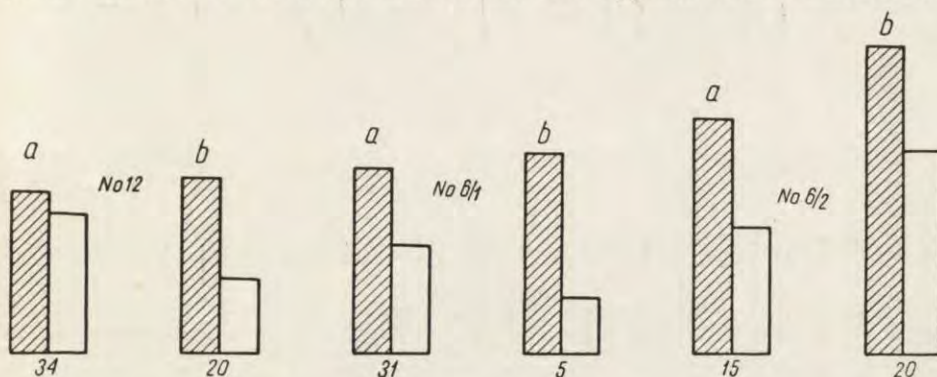


Fig. 3. Mean salivary conditioned responses to buzzer (hatched columns) and specific tactile stimulus (white columns) during chronic extinction (a) and restoration (b) of CR. Nos. of dogs and number of trials in extinction and restoration series are indicated. Note that both in extinction and restoration series the salivary responses to buzzer are larger than to tactile stimuli

7 times in a session, while the buzzer and the tactile stimulus were applied only once per session without reinforcement, in the 3rd or 4th trial, and in the 6th or 7th trial. Their sequence alternated from day to day, so that if in a given session the buzzer came first and the touch second, in the next session their order was reversed.

After the extinction of the instrumental CRs to both stimuli was completed, a restoration series followed with reinforcing the extinguished CSi by food. As known from Wyrwicka's studies (1952a, b) the re-reinforcement of an extinguished instrumental CS by food leads to the re-establishment of the instrumental response to it.

As seen in Table III, the results obtained in all the extinction series were the same. The resistance to extinction of the instrumental CR to the specific tactile stimulus was much stronger than that to the buzzer.

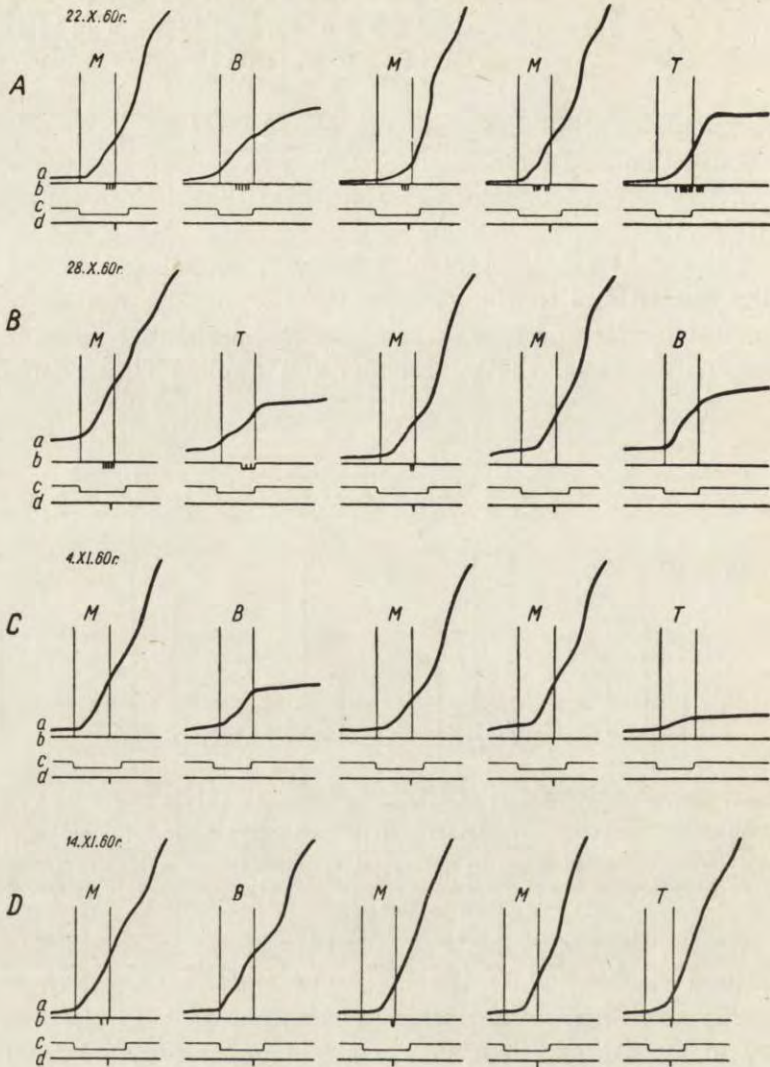


Fig. 4. The fragments of records of experimental sessions in the second extinction-restoration series in dog No. 6

A — 2nd session of the extinction series, B — 7th session of extinction series, C — 12th session of extinction series, D — 5th session of restoration series.

In each record only five successive trials are presented including two extinction trials. a — cumulative curve of salivation; perpendicular lines denote the outset of CS and presentation of food respectively; b — putting the right foreleg on the foodtray; c — CS; M — metronome, B — buzzer, T — specific tactile stimulus; d — presentation of food.

