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FRONTO-HYPOTHALAMIC CONTROL OVER FOOD-REINFORCED CONDITIONED-REFLEX PERFORMANCE AND DIFFERENTIAL INHIBITION IN RABBITS [1]

Halina BALIŃSKA, Stefan BRUTKOWSKI
and Janina STEFANICKA

Laboratory of Animal Physiology, University of Łódź, Łódź, and Department of Neurophysiology, The Nencki Institute of Experimental Biology, Warsaw 22, Poland

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During the past 15 years a series of studies has been presented (reviewed by Brutkowski 1964), indicating that after lesions of the nonmotor frontal cortex area in dog and monkey the previously trained inhibitory conditioned reflexes (CRs) become temporarily disinhibited, that is, at the early postoperative stages the inhibitory conditioned stimuli (CSi) elicit a positive CR. Since it has been found that at least some of the frontally lesioned animals may increase their instrumental, autonomic and emotional reactivity on positive trials, during intertrial intervals and to the presentation of unconditioned stimuli (USi) in situations in which food, water, acid or electric shock are used as reinforcements, it is suggested that the impairment of CR inhibition is secondary to motor or affective hyperreactivity.

Recently, a distinction has been made between the CR inhibition impairment produced by frontal lesions placed on the dorsolateral aspect of the hemisphere and that following lesions situated on the basomedial aspect of the hemisphere (Brutkowski et al. 1963, Brutkowski and Dąbrowska 1963). The first type of impairment has been said to be due to response perseveration or a decreased ability to suppress competing response tendencies, the second type has been said to reflect the

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release of drive functions from cortical inhibitory control. It has been hypothetized that the inhibitory defects resulting from lesions of the basomedial frontal cortex may be related to the disruption of meso-diencephalic mechanisms and that increased reactivity to emotional stimuli causes difficulty with suppression of the CR on inhibitory trials, thereby resulting in disinhibition. The fact that the basomedial frontal cortex has extensive anatomical connections with septum, the hypothalamus, parts of the amygdaloid complex and the brain-stem reticular formation (Clark Le Gros 1948, Maršala and Grofová 1962, Nauta 1964) suggests that it may participate in a large system, the functioning of which makes the inhibition of drives and emotions possible. If this is so, there is reason to expect that lesions in other areas of the system may also produce defects in drive inhibition. Recent observations support the expectation, at least in the case of lesions of the medial nucleus of the hypothalamus (Balińska et al. 1961) or the basolateral portions of the amygdaloid complex (Brutkowski et al. 1960).

Similarly, it would seem reasonable to expect that animals with lesions of the limbic and subcortical structures anatomically interconnected with the dorsolateral frontal cortex might show deficits in the inhibition of the expression of response perseveration. However, no systematic studies have been undertaken to test such expectation.

Several investigations emphasize that a prominent feature of the behavior of frontally lesioned animals is their impaired instrumental activity in performing effectively a food-reinforced or avoidance response (cf. Brutkowski 1964). While some operated animals cease performing the instrumental activity altogether, others show a temporary impairment or more rapid extinction than normals on the instrumental CR. This has been especially noticeable when the lesions encroach on the premotor or cingulate cortex regions, which supports the clinical observation that lesions of the premotor cortex in human patients interfere with the coordination of the movement (Luria 1962).

Not to be able to respond instrumentally is not to be able to display an impairment on inhibition. However, it has been found that once the instrumental performance has recovered an impairment of the previously trained inhibitory CRs occurs. This indicates that lesions of the frontal cortex, including the premotor and cingulate areas, are correlated with two phases in the pattern of behavior: the phase of the abolition or reduction of the CR performance is followed by one of a disinhibition.

The finding that the instrumental CR is abolished or markedly diminished postoperatively has been interpreted to suggest that frontal lesions reduce drives and emotions, Yet, when it is put to experimental test, the interpretation proves to have no substantial value. Regardless of the fact that some drives, e.g. fear (Jaworska and Sołtysik 1966), tend to diminish after frontal lesions, there is ample evidence indicating that, for the most part, the postoperative drive level is elevated. Brutkowski (1964) has commented that instrumental conditioning is not sensitive enough to serve as an accurate measure of emotional behavior and suggested that the impairment of instrumental activity at the early postoperative stages is but a sign of a defect reflecting a destruction of the instrumental reflex arc. It has been suggested (Brutkowski 1959, Stępień and Stępień 1965) that this impairment may be due to a frontal animal's inability to perform two antagonistic movements, e.g. turning of the head toward the source of the CS and lifting of the forelimb, or performing a food-oriented reaction, consisting of searching and sniffing at the food cup, and placing of the forelimb on the food box.

One purpose of the study to be reported is to compare the effects of four types of brain lesions, that is, two frontal and two hypothalamic, in rabbits on the retention of a differentiation type of behavior serving as an indicator of instrumental activity and inhibition. The second purpose is to compare these effects in the rabbit with, at least, some of those which have previously been obtained in other species.

MATERIAL AND METHOD

Animals were 21 experimentally naïve rabbits, ranging in weight from 2.5 to 3.0 kg., and maintained on a daily diet consisting of 100 g. purèe-type potatoes, 100 g. carrots and 80 g. grains of oats. The amount of oats given was an overdose; the spillage was removed before testing. The rabbits were both males and females, and approximately 1.5 years of age. They were housed individually in the home cages throughout the experiment. No water was offered to the animals.

The *experimental room* contained tables, chairs and apparatus. The testing chamber was a cubical compartment with 50 cm inside dimensions, resting on a table. It was of heavy plywooden construction except for an open top and the front side, allowing easy observation. The food box was placed lengthwise on the bottom in the front section of the chamber. It enclosed a rount rotating tray bearing a number of food cups. A small opening in the front center of the food box top enabled the animal to see one food cup at a time. The cup that was in the animal's field of view at the beginning of the testing session was empty; the remaining cups were filled with the experimental food and, on positive trials, were rotated by a hand crank under the opening. The door buzzers which served as CSi were placed away from the testing chamber.

The experimenter sat directly across the chamber and was visible to the animal during the testing sessions.

The animals were brought from their home cages in a carrying cage into the experimental room, removed from the cage and placed directly in the testing chamber. Testing occurred in the morning before the animals received their daily diet. The animal could move freely about the chamber. The suppression of spontaneous activity came about gradually through habituation to the experimental situation.

The general *procedure* employed was that of differentiation (successive discrimination) with the noncorrection method. The task required the rabbit to place the right forepaw on the food box on the positive trial and to withhold this response on the inhibitory trial. The procedure consisted of 4 stages for all animals. *Stage 1*: *Habituation*. This involved the placement of the animals to the testing chamber for 1—3 consecutive days. During this period, each animal was given experience in eating the reinforcement food and trained to associate the food presentation with the operation of the food tray. The food was given when the animals oriented toward the food box. This was sufficient to assure the animal facing the food box for most of the time. Spotaneous activity was small so that the animal remained quietly. *Stage 2*: *Establishment of the positive CR*. For the following days, the animals were taught to perform the correct instrumental response (type II CR, according to Miller and Konorski 1928), which was placing of the right forepaw on the food box. In the initial training trials, a small piece of carrot was shown in the vicinity of the food cup until the animal stepped on the food box to reach for the carrot. Then the animal's forepaw was removed with the experimenter's hand from the food box, placed on the chamber floor, and the animal was allowed to eat the carrot. In further trials, the carrot was shown and placed in the food cup. This phase of training was terminated when the animal readily placed the forepaw on the food box and took the carrot from the food cup. The animals also were consistently given carrot if they performed the response voluntarily. *Stage 3*: *Training of the CR to the presentation of CS*. After the animals were proficient at responding under the conditions described above, the CS+, which was the sounding of Buzzer 1, was presented and remained on until the CR occurred, or, it was presented with the occurrence of the CR, or, when it seemed likely that the animal would perform the forepaw movement. In each instance the CR was immediately followed by the food reinforcement. CRs between the CS presentations were extinguished by nonreinforcements. Each animal received 10 CS presentations a day. Stage 3 continued until the animals performed the response to 30 consecutive presentations of the CS+. *Stage 4*: *Differentiation training* (*establishment of the inhibitory CR*). Within Stage 4 the CS— was introduced. This was Buzzer 2 which was of different intensity and frequency but higher than Buzzer 1. During each testing session 5 positive and 5 inhibitory trials were given in a randomized order. Each positive trial began with the presentation of CS+. The CR was immediately followed by the presentation of the food which was a piece of carrot, weighing 4 g. When the CR failed to occur the food was presented 5 sec. after the onset of CS+. In other words, food was presented on positive trials regardless of whether or not the CR was performed. On each inhibitory trial the CS— was given for 5 sec. and no food was presented. Thus, on positive trials the animals were always reinforced, whereas on inhibitory trials, they were never reinforced. The intertrial intervals were 20 sec., discounting the time for eating. Differentiation training was continued until the criterion of 94 to 96 no placings in 100 inhibitory trials was attained.

Surgery. After reaching criterion all animals were randomly assigned to 5 groups; 17 animals were given a one-stage bilateral surgical operation, 4 animals were given a rest period of 10 days. The animals were operated on aseptically under nembutal anesthesia (40 mg/kg).

Nine animals received hypothalamic lesions; 4 received lesions of the medial portion of the hypothalamus (group HM, rabbits Nos. 1, 2, 3 and 4), and 5 received lesions of the lateral portion of the hypothalamus (group HL, rabbits Nos. 5, 6, 7, 8 and 10). Eight animals received lesions of the frontal cortex, four animals each receiving lesions of either the cortex situated on the medial aspect of the hemisphere (group FM, rabbits Nos. 11, 12, 13 and 14), or the cortex on the dorsolateral aspect of the hemisphere (group FL, rabbits Nos. 15, 16, 17 and 18).

For frontal resections, the animals were fixed in a head holder and the scalp was incised in the midline. Small holes were bored in the skull and enlarged with rongeurs. The dura was cut and the cortex was removed by gentle aspiration, an approximately 18-gauge glass sucker being used. Precautions were taken to avoid tearing the sagittal sinus. After hemostasis the skin was sutured.

In the hypothalamic groups, the lesions were produced stereotaxically. One hole on either side of the midline was bored with a dental trephine. A 0,5 mm stainless steel electrode insulated except for the tip was inserted into the brain, and a direct current of 3 ma was applied for 20 sec. To produce medial hypothalamic lesions the electrode was placed at points 2 mm posterior to the bregma, 1 mm lateral to the midline and 15 mm below the dura surface. To produce lateral lesions, the electrode was placed at points 3 mm posterior to the bregma, 2 mm lateral to the midline and 15 mm below the dura. These operations were accomplished with the Johnson stereotaxic instrument in conjunction with the rabbit head holder and diagrams of Sawyer et al. (1954). Since rabbits following lateral hypothalamic lesions were unable to feed themselves they were given daily subcutaneous injections of 100 cc. of 4 per cent glucose with saline until they began eating voluntarily (Balińska 1963 b). Three to seven days of such injections were sufficient to assure these animals recovering their voluntary eating behavior. Nevertheless, they for ca. 2 to 3 weeks after surgery ate less comparing to the preoperative level and showed great reluctance to accept oats. Immediately after recovery from aphagia they moved slowly, had difficulty in grasping food, showed marked disturbance in chewing and swallowing, and gnashed the teeth while eating. Similarly, rabbits with lesions of the medial frontal cortex at the early postoperative stages were disturbed in taking, chewing and swallowing the food. Their clumsy attempts at eating were accompanied by gnashing of teeth.

Ten days of postoperative rest were allowed for all animals before differentiation testing was resumed. This testing was continued to the same criterion as before operation, except for two rabbits of the HL group (Nos. 8 and 10) in which the postoperative testing was discontinued after 500 trials due to the failure of CR recovery.

Four animals (group C) were not operated on but rested during a 10-day period; they served as an unoperated control for any possible retention loss due to the rest period alone.

Anatomy. When postoperative testing was completed the brain damaged animals were anesthetized with an overdose of nembutal (50 mg/kg), the brains removed, fixed in formalin, dehydrated in alcohols and embedded in paraffin. Serial sections were made at 10 microns and every 10th section was mounted on a slide and stained according to Klüver-Barrera (1953). A parallel series was stained with cresyl violet.

The damage to the hypothalamus was determined, using diagrams from the paper of Sawyer et al. (1954). Figs. 1 and 2 show diagrams of the representative cross sections of the brains of the animals that were given lesions of the lateral or medial hypothalamus. The frontal lesions were reconstructed, using

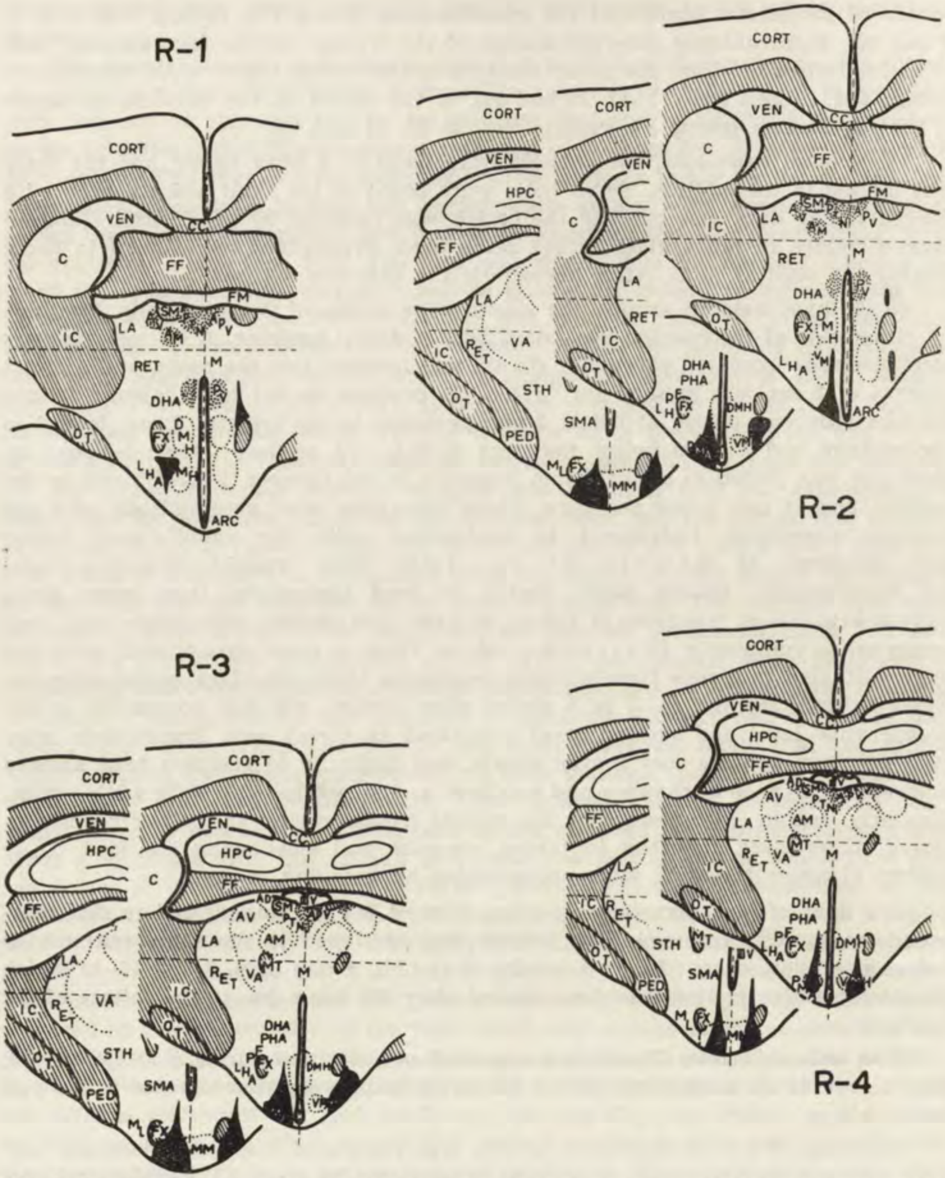


Fig. 1. Reconstructions of medial hypothalamic lesions (group HM, rabbits Nos. 1-4) plotted on standard plates of Sawyer et al. (1954).The lesions are indicated by solid black. The abbreviations for Figs. 1-2 are as follows :

AD, N. anterodorsalis; AM, N. anteromedialis; APV, N. paraventricularis anterior; ARC, N. periventricularis arcuatus; AV, N. anteroventralis; C, N. caudatus; CC, Corpus callosum; CORT, Cerebral cortex; DHA, Dorsal hypothalamic area; DMH, N. dorsomedialis hypothalami; FF, Fimbria of fornix; FM, Foramen of Munro; FX, Fornix; HPC, Hippocampus; IC, Internal capsule; LA, N. lateralis anterior; LHA, Lateral hypothalamic area; M, Massa intermedia (nuclei of midline)