In A, both buzzer and tactile stimulus elicit strong motor and salivary reaction. In B, tactile stimulus still elicits motor response, while buzzer fails to do so. In C, both buzzer and tactile stimulus do not produce motor response; note the considerable salivation to B. In D, on 5th day of restoration tactile stimulus produces motor response, while buzzer does not. Note the gradual decrease of motor responses to metronome in the course of extinction series

Table III

Speed of extinction and restoration of instrumental CRs to buzzer and specific tactile stimulus

Nos. of dogs	12		6/1		6/2		9		8	
Extinction to buzzer	7	7	3	7	6	6	8	8	5	8
Extinction to specific tact. stimulus	27	31	8	22	11	11	31	32	10	13
Restoration to buzzer	(20)	(20)	(5)	(5)	(20)	(20)	7	9	—	—
Restoration to specific tact. stim.	2	2	2	2	2	2	2	2	—	—

The first column for each dog denotes the first trial in which the instrumental response was absent in the extinction series, or the first trial in which the instrumental response reappeared in the restoration series. The second column denotes the same for three consecutive trials. The figures in brackets denote that after a given number of trials the instrumental response did not reappear.

On the contrary, in the restoration series, the reappearance of the instrumental movement in response to the touch occurred already after a few reinforcements, while to the buzzer it occurred much later, or even failed to appear.

The extinction and restoration of the salivary reflex took a quite opposite course, namely, its resistance to extinction and promptness of restoration was greater to the buzzer than to the touch (Fig. 3).

In Fig. 4 representative fragments of records of the second extinction-restoration series in dog No. 6 are shown. It is seen that the motor reaction to the buzzer disappears sooner than that to the tactile stimulus, while the salivary reaction drops earlier to the latter stimulus. It is also seen that during the extinction series there is some impairment of the instrumental CR to the positive CS (metronome), which either elicits a less vigorous motor response, or even fails to elicit it.

DISCUSSION

Our results demonstrate that the association between the CS and the instrumental response is particularly strong when the CS is represented by a tactile stimulus applied to the distal part of the leg involved in

this response. These results are supported by other tests, such as acute extinction of the CR or satiation of the animal, as reported in another paper (Wyrwicka and Dobrzecka 1960). Here, also, the instrumental response to the touch of the leg was much more persistent than the same response elicited by either the auditory stimuli, or tactile stimuli applied to other parts of the body. Similar results were obtained independently by Zewald (1959).

Thus, the old and well documented Pavlovian principle of the dependence of the CR strength on the CS strength should be reformulated by stating that for different types of CRs there exists a different hierarchy of strength. According to our present evidence, for the classical salivary CR the auditory CS are stronger than the tactile CS applied to the leg, whereas for the instrumental CR the opposite is true. Thus a noticeable discrepancy exists between the type I salivary CR and type II motor CR, which is seen even in regular CR experiments, and may be even more clearly manifested by special tests, such as satiation of the animal, acute or chronic extinction, etc.

The problem arises what is the explanation of this peculiar motogenic potency of the specific tactile stimulus in comparison with other stimuli to which an instrumental CR is established.

In an attempt to approach the physiological mechanisms of CRs and their properties discovered by the Pavlov school Konorski has suggested that in the course of conditioning "actual" connections are formed between the respective centres on the basis of "potential" connections developed in ontogeny (cf. Konorski 1948, chapt. IV). Thus, the maximal strength of the given CR and its relative resistance to extinction depends on how powerful are the innate connections between the given centres.

On the basis of an ample experimental evidence, Wyrwicka (1952a, b) has shown that the "arc" of an instrumental food CR consists of two components. The connections between the centre of the CS and the centre of the instrumental response run both through the feeding centre*, and directly (Fig. 5a). The first connections ($S \rightarrow F \rightarrow R$) are responsible for the fact that the instrumental food response is "driven" by the excitation of the feeding centre, and is reduced or abolished by satiation. The direct connections ($S \rightarrow R$) are responsible for the selection by the animal of the appropriate instrumental response out of many in dependence of which CS is operating in a given moment.

* In this paper, we understand by "feeding centre" the whole system of "centres" situated in the diencephalon and telencephalon related to food intake without going into its anatomical substrate and functional organization.

Now, one may suppose that the exceedingly strong motogenic potency of the specific tactile stimulus is due to the powerful direct connections existing between the centre of this stimulus and the relevant motor centre (Fig. 5b). The presence of such connections is manifested, among other things, by the innate cortical placing reaction to the touch applied

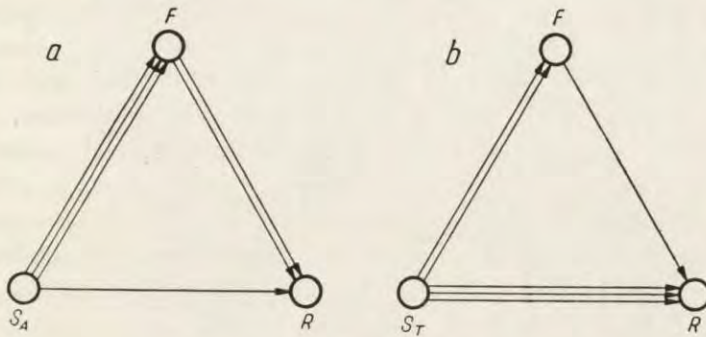


Fig. 5. Schematic representation of the instrumental CR arc to the auditory stimulus (a) and to the specific tactile stimulus (b)

S_A — centre of auditory stimulus, S_T — centre of specific tactile stimulus, F — feeding centre, R — centre of instrumental response. The number of lines between centres denote the strength of particular connections

to the anterior aspect of the wrist. These very connections are "utilized" in the formation of the instrumental CR involving the movement of the touched leg.

This hypothesis seems to explain all properties of the instrumental CR to the specific tactile stimulus described in this paper.

First, as seen in Table I and II, and as confirmed by many other experiments not described in this paper, the instrumental CR to the specific tactile stimulus is established with great speed, and sometimes even after a few trials. It happens that in response to the first touch applied to the rostral side of the leg the animal raises this leg, and if this movement is reinforced by food, the instrumental CR is formed almost immediately. This result is self-evident in view of our previous considerations.