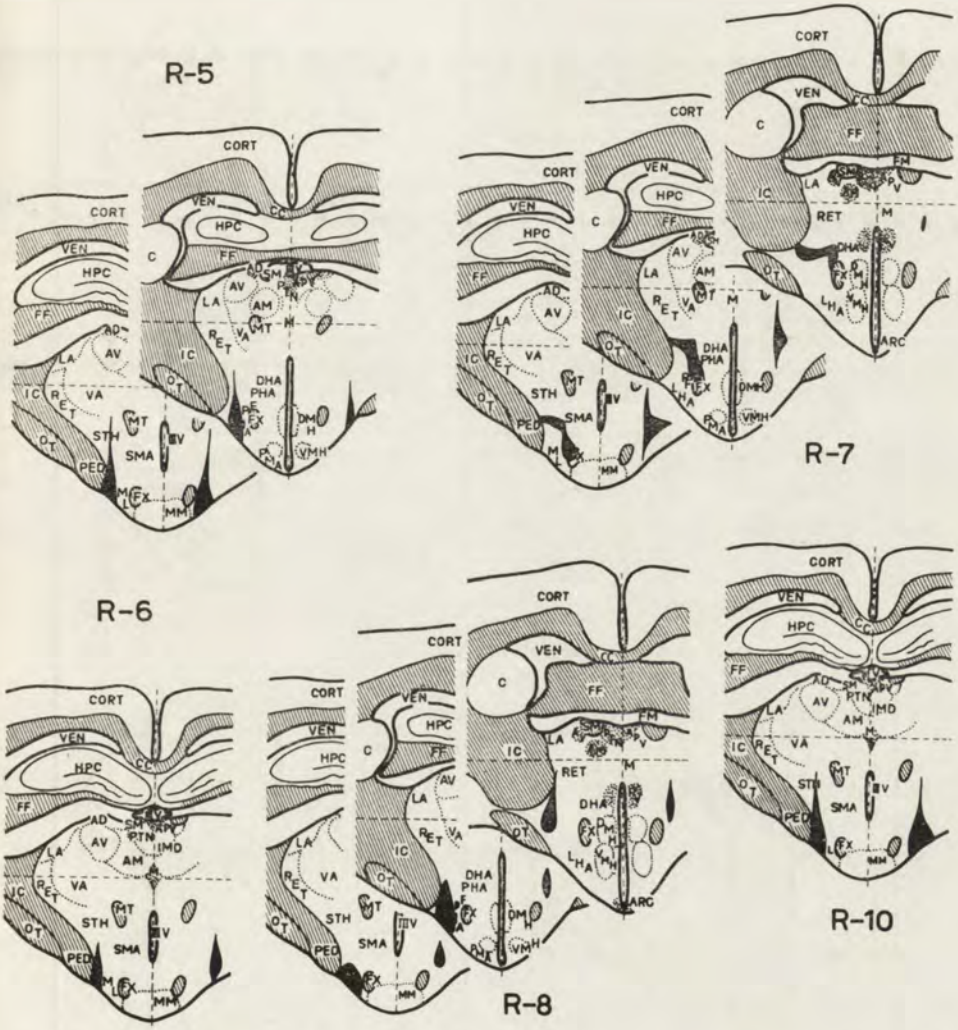
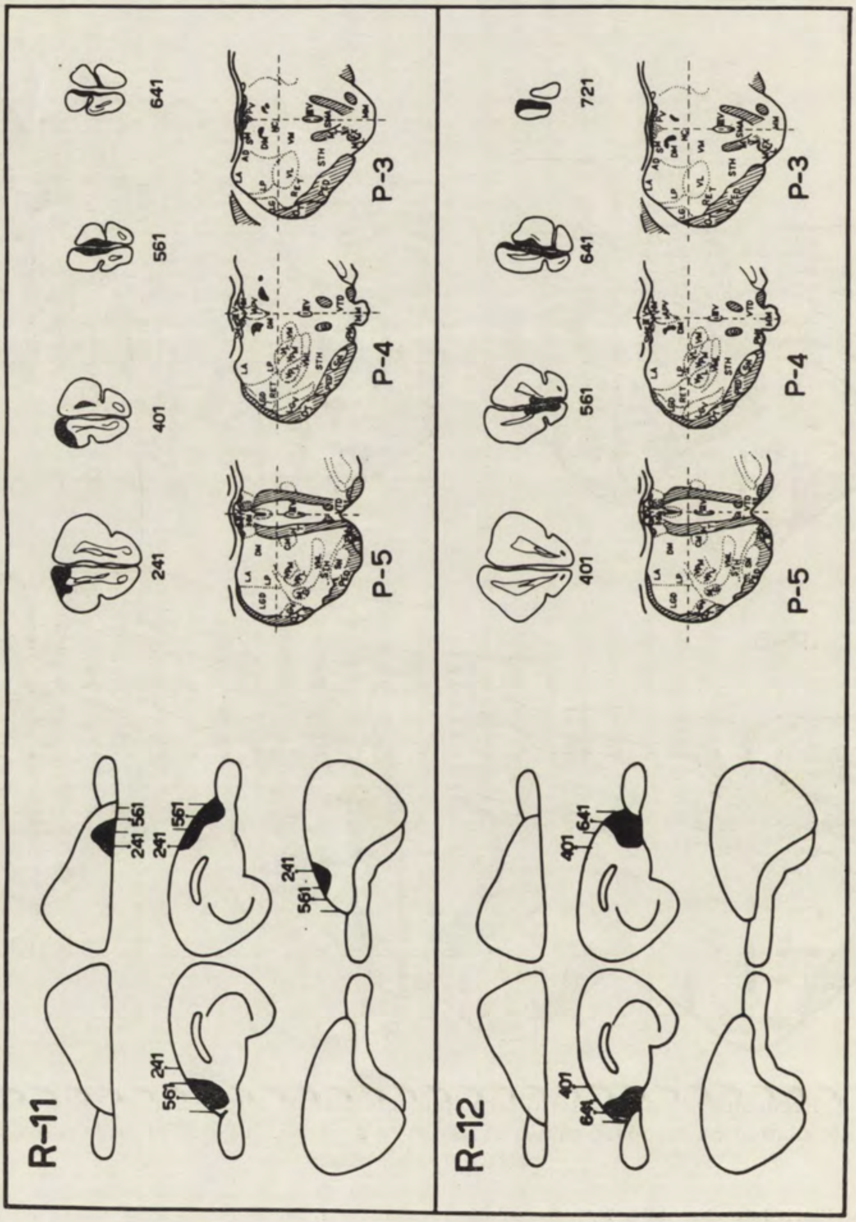


Fig. 2. Reconstructions of lateral hypothalamic lesions (group HL, rabbits Nos. 5-8 and 10) platted on standard plates of Sawyer et al. (1954). The lesions are indicated by solid black

mammillaris lateralis; MM, N. mammillaris medialis; MT, Mammillothalamic tract; OT, Optic tract; PED, Basis pedunculi; PF, Perifornical area; PHA, Posterior hypothalamic area; PTN, N. parataenialis; PV, N. paraventricularis; RET, N. reticularis; SM, Stria medullaris; SMA, Supramammillary area; STH, Subthalmus; VEN, Ventrcle; VMH, N. ventromedialis hypothalami; III V, Third ventricle.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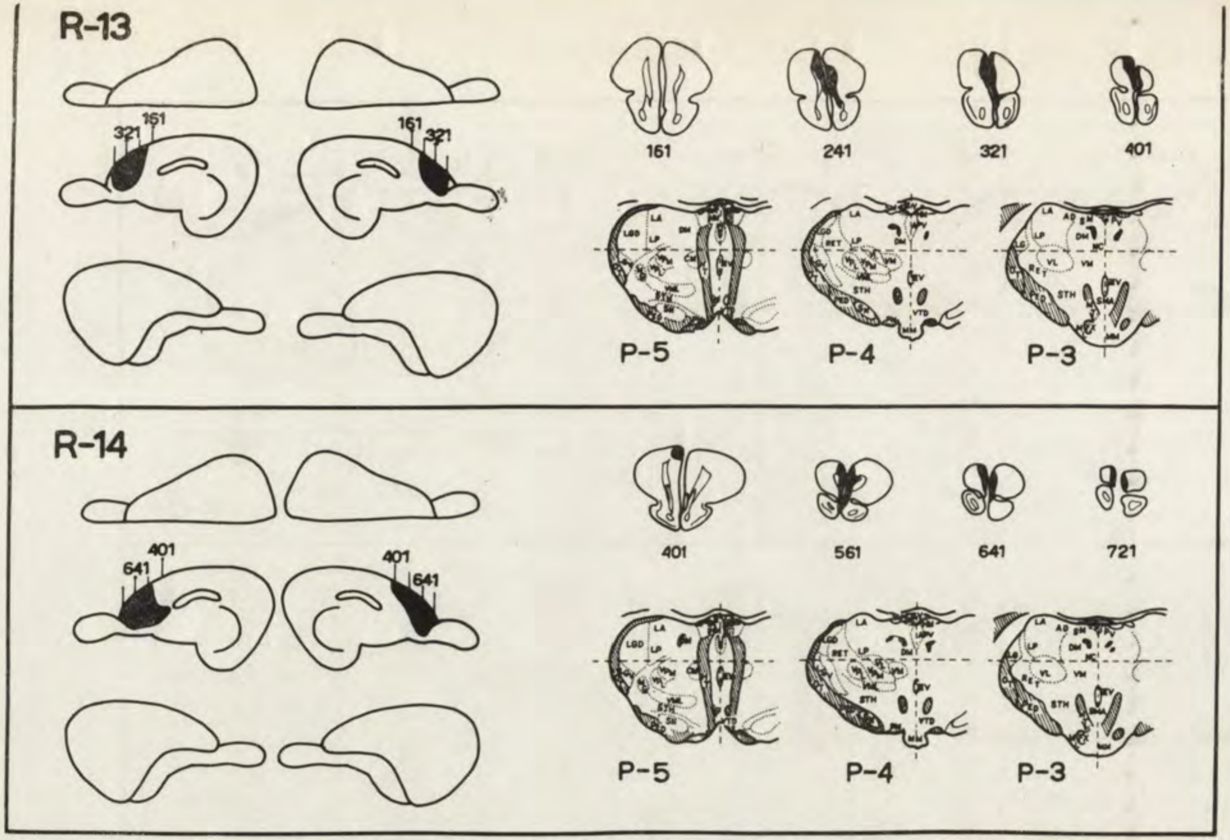
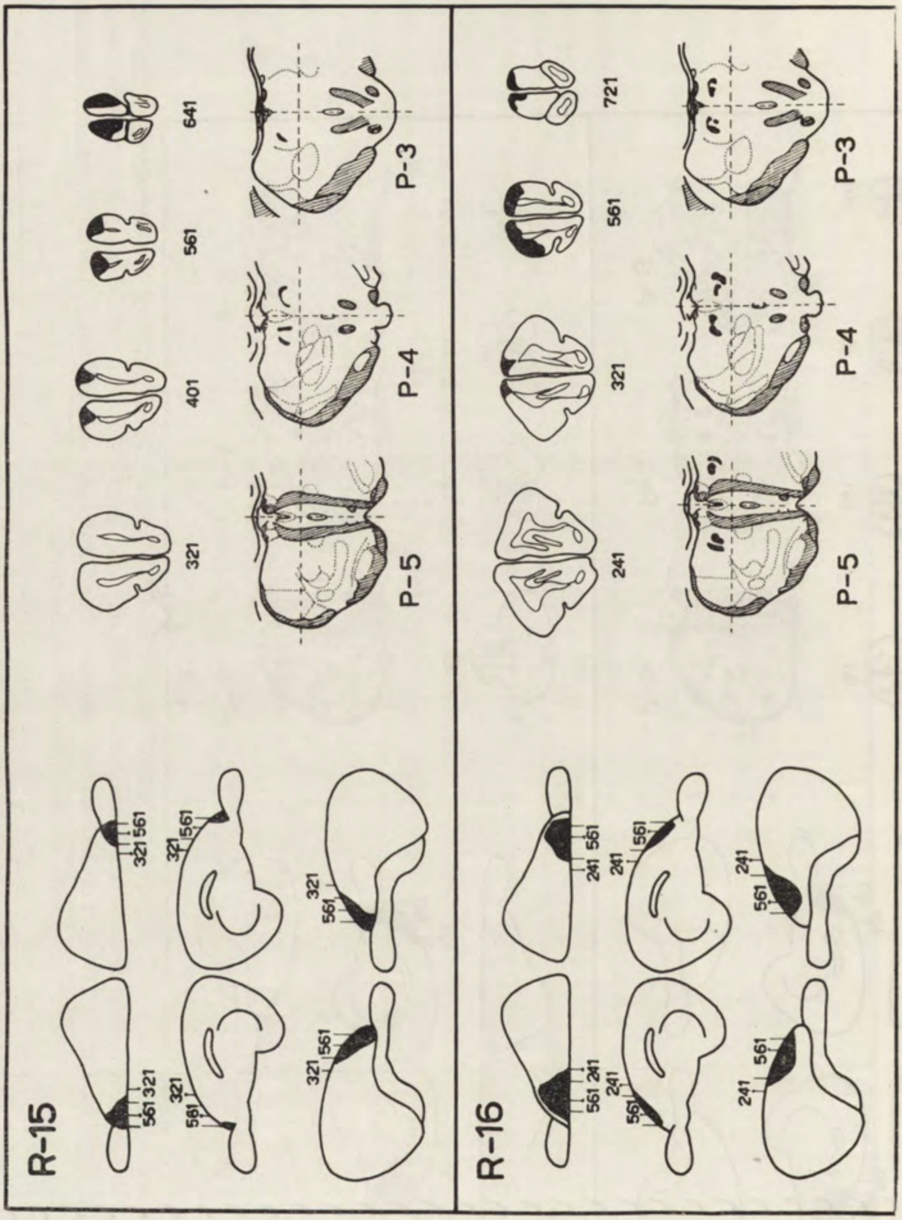


Fig. 3. Diagrams showing the extent and depth of cortical lesions and retrograde degeneration of the dorsomedial nucleus of the thalamus for rabbits with medial frontal resections Nos. 11-14 (Group FM) Sketches adapted from Rose and Woolsey (1948) and Sawyer et al. (1954). The lesions and degenerations are indicated by solid black. The abbreviations used in this figure are as follows :

AD, Anterior commissure; APV, N. paraventricularis anterior; CM, N. centrum medianum; DM, N. medialis dorsalis; FX, Fornix; G. Mammillotegmental tract; HM, N. habenularis medialis; HT, Habenulointerpeduncular tract; LA, N. lateralis anterior; LGD, Lateral geniculate body, dorsal part; LGV, Lateral geniculate body, ventral part; LP, N. lateralis posterior; ML, N. mammillaris lateralis; MM, N. mammillaris medialis; MT, Mammillothalamic tract; NC, N. centralis; OT, Optic tract; PED, Basis pedunculi; PM, Peduncle of mammillary body; PV, N. paraventricularis; RET, N. reticularis; SM, Stria medullaris; SMA, Suppramammillary area; SN, Substantia nigra; STH, Subthalamus; VL, N. ventralis lateralis; VM, N. ventromedialis; VML, Ventral medullary lamina; VPL, N. ventralis posterolateralis; VPM, N. ventralis posteromedialis, VTD, Ventral tegmental decussation; III V, Third ventricle; III, Oculomotor nerve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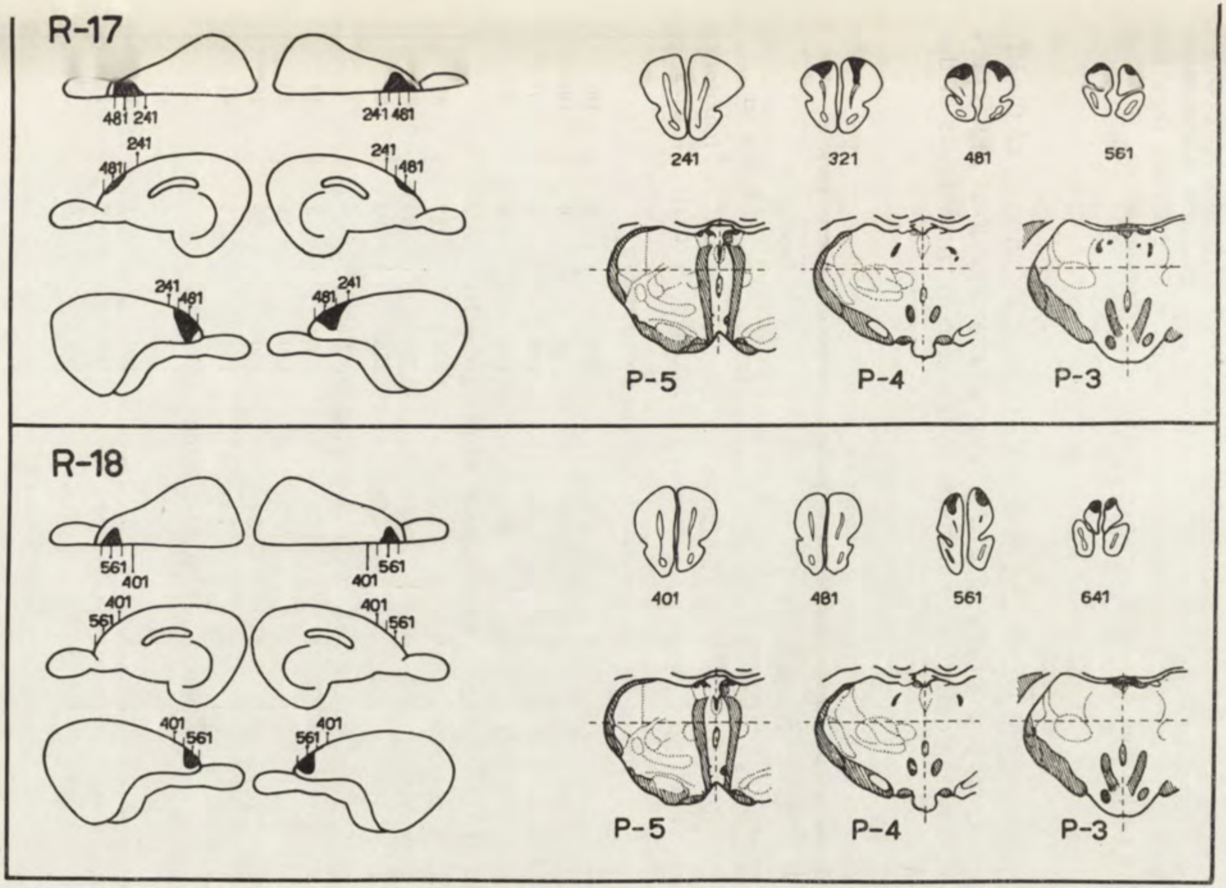