The finding indicating that the instrumental CR to the specific tactile CS is stronger than the CR to other stimuli is also obvious.

In addition, we have found that if the given instrumental CR is formed at first to the specific tactile stimulus, the transfer of this reflex to other stimuli is very slow or even impossible. This fact may be explained by the preponderance of the $S \rightarrow R$ connections over $F \rightarrow R$

connections in the structure of the respective CR arc (cf. Fig. 5b). In consequence, when a new stimulus, "neutral" in this respect, is introduced and reinforced by food, it cannot utilize the direct pathway $S \rightarrow R$, while the established pathway $F \rightarrow R$ may be too weak to secure a proper transfer. Since the new stimulus is simply reinforced by food without the performance of the learnt movement, the classical food CR is readily formed to this stimulus, as evidenced by the conditioned salivary response elicited by it. According to the ample experimental evidence provided by Konorski and Miller (1930, 1933, 1936) and Konorski and Wyrwicka (1950), the classical food conditioned response established to a given stimulus inhibits the instrumental response. This makes the transfer of this response to a new stimulus even more difficult.

Now, we have to explain the increased resistance to extinction of the instrumental CR to the specific tactile stimulus and its prompt restoration in comparison with the CR to other stimuli.

Extinction of the instrumental CR may theoretically occur along two pathways. First, the inhibitory process may affect the pathway $S \rightarrow F$ owing to the fact that the CS is not reinforced by food; since centre F is no longer stimulated by the CS, the connections $F \rightarrow R$ are not put into action. The evidence of the operation of this mechanism is provided by the fact that usually the extinction of the instrumental response occurs *pari passu* with the diminution of the salivary response to the CS (Konorski and Miller 1936, Konorski and Wyrwicka 1952). Secondly, inhibition may also occur along the pathway $S \rightarrow R$, i.e. the movement R, no longer leading to food reinforcement, is "stamped out". The fact that the extinguished instrumental response immediately reappears as soon as the stimulus is again reinforced by food (Wyrwicka 1952a, b), provided that extinction was not overtrained, (Szwejkowska 1959) shows that the first and not the second of these two mechanisms is actually in operation, since otherwise the re-reinforcement of the CS should lead to the formation of the classical and not instrumental CR to this stimulus.

In view of these considerations we may assume that extinction of the instrumental response to ordinary CSi occurs as soon as conditioned excitation in centre F becomes too weak to produce a superthreshold excitation in centre R. On the other hand, the instrumental response to the specific tactile stimulus still persists, since it is facilitated by powerful connections existing between S and R.

However, this does not fully explain all the events observed in the course of extinction-restoration experiments. We noticed that in the course of extinction the positive CS (metronome) also became less moto-

genic than it was before, and often failed to elicit the trained movement. It was also observed that the restoration of the extinguished instrumental response to the auditory CS was strongly defective (see Table III) in spite of the fact that the restoration of the salivary conditioned response was prompt and complete (cf. Fig. 4d). One should stress that these effects have never been observed in any other chronic extinction-restoration experiments performed in our laboratory, and they are certainly connected with the general weakness of the instrumental CRs to the auditory stimuli trained side by side with those to the specific tactile stimulus. The evidence supporting this view will be provided in the next paper of this series. Anyhow, the deterioration of the instrumental CR to the positive CS in the extinction series, as well as a defective restoration of the instrumental response to the extinguished auditory stimulus, would suggest that in the course of extinction the direct pathway $S \rightarrow R$ has also been partially affected by inhibition. This inhibition could easily attenuate the instrumental CR to the auditory stimuli, leaving their salivary effects undisturbed.

In another paper, which is now in preparation, we shall provide evidence showing that the physiological connections dealt with in this paper have in fact a definite anatomical basis. It will be shown that by cutting the fibers connecting the sensory and motor cortex of the contralateral hemisphere all the extraordinary properties of the specific tactile stimulus are abolished and this stimulus does not differ from other instrumental CSi.

SUMMARY

1) Instrumental food CRs consisting in placing the right foreleg on the platform situated before the dog were trained to various stimuli, and among them to the tactile stimulus applied to the anterior side of the wrist (specific tactile stimulus).

2) If the instrumental CR is trained first to the specific tactile stimulus, its transfer to auditory stimuli is prevented. If, however, the tactile stimulus applied to the body is first used in the instrumental CR training, the transfer to other stimuli occurs without difficulty.

3) The instrumental response to the specific tactile CS is stronger than that to the auditory CS, while the salivary conditioned response is stronger to the auditory CS.

4) When the specific tactile CS and the auditory CS cease to be reinforced by food, the resistance to extinction of the instrumental response to the former stimulus is much greater than to the latter, while in respect to the salivary response the reverse is true. The re-reinforcement

of the stimuli leads to a much more prompt restoration of the instrumental response to the specific tactile than to the auditory stimulus, while the restoration of the salivary response is more prompt to the auditory stimulus.

5) The peculiar motogenic potency of the specific tactile CS in comparison with other instrumental CSi is discussed.

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FOOD INTAKE AND DEFECATION IN THE GOOSE, *ANSER ANSER* L.

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It was reported by Rybicki and Lubańska (1959) that the anterior sections of the alimentary tract (ingluvies, proventriculus) of geese fed chiefly on a green plants diet differed from those of geese reared on a non-green diet. It might be expected that the structural diversities of the alimentary tract of geese living on different diet would be reflected in the character of its functions.

The present work was aimed at investigating the amount of food consumed and the defecations of geese living on green plants compared with those kept on a diet lacking this component.