Fig. 4. Diagrams showing the extent and depth of cortical lesions and retrograde degeneration of the dorsomedial nucleus of the thalamus for rabbits with dorsolateral frontal resections Nos. 15-18 (group FL). Sketches adapted from Rose and Woolsey (1948) and Sawyer et. al. (1954). The lesions and degenerations are indicated by solid black

diagrams from the paper of Rose and Woolsey (1948). Figs. 3 and 4 show these reconstructions, the distribution of the degeneration in the dorsomedial nucleus of the thalamus and representative cross sections through the lesions of the brains of the animals that were given dorsolateral and medial frontal resections.

The cortical reconstructions were made from projections of the sections, supplemented by reference to photographs of the whole brains. Thalamic degeneration was established by microscopic examination and recorded on diagrams from the paper of Sawyer et al. (1954).

RESULTS

CR performance. As seen from Table I, all animals of the HL group and 3 animals out of 4 of the FM group showed deficit in CR performance, but the deficit was appreciably greater in the animals of the HL group.

Table I

Scores of pre- and postoperative trials and errors to the criterion

Rabbit No.	Preoperative			Postoperative		
	Trials (positive or inhibitory)	Errors on positive trials	Errors on inhibitory trials	Trials (positive or inhibitory)	Errors on positive trials	Errors on inhibitory trials
Medial hypothalamic lesions, group HM						
R-1	225	0	53	300	0	100
R-2	100	2	20	250	0	108
R-3	200	1	37	150	0	70
R-4	170	0	53	150	2	65
Lateral hypothalamic lesions, group HL						
R-5	150	10	39	300	127	37
R-6	180	0	59	300	66	67
R-7	140	2	24	250	99	21
Medial frontal lesions, group FM						
R-11	195	4	83	150	5	49
R-12	245	4	85	150	31	20
R-13	165	3	34	150	20	20
R-14	235	0	79	150	1	41
Dorsolateral frontal lesions, group FL						
R-15	160	1	52	150	2	18
R-16	255	6	76	100	1	14
R-17	165	3	37	100	0	17
R-18	200	0	85	100	0	6
Unoperated, group C						
R-19	135	0	40	50	0	0
R-20	165	0	47	50	0	0
R-21	275	0	77	50	0	0
R-22	120	5	47	50	0	0

HL group: Two of the animals, rabbits Nos. 8 and 10, were permanently deficient in their CR behavior. During the entire period of postoperative observation these two animals were apathetic and showed a clear-cut descrease of motility and reactivity in the experimental situation. They neither approached the food box nor took the experimental food offered on the positive trials despite the fact that they ate their daily diet in their home cages. The other three animals (Nos. 5, 6 and 7) did not end their ability to perform the placing response except as a transitory phenomenon. Although, of these three animals, one (No. 5) stopped and two others (Nos. 6 and 7) greatly diminished the instrumental performance in the initial postoperative period (Table II), they all, at the same time, clearly showed signs of an excessive primordial food activity in terms of an increased sniffing and searching at the food box. They also took the food offered on the positive trials. However, they throughout the entire period of reduced instrumental responsiveness were surprisingly slow and placid. With further training, they became more active and executed the placing response sporadically on both positive and inhibitory trials, and during intertrial intervals (Table III). This sporadic responding

Table II

Distribution of errors on positive trials in the postoperative period

Rabbit No.	50-trial blocks					
	1	2	3	4	5	6
Medial hypothalamic lesions, group HM						
R-1	0	0	0	0	0	0
R-2	0	0	0	0	0	
R-3	0	0	0			
R-4	2	0	0			
Lateral hypothalamic lesions, group HL						
R-5	50	44	18	12	2	1
R-6	41	13	5	4	2	1
R-7	40	38	15	5	1	
Medial frontal lesions, group FM						
R-11	5	0	0			
R-12	25	6	0			
R-13	18	2	0			
R-14	1	0	0			
Dorsolateral frontal lesions, group FL						
R-15	2	0	0			
R-16	1	0				
R-17	0	0				
R-18	0	0				

represented the most striking effect of the lateral hypothalamic lesions at the early stages of the CR recovery. It was evidently clear that the animals after recovery from aphagia showed a full motor efficiency and could perform the instrumental response but they apparently had great difficulty in performing the response consistently. This may have been due to the interference of this response with the increased food-oriented activity. Eventually, the animals recovered their preoperative type of eating and attained the full level of proficiency in CR performance. An excessive intertrial responding remained high throughout many postoperative experimental sessions, but it eventually declined (Table III).

Table III

Distribution of CR performances during intertrial intervals in the postoperative period

Rabbit No.	100-intertrial blocks					
	1	2	3	4	5	6
Medial hypothalamic lesions, group HM						
R-1	80	84	50	26	23	23
R-2	121	79	67	57	13	
R-3	57	67	16			
R-4	64	71	20			
Lateral hypothalamic lesions, group HL						
R-5	0	0	30	44	54	79
R-6	24	70	78	62	57	41
R-7	0	22	16	15	10	
Medial frontal lesions, group FM						
R-11	83	75	66			
R-12	0	0	18			
R-13	20	19	27			
R-14	44	26	3			
Dorsolateral frontal lesions, group FL						
R-15	5	3	4			
R-16	8	10				
R-17	2	8				
R-18	0	0				

FM group: One animal (rabbit No. 14) was unimpaired. Three remaining animals, rabbits Nos. 11, 12 and 13, showed a temporary decrement in terms of an inability to perform a consistent CR (Tables I and II) which was intimately associated with gross behavioral changes similar to those seen in HL animals in the early postoperative period. Thus the FM animals, like the HL animals, were apathetic, displayed decreased motor activity and ate less than before surgery. However, the initial fall in responding and food intake was within a few days followed by the recovery of feeding behavior and alertness in conjunction with an increased instrumental reactivity (Tables II and III) and an augmentation of the orienting reflex in response to the presentation of the CS+. It is interesting to note that great reactivity in terms of an excessive orienting reflex to the presentation of an acoustic CS+ in dogs with lesions of the premotor cortex was reported by Stępień and Stępień (1965). Thus in striking contrast to the HL animals, the disturbance in instrumental performance in the FM animals was confined to the immediate postoperative period.