MATERIAL AND METHODS

Experiments were conducted on two groups of *Anser anser* L. geese, marked K and D. Each group of 5 geese was kept on a different diet from that when they were goslings to the beginning of the experiment.

The geese in D group were fed on green plants with the addition of wheat bran (5—44 g. a day, depending on the age of the goose), sometimes meat and bone meal (3—20 g. a day) and, from time to time, small amounts of grated carrot. The geese in K group were fed on a non-green diet; they were given instead such food as: potatoes, wheat bran, wheat, barley corn, cheese, bread, oatmeal, meat and meal, oats, eggs, minerals, carrot, juice. Detailed data on their living conditions and diet composition were presented earlier (Rybicki and Lubańska 1959).

Once a month, from June through to October, one goose out of each group was subjected to a 24-hour investigation. The resulting data are shown in Table I.

As is seen, each pair was older than the preceding one.

During the experiment the geese were kept singly, in wooden boxes with glass bottoms, and were fed only with the green plants *Lolium perenne* L., *Sonchus*

oleraceus L. The amount of food, both green plants and water, and times of feeding were recorded.

The geese were given green plants and water ad libitum for the first 12 hours of the experiment. The weight of the green plants eaten by each goose may therefore be regarded as the maximum amount of food taken in during this time. Goose K₂ of the second pair was an exception because with still one hour to go to the end of the full 12-hour feeding cycle it did not receive further food even though it had already eaten all that was given previously.

Table I

Date of the experiment, weight and age of the goose

Date of experiment	Symbol of goose	Age of goose /days/	Body weight /kg/	Symbol of goose	Age of goose /days/	Body weight /kg/
4/VI	D ₁	20; 20	0.38	K ₁	20; 20	0.42
25/VII	D ₂	20; 36	0.61	K ₂	20; 36	1.21
29/VIII	D ₃	55; 71	1.08	K ₃	55; 71	1.77
25/IX	D ₄	82; 98	2.14	K ₄	82; 98	2.35
15/X	D ₅	102; 118	2.60	K ₅	153; 153	3.18

Numbers in columns 3 and 6 refer to the days during which the geese were kept on a particular diet (first row of numbers) and the number of days of their age (second row of numbers).

The time of every defecation was recorded in the 24 hours starting from the beginning of the first food intake. The portions of feces were collected in crucibles and weighed.

RESULTS

Food and Water intake

The amount of food and water taken during the experiments changed proportionally to the age of geese and length of time they were under breeding conditions.

Plant intake was as follows:

D₁ — 120 g., D₂ — 300 g., D₃ — 730 g., D₄ — 1170 g., D₅ — 1700 g.
 K₁ — 120 g., K₂ — 320 g., K₃ — 450 g., K₄ — 455 g., K₅ — 100 g.

Consumption of green plants by geese of D group increased as the birds grew older. The K group reached its maximum earlier with a subse-

quent decrease according to the age of the goose so that consumption of plant food by the oldest goose, K_5 , was at the same level as that of the youngest goose K_1 .

Water intake was:

D_1 —180 g., D_2 —98.0 g., D_3 —460.1 g., D_4 —686.9 g., D_5 —926.0 g.
 K_1 —102 g., K_2 —39.2 g., K_3 —276.6 g., K_4 —532.1 g., K_5 —205.6 g.

The total amount of water intake by the geese in D group is higher than that of corresponding geese in K group.

Frequency of water intake (in number of times per hour):

D_2 —4, D_3 —7, D_4 —12, D_5 —11; K_2 —2, K_3 —7, K_4 —11, K_5 —6

In both groups the frequency of water intake (up to the 4th pair inclusively) increased with age. But, it should be emphasized that, although the frequency of water intake in older geese of both groups is very similar, the ratio between the plant intake and that of water is dissimilar.

Table II

Consumption rate of 10 g. of green plants in series D and K (in minutes)

Symbol of goose	Feeding periods			Daily average	Symbol of goose	Feeding periods			Daily average
	From start to 12 o'clock	12—4p.m.	4p.m. to the end of feeding			From start to 12 o'clock	12—4p.m.	4p.m. to the end of feeding	
1	2	3	4	5	6	7	8	9	10
D_1	83	82	62	76	K_1	54	83	104	80
D_2	29	30	30	30	K_2	21	22	21	21
D_3	10	8	11	10	K_3	15	13	39	22
D_4	15	5	7	9	K_4	16	68	21	35
D_5	7	3	5	5	K_5	70		68	69

The speed of intake of green plants (10 g.) in each of the enumerated periods is the mean value computed on the basis of the speed of consuming the successive feeds by the geese.

Goose K_5 ate only two portions of food during the experiment.

The D group drank larger quantities of water, but in comparison to the amount of plants consumed, the requirement of water was higher in the K group (Table III, Fig. 1, 2).

The experiments show a relation between plant and water consumption in older geese of each group (3rd, 4th, 5th pairs). It was found that periods of more intense feeding (Table II) were accompanied in

most cases by an increase in water intake (Fig. 1). The exceptionally low plant consumption in goose K₅ is matched by a similarly small water intake. There was some relation between the amount of plants eaten and the quantity of water drunk.

Observations showed that geese of both groups fed with varied intensity during the day.

There was a very distinct rhythm among the older geese of D group (D₃, D₄, D₅) of diurnal feeding.

Comparing the average speed of plant consumption in the geese of the two series (cols. 5 and 10) it was noted that in group D the speed increase was dependant on age and on how long the goose was on a green plant diet. There was a wide speed range. Goose D₅ consumed 10 grammes of plant food about 15 times as fast as goose D₁. The rate of food intake of K₁, the youngest goose of K group (20 days old) reared on a completely non green diet, does not differ from that of goose D₁. The rate increases with the older specimens (K₂, K₃) but clearly diminishes in the oldest geese (K₄, K₅).