HM group: These animals, on the other hand, markedly increased their CR performance immediately after surgery (Tables I and III). The general trend of results related to CR responding and gross behavior indicates a close similarity between these animals and the FM animals after the cessation of the depression stage. Thus, in both the HM animals and the FM animals following the recovery of consistent CR performance the placing response became violent and occurred in series, sometimes turning into scratching. In many instances, the animals persisted to keep the forepaw on the food box, or, did not finish eating the portions offered but, instead, prepared for the next trial, gnawing at the food cup and making an anticipatory series of placing responses. The animals ate hurriedly but clumsily, spilling the food around. They often executed not only the previously acquired right forepaw reaction but also a response with the left forepaw, or they stepped on the food box with both forepaws simulataneously. During intertrial intervals, the animals showed an excess in responding or raised their forepaws alternately but refrained from placing them on the food box. The instrumental response became amplified and, at the same time, disorderly and clumsy as compared with the precision with which it was performed prior to surgery. All these manifestations appeared to be an indicator of an increased liveliness and motivation of the animals of these two groups.

The animals with lesions of the dorsolateral division of the frontal cortex (*FL*) and the unoperated control animals (*C*) did not show appreciable changes either in gross behavior or in CR performance (Table I and II). There was some intertrial responding in the FL animals, which was, however, inferior to that in the remaining groups (Table III).

CR inhibition. As may be seen in Table I, all animals of the four operated groups, except for the two of the HL group who stopped performing the instrumental response (Nos. 8 and 10), were impaired in their ability to refrain from responding on inhibitory trials. The impairment in the FL animals was least and shortest in duration; it did not persist beyond the immediate postoperative period (Table IV). The remaining three groups showed a more enduring impairment. However, of these three groups, the FM group appeared to be less severely impaired. With continued training all groups approximated their preoperative levels of inhibition but group HL required more training postoperatively than preoperatively (Tables I and IV).

Table IV

Distribution of errors on inhibitory trials in the postoperative period

Rabbit No.	50-trial blocks					
	1	2	3	4	5	6
Medial hypothalamic lesions, group HM						
R-1	45	21	11	8	14	1
R-2	43	30	16	12	7	
R-3	45	19	6			
R-4	40	24	1			
Lateral hypothalamic lesions, group HL						
R-5	0	0	23	6	6	2
R-6	6	23	8	14	12	4
R-7	4	14	3	0	0	
Medial frontal lesions, group FM						
R-11	17	19	13			
R-12	7	10	3			
R-13	5	9	6			
R-14	14	18	9			
Dorsolateral frontal lesions, group FL						
R-15	7	10	1			
R-16	12	2				
R-17	12	5				
R-18	5	1				

Table IV permits comparison of error scores divided into 50-trial blocks for the individual animals of the four operated groups (excluding the two unresponsive rabbits Nos. 8 and 10 of the HL group). It is seen that FM, HM and HL animals clearly differ in the distribution of errors. While the HM animals show the greatest number of errors early in the postoperative period, the maximum deficit in the FM and HL animals does not occur until from the 2nd to the 3rd 50-trial block. In view of the data presented in Tables I and II, it becomes evident that the low error score in the FM and HL groups in the initial period is attributable to the absence of a consistent CR performance in the early postoperative period in the animals of these two groups. Thus the impairment of inhibition in HL and FM animals is a time-dependent phenomenon.

However, in spite of the difference in the distribution of errors in inhibitory trials, an examination of gross behavior changes during testing suggests that the nature of the inhibitory defects in the FM, HM and HL animals is the same. The best guarantee of comparability appears to be an excessive searching behavior, consisting mostly of manoeuvering in the vicinity of the food box with much sniffing, inserting the mouth into the food cup and making efforts to reach for the food directly, which in all the animals of these three groups was particularly pronounced at the early stage of the impairment of differential inhibition (in the HL animals also prior to the impairment), thus making these groups at this stage undistinguishable. This suggests the possibility that the inability to withhold responding on inhibitory trials in the FM, HM and HL animals may have been caused by an increased drive for food. No searching was ever seen in the FL animals.

Observations of the behavior of the HL animals in the later postoperative period suggest that an important factor in the impairment of differential inhibition derives from the tendency of the animals to obstinately perseverate the instrumental response. It is then likely that the behavioral deficit of the HL animals seen late after surgery reflects not only an increased drive for food but even more so the somatoperseverative tendencies.

The unoperated control animals (group C) continued to do the same undisturbed performance on inhibitory trials (Tables I and IV) and the same behavior as had characterized these animals prior to the rest.

Other behavioral observations. Rabbit No. 4 of the HM group and all the rabbits of the FM group showed rage responses together with an excessive susceptibility to all types of tactile stimuli. A violent aggressive-defensive reaction was elicited by touching an operated animal, or, when attempts were made to take out the animal from the cage: the animal wriggled, escaped, or, emitting squealing sounds, attacked one's hand extended. These findings are in agreement with those of Brutkowski et al. (1961), who reported an elevation of tactile sensibility in conjunction with angry behavior in dogs with a damage to the genual area of the anterior cingulate gyrus, and of Romaniuk (1962), Balińska (1963 a), and Lewińska (1964), who reported aggression in rabbits with a damage to the ventromedial nucleus of the hypothalamus.

The HM animals showed a definite preference to overeat oats and potatoes over carrots, whereas the HL animals preferred carrots over oats and potatoes, which confirms the previous observation of Balińska (1963 a, b). Before surgery, the animals showed a preference for carrots.

DISCUSSION

The observations reported here clearly demonstrate that medial frontal cortex together with the medial and lateral portions of the hypothalamus in the rabbit constitute one basic system which participates in mediating the type of inhibition referred to as "drive inhibition". The medial frontal cortex and the lateral hypothalamus serve also in maintaining the food-reinforced instrumental CR. It is interesting to note that these two structures likewise mediate the performance of an avoidance response (Balińska and Wyrwicka 1961, Brutkowski and Wojtczak-Jaroszowa 1963, Balińska et al. 1964). The medial hypothalamus appears to be crucial only for inhibition. Lesions destroying the medial hypothalamus impair the differential inhibition but do not intefere with the instrumental CR.

The major result is that rabbits with lateral hypothalamic lesions who show aphagia in association with a deficit in CR performance in the early postoperative period, after recovery of food intake made possible by subcutaneous hydration, may develop an excessive food-directed activity which is subsequently followed by an increased performance of the food-reinforced CR in conjunction with a drastic impairment of differential inhibition. This is in agreement with an earlier finding that the lateral hypothalamic lesioned rabbits who have recovered their feeding behavior and previous performance of the food-reinforced CR greatly increase their searching habit and the response rate in extinction (Balińska and Brutkowski 1964).

In general, the effect on a differentiation task of lesions of the frontal cortex in the rabbit is similar to that in the dog and monkey. However, differences are also obtained. Rabbits and dogs with lesions of the medial frontal cortex (presumably homologous to the orbital frontal cortex of the monkey) show an abolition or reduction of CR performance early in the postoperative testing and then later an increase in performance together with a deficit in differential inhibition. Monkeys with orbital frontal lesions are also deficient on differential inhibition but, in contrast to rabbits and dogs with medial frontal lesions, their CR performance is not affected. On the other hand, rabbits, dogs and monkeys with dorsolateral frontal lesions, are unimpaired on CR performance and only minimally impaired on CR inhibition in the differentiation-type test. An increase in sniffing and searching behavior in subprimate subjects with lesions of the medial frontal cortex suggests that the deficit produced by medial frontal lesions on a differentiation task reflects an elevation of drive functions. Although there is no direct evidence of an increase in drives in monkeys with orbital frontal lesions, a careful examination of the effects of orbital frontal lesions in the monkey on various sorts of behavioral tests indicates that the deficit in differential inhibition after lesions of the orbital frontal cortex in the monkey may be attributed to an increase in the drive sphere (Brutkowski et al. 1963). On the other hand, an analysis of the error-producing factors in animals with lesions of the dorsolateral frontal cortex (Brutkowski and Dąbrowska 1963, Brutkowski et al. 1963), and those with lesions of the lateral hypothalamus in the later postoperative period suggests that the deficit in differentiation performance in these two groups of animals may be related to the somatoperseverative tendency.

Since no information is available on the effect of hypothalamic lesions on differentiation in mammals other than rabbits, it is not possible to compare the effect of hypothalamic lesions on CR performance and inhibition in differentiation behavior between rabbits and other species. Data from this study lead to the conclusion that hypothalamic lesions produce an impairment in differentiation which is qualitatively similar, but quantitatively more severe than that produced by frontal lesions.