For a more exact estimation of the changes in plant and water intake during their growth period it is necessary to take into account the changes in body weight during the experiments (Table III).

Table III

Plants and water consumption per 1 kg. of body-weight during the 24 hour experiment

Symbol of goose and its body weight g.	Amount of food consumption					Symbol of goose and its body weight g.	Amount of food consumption				
	g.			%			g.			%	
	plants	water	total	plants	water		plants	water	total	plants	water
1	2	3	4	5	6	7	8	9	10	11	12
D ₁ - 380	315.8	284.0	599.8	52.6	47.4	K ₁ - 420	285.7	242.0	527.7	54.1	45.9
D ₂ - 610	491.8	160.5	652.3	75.4	24.6	K ₂ -1210	264.5	32.4	296.9	89.1	10.5
D ₃ -1080	675.9	425.3	1101.2	61.4	38.6	K ₃ -1770	254.2	156.1	410.3	62.0	38.0
D ₄ -2140	546.7	320.8	867.5	63.0	37.0	K ₄ -2350	193.6	226.3	419.9	46.0	53.9
D ₅ -2600	653.8	356.0	1009.8	65.0	35.0	K ₅ -3180	31.4	64.7	96.1	32.7	67.3

We would like to draw attention to the young geese. The first pair was very young, at an early stage of development, and since they were only a short time on different diets, their food requirements and reaction to the food were similar. The 2nd pair, contrary to D₁ and K₁, differs as to the quantity of plants eaten per 1 kg, of body weight and as to

body weight. They were on a different diet for the same number of days as the first pair but they were older goslings and therefore at another stage of development. This shows the great plasticity of the goose organism in the early stages of development, up to the 20th day of life.

Based on the preceding data the total food intake by both groups is as follows.

The geese that had been on an intensive food diet (group K) and were then transferred to a green-plant diet, display a diminution in plant consumption as they grow older. The amount of plant food consumed per 1 kg. of body weight steadily decreases so that the older geese of this series eat smaller quantities of plant food than those permanently living on green plants. Water requirements increase with a green plant diet. It seemed as if the green plants became something of an "alien" food, compulsorily consumed by the geese in K group especially by the older ones, which had lived longer on an intensive food diet. This limitation in green-plant consumption became increasingly noticeable in geese — K₂, K₃, K₄, and was most prominent in K₅ which stopped eating altogether. This wide range between the consumption of K₄ and K₅ can be explained by the difference in length of their previous diet: K₄ — 82 days, K₅ — 153 days.

With the geese on a green-plant diet, the increase in plant consumption per 1 kg. of body weight connected with the age of the bird, reached its maximum in goose D₃, and was established within certain limits, starting from goose D₃. It follows that in D group, from the 71st day of life and 55th day of the green-plant diet, the increase in plant consumption was proportionate to the increase in body weight. Starting from this goose (D₃) the percentage of plants eaten and water drunk during a feed, became stabilised as did the diurnal rhythm of food intake. A considerable increase in body weight was observed between goose D₃ and D₄ (see Table I). This may mean that for geese living on green plants, the period of adaptation of their organisms to that kind of food is of great importance.

Defecation

The increase in food intake with the age of the goose was reflected in defecation, and the increase in the rate of food consumption with age corresponds to the frequency of defecation.

Total amount of feces:

D₁ — 212.4 g., D₂ — 334.5 g., D₃ — 1038.4 g., D₄ — 1483.8 g., D₅ — 2238.7 g.
K₁ — 198.2 g., K₂ — 354.1 g., K₃ — 548.8 g., K₄ — 744.0 g., K₅ — 229.4 g.

Table IV

Maximal, minimal and average defecations of geese

Sym. of goose	Minim. defecation g.	Maxim. defecation g.	Average but most frequent defecation		% of defecation of weight greater than average (column No. 4)	Sym. of goose	Minim. defecation g.	Maxim. defecation g.	Average but most frequent defecation		% of defecation of weight greater than average (column No. 10)
			g.	%					g.	%	
1	2	3	4	5	6	7	8	9	10	11	12
D ₁	0.94	9.4	1—2	55.4	41.9	K ₁	0.27	3.5	1.0—2	53.3	34.4
D ₂	0.24	7.4	1—3	63.1	19.7	K ₂	0.45	16.6	2.0—4	42.9	37.4
D ₃	0.18	15.4	3—8	71.3	16.0	K ₃	0.44	12.2	3.0—5	42.2	25.6
D ₄	0.37	23.4	5—9	43.4	31.9	K ₄	0.35	12.4	3.0—5	35.8	40.8
D ₅	0.77	29.1	2—4 10—13	18.3 31.4	19.1	K ₅	0.10	9.8	0.5—2	50.0	33.0

The increase in quantity of feces with age in D group was accompanied by an increase in the % of weight of a single defecation (Table IV).

From among all the geese D₃ and K₂ were especially interesting. In D group, the conspicuous increase in the weight of a single feces began from goose D₃. In K group the maximum weight of a single feces was that of K₂. Considering the size and percentage of an average and maximum excreta it may be supposed that the excreta of the older geese in K group do not differ to a greater extent than those of K₂.

From time to time among the older geese in D group a single defecation of exceptional weight occurred during the night, or at dawn. As this was several hours after feeding, it may be presumed that it came from the caeca. This is shown by its somewhat different appearance and smell of rotten matter. A greater quantity of this type of defecating occurred in group D than in K, which leads to the supposition that their occurrence is connected with a permanent diet of green plants.

Nos. of defecations in 24 hours:

D₁ — 73, D₂ — 152, D₃ — 181, D₄ — 196, D₅ — 245

K₁ — 122, K₂ — 91, K₃ — 136, K₄ — 154, K₅ — 112

In D group the quantity and number of defecations increased with age. This was not so obvious with K group.

In D group on a green plant diet the intervals between defecations decreased with age (Table V). This is seen most clearly in the percentage occurring at intervals of 1—5 min.

Table V

Percentage of defecations at various intervals of time

Intervals between excretions	Symbol of goose									
	D ₁	D ₂	D ₃	D ₄	D ₅	K ₁	K ₂	K ₃	K ₄	K ₅
1'	0	1.3	2.8	5.6	4.9	3.4	0	3.6	7.2	1.8
2'	1.4	4.6	7.7	6.7	8.2	1.7	1.1	5.2	8.5	4.5
3'	0	5.3	11.6	16.0	20.6	4.2	1.1	8.2	8.5	9.0
4'	0	9.2	11.4	17.5	23.5	7.6	3.4	8.8	11.3	9.0
5'	2.7	10.5	14.1	16.0	16.1	8.4	3.4	11.1	10.0	9.0
1'—5'	4.4	30.9	47.6	61.8	73.3	25.3	9.0	36.9	45.5	33.3
6'—10'	26.0	40.2	33.8	27.7	19.5	40.3	43.4	32.0	30.3	29.8
11'—15'	30.1	21.0	8.8	6.5	3.2	16.8	25.5	18.7	12.5	13.5
16' →	39.8	7.9	9.8	4.0	4.0	17.6	22.1	12.4	11.7	23.4

Table VI

Average number of defecations per hour during 24 hours

Symbol of goose	Hours of observation						Symbol of goose	Hours of observation					
	1—4	5—8	9—12	13—16	17—20	21—24		1—4	5—8	9—12	13—16	17—20	21—24
1	2	3	4	5	6	7	8	9	10	11	12	13	14
D ₁	3	3.5	4	5.5	1.5	1	K ₁	7	7.5	5.5	5	4	1
D ₂	6	9	6	9	5	2	K ₂	5	6	5	5	2	1
D ₃	9	13	12	4	4	2	K ₃	6	11	6	5	3	2
D ₄	8	14	13	9	2	3	K ₄	6	9	10	6	5	2
D ₅	11	17	15	12	4	2	K ₅	8	6	5	5	2	2

The geese of K group which lived on a non-green diet, showed a less obvious regularity of rhythm in defecation.

Among the older pairs, the percentage of defecations with the shortest intervals (1—5 min.) was always higher in D group than in K group which means that a permanent diet of green plants accelerated defecation.

The intervals between defecations became so short with increasing

age that the older geese of D group defecated almost permanently as shown in Table VI.

Among the older geese of D group the number of defecations was considerably greater during intensive feeding, between the 5th and 12th hours of the experiment (12—16 days), than at any other time. Geese of K group showed an increase in the number of excretions during the feeding period (1—16 hour of the experiment) in comparison with the period of rest (17—24).

It follows from Tables II and VI that the number of defecations at various times during the experiment depends on the feeding period; and therefore on how full the alimentary tract is. This dependence is more distinct in D group than in K.

It follows from these observations that defecations increased with age among geese of both groups although it was more obvious with those on a green-plant diet.

Comparison of Food Consumption and Defecation

A. *The Course of Consumption and Defecation.* The course of the daily consumption of food and defecation in older geese of both groups is shown by the curves in Figs. 1 and 2.

The curves (Fig. 1) show that the quantity of water drunk during feeding increases or decreases in proportion to the plant consumption.

A comparison of the two curves (total food, defecation) shows that the speed of consumption varied, sometimes being higher than the rate of defecation. Since the rhythm of food intake fluctuated and the rhythm of defecation only increased and decreased gradually, it might be expected that greater amounts of food, consumed periodically, are stored for some time in the anterior part of the alimentary tract, but that the food mass passes steadily through the intestine without a break.

It may be deduced (Fig. 2) from the course of the water- and plant-intake curves that a steady plant intake is accompanied by a periodically increased water consumption.

As can be seen (Figs. 1, 2) during the first 3—4 hours of feeding, the course of feeding and excretion were identical in geese of both groups. The differences in plant consumption and defecation occurred among the older geese of both groups, after the first 3—4 hours. During this period the geese of D group showed an increase in plant consumption but in K group it remained at a lower level than during the first hour of the experiment.

As the examples (Figs. 1, 2, Tables II, VI) show, the diurnal rhythm

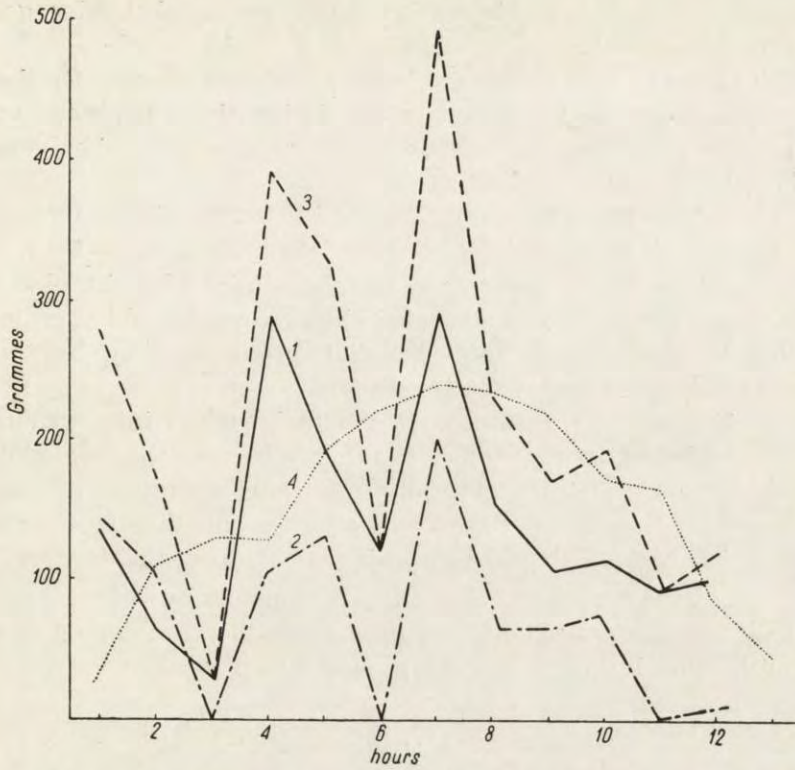


Fig. 1. Food (green plants + water) consumption and defecation in goose D₅ during its feeding period
 1 — plant-stuff consumed, 2 — water drunk, 3 — total food (green plants + water) consumption, 4 — defecations