SUMMARY AND CONCLUSIONS

Bilateral damage to the dorsolateral frontal cortex, medial frontal cortex, lateral hypothalamus or medial hypothalamus in the rabbit disturbed differential inhibition. The disturbance that followed hypothalamic lesions was more severe than that produced by frontal lesions. The animals that received lesions of the medial hypothalamus and dorsolateral portion of the frontal cortex displayed the greatest impairment of inhibition immediately after surgery. In animals with lateral hypothalamic lesions and in those with medial frontal lesions, the inhibition impairment required time for its full development and was preceded by the abolition or reduction of CR performance. In some animals with lateral hypothalamic lesions, a permanent abolition of CR performance occurred. Accordingly, the medial frontal cortex and lateral hypothalamus appear to be implicated in both CR performance and differential inhibition.

The deficit in CR performance in the animals with medial frontal cortex was associated with a decrease in food intake and that in the animals with lateral hypothalamic lesions was associated with aphagia. During the impairment of differential inhibition, the animals with lesions of the medial frontal cortex, medial hypothalamus and lateral hypothalamus showed an excessive food-oriented behavior and an augmented CR performance during intertrial intervals. However, such was not the case for the animals with lesions confined to the dorsolateral frontal cortex. These preparations displayed neither excess in food-oriented activity nor exaggerated intertrial performance. Thus lesions involving the medial frontal cortex, unlike those involving the dorsolateral frontal cortex, reflect the behavioral changes resulting from lesions of the lateral hypothalamus as well as those of the medial hypothalamus. These physiological observations are in consonance with the anatomical finding, indicating an association between the medial frontal cortex and the lateral and medial hypothalamic regions. The close correspondence between the increased food-oriented activity and the impairment of differential inhibition associated with food-reinforced performance in animals with lesions of the medial frontal cortex, medial hypothalamus and lateral hypothalamus suggests that an increase in the drive for food is the factor determining the disinhibition of previously suppressed response tendencies. It is concluded that the complex composed of the medial frontal cortex, and the medial and lateral hypothalamus constitute a neural substrate for the type of inhibition referred to as "drive inhibition". It is clear that the effects of some brain lesions on CR performance and inhibition must be considered in terms of the time after surgery.

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SOME PROBLEMS CONCERNING THE PHYSIOLOGY AND MORPHOLOGY OF THE MOTOR ANALYZER[1]

L. S. GAMBARIAN and A. A. GARIBIAN

Laboratory of Neurobionics, The Orbeli Institute of Physiology,
Academy of Sciences of the Armenian SSR, Erevan, USSR

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Pavlov (1951) who designated the neural sensory substrates made up of receptors, afferent nerve fibres and receiving areas in the brain — "analyzers", pointed out in 1911 to the existence of the motor analyzer as that which gives information concerning movement, position and tension of the body.

The sensory function of muscles was first suggested in 1826 by the experiments of Bell. On the basis of a large body of evidence, Bell established the fact that muscles are not only motor but also sensory in function, and that brain and muscles are interconnected by both afferent and efferent pathways. In this neural circuit, efferent fibres transmit messages that cause a twitch of the muscle, and afferent fibres arising from the muscle give the sense of the changes within the muscle to the brain thereby regulating the posture and movement. It is obvious that in the absence of this ascending signalization, referred to as "muscle sense", no coordination of the motor activity is possible.

Bell's observations and ideas, which basically have retained importance to the present days, were substantially extended by subsequent investigators. Sechenov (1952), who elaborated the concept of brain reflexes, clearly indicated that the "obscure" muscle sense contributes considerably to the control of movement and formulation of elementary thinking process. Sherrington (1906) demonstrated that sense organs

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of the muscles, tendons and joints, which have been called by him "proprioceptors", are important in the reciprocal innervation of antagonistic muscles. Studies of Bekhterev (1905) and his associates established the existence of ascending pathways conducting impulses that subserve proprioception, and those of Pavlov (1951) determined the cortical topography of the proprioceptive sensation. With the use of the conditioned-reflex method Krasnogorski (1911) showed that the motor area is the region of the cerebral cortex which receives projection of proprioception. It has thus been shown that the motor analyzer, like all other analyzers (cutaneous, visual, acoustic, etc.), consists of the following three neural components: (1) receptors which transform the energy of the stimulus into the neural process, (2) sensory pathways which send the impulses from the muscle, tendon and joint receptors to the central nervous system, and (3) the cortical sensory area in which the ultimate analysis and sythesis of the complex perception pattern occur. The morphologic and physiologic evidence obtained since then has extended considerably our knowledge concerning the anatomy and function of each of these three components.

The sense organs of the motor analyzer are the muscle spindles, the Golgi tendon organs, and Pacinian corpuscles. The muscle spindle contains (from 2 to 12) cross-striated intrafusal fibres enclosed in a fibrous capsule. It differs from the regular, or extrafusal fiber, in several points. Each intrafusal muscle fiber consists of two contracticle striated poles interconnected by a noncontracticle nuclear bag. Sensory pathways of the intrafusal fiber arise from both the nuclear bag and the surrounding myotube region (Creed et al. 1932, Granit 1955). The contracticle portion of the intrafusal fiber is innervated by small motor fibers, recognized as gamma efferents.

Knowledge of how the muscle sense organs function has principally come from the studies by Matthews (1929, 1931), Hunt (1951, 1952, 1953) and Granit (1955). It has been found that stretch of the muscle causes firing of the spindle receptor, and contraction results in ceasing the firing. This comes about because the contraction removes tension from the intrafusal fibres, which are "in parallel" with the extrafusal fibres. However, if intrafusal stimulation occurs during muscle contraction the nuclear bag is put under tension and the spindle receptor continues to discharge.

Leksell (1945) demonstrated that the intrafusal system is activated by the gamma efferents, innervating the contractile zones of the spindles, and the activity originating in the nuclear bag maintains the discharge of the alpha-motoneurons, innervating the extrafusal muscle fibres. This interaction of alpha- and gamma-efferent systems, determined by an afferent discharge of the spindles thus provides a mechanism for maintaining a continuous tension of the muscles.

The Golgi tendon organs, located near the junction of muscle and tendon or in the spindle endings, are activated by both muscular contraction and stretch. To sum up, spindles are "length recorders", whereas tendon organs are "tension recorders" of the muscles (Granit 1955).

The Pacinian corpuscles, which occur in a small number in the fleshy tissue of the muscle but are numerous in the true skin and in the fascia of the muscle and bones, respond to weak mechanical stimuli and display a rapid adaptation. They are considered, accordingly, to subserve vibratory sensibility (McIntyre 1962, 1963).

Nerve impulses underlying sensation of posture, when set up in the sense organs, pass into the spinal cord by means of posterior nerve roots and reach the alpha-motoneurons directly (a monosynaptic reflex arc), or, after transfer through an intermediate neuron system, including cells of the cortical subdivision of the motor analyzer.

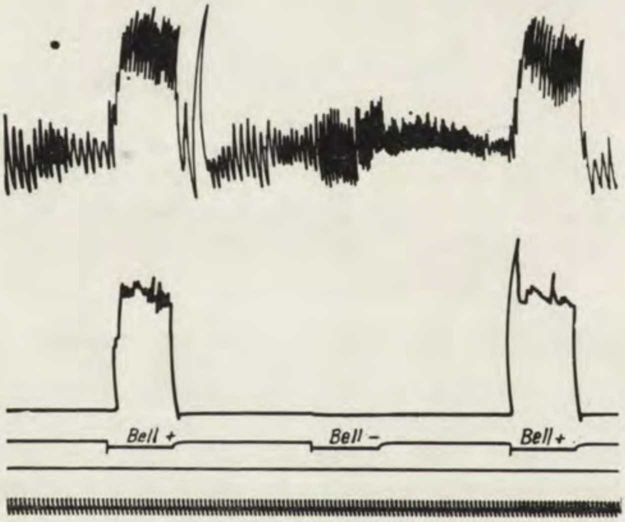

Fig. 1. Conditioned flexor reflexes of a dog, reinforced with electric shock administered to the foot, two days after the removal of the dorsal columns over the spinal cord segments Th6-Th8. Breathing, leg flexion, CS presentation, electric shock (US), time (to be read from the top to the bottom). The time is marked in seconds. Plus and minus indicate CS+ and CS−, respectively. No shock was given since the avoidance response was made

It is generally considered (Kononova 1957, Adrianov and Mering 1959) that the central portion of the motor analyzer consists of the dorsal column, the medial lemniscus and the spinothalamic tract, terminating in the "kinesthetic" cells of the cerebral cortex. However, there is now increasing reason to question the value of this view.