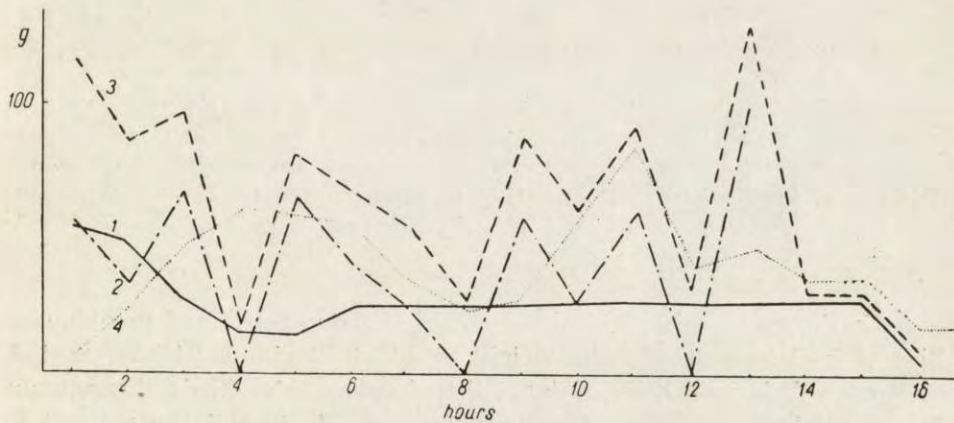


Fig. 2. Food consumption and defecation in goose K₄ during its feeding period
 1 — plant-stuff consumed, 2 — water drunk, 3 — plants+water consumed, 4 — defecations

of plant consumption and defecation differ among the older geese of both groups.

B. *Utilization of Food Consumed by Geese of Both Groups.* On the basis of the figures showing total food intake during the experiment and defecations, the percentage of food retained in relation to that consumed was computed for geese of both groups.

D₁—7⁰/₀, D₂—16⁰/₀, D₃—13⁰/₀, D₄—20⁰/₀, D₅—15⁰/₀,

K₁—11⁰/₀, K₂—1⁰/₀, K₃—24⁰/₀, K₄—25⁰/₀, K₅—25⁰/₀.

A comparison of the percentage of food retained by the older geese of both groups (3rd, 4th and 5th pairs) shows a considerably greater food utilization by geese on an intensive diet (group K) than by those on a permanently green plant diet (group D).

In considering food utilization it should be taken into account that there are probably in the feces, together with particles of indigested food and some products of metabolism, various quantities of sand. All these ingredients influence the weight of feces and therefore figures on the utilization of food should be considered as approximate only.

Because of the very great consumption of plants by geese of D group, the calculations presented above, do not show the true degree of green-plant utilization by geese of both groups during a day.

Table VII

The quantity of retained food in % of body-weight

Symbol of goose and its body weight	Food consumed g.	Defecations g.	Quantity retained		Symbol of goose and its body weight	Food consumed g.	Defecations g.	Quantity retained	
			g.	%				g.	%
1	2	3	4	5	6	7	8	9	10
D ₁ — 380 g.	228.0	212.4	15.6	4	K ₁ — 420 g.	222.0	198.2	23.8	6
D ₂ — 610 g.	398.0	334.5	63.5	10	K ₂ —1210 g.	359.2	354.1	5.1	1
D ₃ —1080 g.	1190.1	1038.5	151.6	14	K ₃ —1770 g.	726.6	548.8	177.8	10
D ₄ —2140 g.	1856.9	1483.8	373.1	17	K ₄ —2350 g.	987.1	744.0	243.1	10
D ₅ —2600 g.	2626.1	2238.7	387.4	15	K ₅ —3180 g.	305.6	229.5	76.1	3

As is shown in Table VII, the geese of D group consumed great quantities of food (cols. 2—7), the weight of which, during a 24-hour period, often exceeded their body weight: therefore in older birds the amount of food retained, both the actual amount (cols. 4—9) and the amount in percentage of their body weight (cols. 5 and 12) was greater in D group than in K.

DISCUSSION

In geese living on a diet with green plants as the main component (D group), the daily consumption of food as well as the total and single defecations were considerably greater than in geese living on non-green diet. (see: Tables III, IV, VI.)

The differences in the degree of consumption were clearly shown by the proportion of the amount of food consumed to the body weight of the geese in both groups. They are:

$$D_1 — 0.60, D_2 — 0.65, D_3 — 1.10, D_4 — 0.87, D_5 — 1.01$$

$$K_1 — 0.53, K_2 — 0.30, K_3 — 0.41, K_4 — 0.42, K_5 — 0.10$$

In D group the relation in the size of the daily food-consumption to the body weight distinctly increased in older birds, beginning with D_3 . In K group this relation, from K_2 onwards was very small.

A great increase in food consumption, as revealed in goose D_3 , fed on green plants for 55 days, permits us to assume that it results from the adaptation of the organism to a diet of this kind. After the adaptation period, lasting for about 50 days, the weight of the daily food mass approaches, and even exceeds, the body weight of the goose. Such a considerable food-mass passing through the organism in one 24-hour period must correspond to the size of the alimentary tract capacity.

It might be supposed that the amount of food consumed and the size of defecations are an indication of the capacity of the alimentary tract. In the geese of group D the amount of food consumed, the quantity of feces as well as the size of single defecations increase with age. The hypothesis of an enlarged capacity of the alimentary tract in geese living permanently on a green plant diet is supported by the fact that their maximum defecation weight reached 29 gm., whereas that of geese living on a non-green diet did not exceed 16 gm. (Table IV).

The differences in the increase of the alimentary tract capacity during the growing period of geese living on various diets may be estimated by the quantity of food consumed. Geese living on intensive food (series K) ate, on the days preceding the 24-hours experiment, the following amounts of food:

$$K_1 — 218 \text{ g.}, K_2 — 342 \text{ g.}, K_3 — 378 \text{ g.}, K_4 — 490 \text{ g.}, K_5 — 450 \text{ g.}$$

Supposing the intake by the youngest geese, K_1 , to be 100 units of consumption, in the geese of group K it was as follows:

$$K_1 — 100\%, K_2 — 157\%, K_3 — 173\%, K_4 — 225\%, K_5 — 206\%.$$

Analogous computations for the geese of D group reveal a considerable

rable increase in consumption in the group living on green plants from the gosling stage:

D_1 — 100%, D_2 — 250%, D_3 — 608%, D_4 — 978%, D_5 — 1416%.

A considerably greater increase in the capacity of the alimentary tract among geese of group D than among those of group K, as postulated on the basis of the preceding data, was confirmed by measurements of the length of the alimentary tract made by Rybicki and Lubańska (1959). In goose K_5 it was 265 cm., in goose D_5 — 368 cm.

The mass of maximum defecations and their frequency seem to indicate a greater elasticity of the alimentary tract among the older geese in D group than among those of K group (Tables IV, VI, VII).

On the basis of observations on the frequency of defecations, the rate of the passing of food through the alimentary tract may also be estimated.

A comparison of the intervals between defecations by geese of both groups shows that they are of shorter duration among geese of D group. The shorter intervals between defecation and the longer alimentary tracts of the geese of this group (D) seem to support the statement that the food mass passes more quickly through the alimentary tract of the geese of D group. The data presented in Tables V and I show that in D group the speed of passage of the food through the alimentary tract depends on the age of the goose and on the period preceding the experiment, during which they were fed on green plants. Among K group the shortening of the intervals between defecation decreased, but only slightly, with age (Table VI.)

The time of retention of food in the alimentary tract was estimated from the moment of consumption of the first plants to the defecation of this feed (Table VIII, cols. 2, 3, 5, 6). A first feces of a different colour (green) from the previous ones, was acknowledged as that of the morning feed.

Table VIII shows that in both groups the time of the retention of food in the alimentary tract was shortened with increasing age. It was always shorter in geese of D group.

It should be noted that among geese of group D both the maximum speed of food consumption and the greatest frequency of feces occurred in the middle of the day (Table II, VI). This points to the existence of a relation between the degree of filling of the alimentary tract and the speed of the passage of the food down the alimentary canal, i.e. the retention time of the food in it. This would indicate that the time of retention of food in the alimentary tract of a goose, as shown in Table VIII, could not be treated as stable throughout the whole, 24-hour experiment.

Table VIII

Time of food retention in the alimentary tract

[Symbol of goose	Food retention period (from giving the food to the time of its excretion) in hours		Symbol of goose	Food retention period (from giving the food to the time of its excretion) in hours	
	1	2		3	4
D ₁	9 ⁰⁷ —13 ³⁷	4 h.30 min.	K ₁	9 ¹⁰ —12 ²²	3 h.12 min.
D ₂	7 ⁵⁵ —10 ⁵⁸	3 h.03 min.	K ₂	7 ⁵⁵ —11 ²²	3 h.27 min.
D ₃	9 ¹⁵ —11 ⁰⁰	1 h.45 min.	K ₃	9 ¹⁵ —11 ³⁸	2 h.23 min.
D ₄	8 ²⁰ — 9 ³⁵	1 h.15 min.	K ₄	8 ²² —10 ¹⁴	1 h.52 min.
D ₅	8 ⁵³ —10 ⁰⁹	1 h.16 min.			

The different utilization of food by geese of both groups is probably due to the speed of the passage of the food and to the length of time it remained in the alimentary canal.

SUMMARY

From experiments on the green-plant consumption and defecation of geese living permanently on a green plant diet, and others on a non-green diet, the following conclusions can be drawn:

1) Geese kept for a longer period of time on a non-green diet lose their faculty to consume this kind of food (Table III).

2) Geese fed chiefly on green plants from the gosling stage undergo an adaptation period to this kind of food, which lasts for about 50 days. A considerable increase in green-plant consumption then occurs fulfilling the needs of the growing organism (Tables I, III).

3) The speed of the passage of food down the alimentary canal increases as the geese grow. Green plants, provided as basic food, stimulate the process (Table V).

4) The speed of the passage of food down the alimentary canal depends on how full the alimentary canal is (Tables II, VI; Fig. 1).

5) The capacity of the alimentary tract of geese fed on green plants is greater than that of geese living on an intensive diet lacking this component (Tables III, IV).

6) The walls of the alimentary tract of geese living on green plants are more elastic than those of geese living on an intensive diet, without green plants (Tables IV, VI).

7) The length of time it takes for consumed plants to pass through the alimentary tract shortens as the geese grow older. It is shorter in

birds living permanently on a green plant diet than in those living on a non-green diet (Table VIII).

I should like to thank Docent Dr. M. Rybicki for the planning of this work and for his great help in carrying out the experiments.

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