Experiments carried out in our laboratory (Gambarian 1957, 1963, Grigorian 1957, 1959, 1963) indicate that when dorsal columns are cut or removed over a few spinal segments in the dog, the previously established motor conditioned reflexes (CRs) remain unaffected (Fig. 1). Furthermore, such lesions do not interfere with the acquisition of the motor CRs (e.g., CRs reinforced by food presentation or electric shock) even after the enucleaction of the eyes. It has moreover been indicated that dogs who after an amputation of two legs are still able to perform locomotor activity, continue to do so following the removal of the dorsal columns over a distance of a few segments (Fig. 2).

Fig. 2. The dog *Anitra*, one day after the removal of the dorsal columns over the spinal segments Th6-Th7 (After L. S. Gambarian 1963)

Considering the fact that anatomical connections are arranged to form a circuit and that coordination exists within biological systems, it is suggested that ascending pathways other than those discussed above account for a coordinated locomotor performance in an animal with the damage to the dorsal column system. This view has been found persuasive.

There is morphologic evidence (Gambarian 1959, 1963, Grigorian 1960) that following section of the dorsal columns a fiber degeneration occurs not only in these columns but also in the ventrolateral white matter of the spinal cord.

On the basis of their histologic analysis, Brodal and Wallberg (1952) have suggested that the pyramidal tract contains afferent fibres subserving extero- and proprioception. Brodal and Kaada (1953) have confirmed this electrophysiologically. Although some studies do not bear out this suggestion, the existence of extero- and proprioceptive fibres within the pyramidal tract has conclusively been proved by the recent experiments of Towe and Jarburr (1959), and Batsel (1963).

Evidence that the dorsal column lemniscal system, recognized as the classical pathway concerned with deep sensibility contains but a few fibres transmitting impulses from joints and muscles has been provided by the experiments of McIntyre (1953, 1961, 1963). It has been found that the largest Group I (12—22 microns) fibres arising from both the primary or nuclear bag endings of the muscle spindles and tendon organs do not run within the dorsal column and project to the cerebellum; Group II fibres (4—12 microns) originating in the secondary or myotube endings of the spindles and, in part, in the Pacinian corpuscles project to both the cerebral cortex and cerebellum; Group II fibres which run within the dorsal column appear to arise from the Pacinian or Pacinian-like corpuscles. However, according to Amassian and Berlin (1958), Group I fibres from muscles and joints conduct impulses to the cortex.

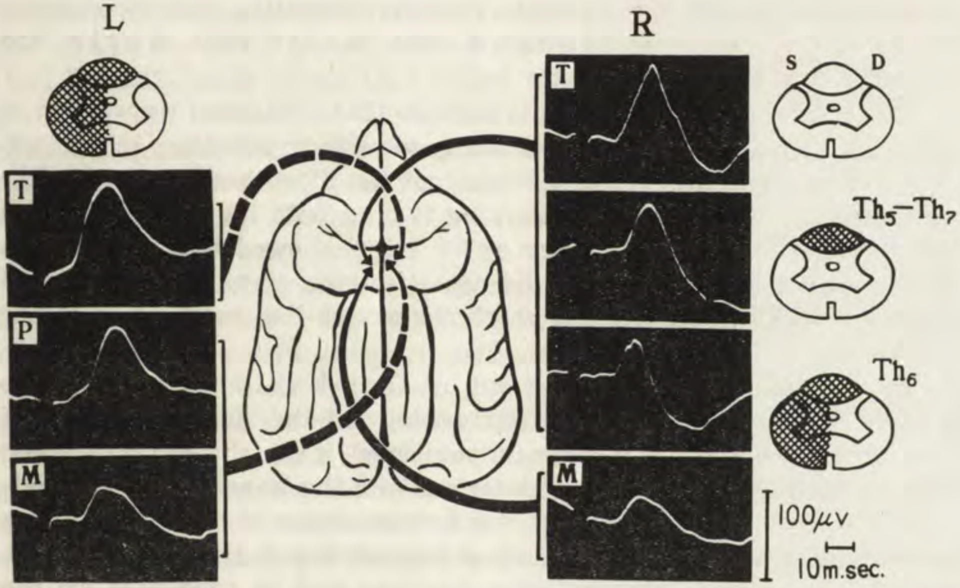

Fig. 3. Bioelectric potentials (recorded from the posterior portions of the sigmoid gyrus) evoked by electric shocks administered to the right (R) and left (L) hindfeet. T = n. tibialis, M = rami musculares, P = n. peroneus communis. Lesions of the spinal cord, after which the evoked potentials were recorded, represented on diagrams of coronal sections. The arrows indicate the areas from which the potentials were obtained (After L. S. Gambarian 1963)

More recently, a series of studies (Gardner and his associates 1952, 1953a, b, 1957, Gambarian 1960, 1963) has appeared indicating that impulses elicited by exciting afferent fibres of spindle origin in the extremities continue on to the sensorimotor cortex when all spinal cord pathways are sectioned except those of the ventrolateral tract (Fig. 3). The main conclusion reached from these studies is that dorsal columns are not the only pathways, containing fibres of the motor analyzer. Apparently, the lateral and ventral portions of the spinal cord white matter are also open to proprioceptive impulses. This conclusion has been confirmed by numerous chronic experiments (Gambarian and Grigorian 1957, Grigorian 1957, 1960, Gambarian 1963, Gambarian and Garibian 1963).

The evidence that proprioception has a double pathway in the spinal cord suggests a similar anatomic arrangement in the brain stem. Indeed, it has been found that supplementary spinal tracts subserving prorioceptive function supply the midbrain reticular formation and the anterior lobule of the cerebellum (Haddad 1953, Morin 1953, Morin and his ascociates, 1953a,b, 1957).

The results of our experiments indicate that a bilateral transection of the medial lemniscus does not end ability to perform voluntary movement. Three days after surgery, an operated cat can move his extremities like an intact cat. He is capable of learning to open with his forepaw a small can to reach for the food. Tarnecki (1962) showed that interruption of the medial lemniscal fibres did not affect the previously established instrumental CR, consisting of rhythmic scratch-like movements of the hindpaw.

In acute experiments, carried out by Gambarian and Tarnecki in the Department of Neurophysiology of the Nencki Institute of Experimental Biology in Warsaw (unpublished), it was shown that a lesion of the medial lemniscus does not interfere with the transmission of impulses to the sensorimotor cortex, elicited by stimulation of the nerves arising in the hindleg muscles. These findings suggest that in the absence of the medial lemniscus the proprioceptive impulses may be conducted via the reticular formation and the cerebellum.

It has long been known that the cerebellum possesses a definite afferent input from the spinocerebellar tract of Flechsig and Gowers and the nuclei of Goll and Burdach. More recent studies of the proprioceptive projections have revealed a topographic localization of the cerebellar cortex (Snider 1950, Firsov 1958). Electrophysiologically, Adrian (1943) was the first to show that the body surface, including the hindlimb, forelimb and face, is projected into the cerebellum in a way compararable to the somatotopic organization in the cerebral cortex. According to McIntyre (1961, 1963) the afferent fibers from the myotube and nuclear bag and those from the Golgi tendon organs project onto the cerebellum.

A projection of the supplementary spinal proprioceptive pathway in the cerebellum of the cat and monkey has been shown by Morin et al. (1957). Bekaia and Moniava (1963) have determined electrophysiologically the pathways between "the sensorimotor area" of the cerebellum and the sensorimotor area of the cerebral cortex. It has been shown that these pathways originate in the paramedial and anterior lobules of the cerebellum and reach the cerebral cortex via the ipsilateral dentate nucleus, the anterior peduncle of the cerebellum, the mesencephalon (in which a partial crossing occurs), the thalamic ventral nucleus and the red nucleus.

It then becomes obvious that the cerebellum is an area of termination of the afferent pathways of the motor analyzer.

To summarize, the cerebral cortex receives impulses from the muscle receptors via two projection systems, i.e., the brain stem and the cerebellum (Snider 1950, Gambarian 1963). Sjöquist and Weinstein (1942), have found that injury of either the medial lemniscus or the superior peduncle of the cerebellum has little permanent effect on a previously established proprioceptive habit (discrimination of weight). However, a combined lesion of both conducting pathways produces a loss of the habit. In other words, the habit remains undisturbed, provided one of these pathways is not damaged.

Experiments carried out in our laboratory (Gambarian 1960, 1963) have shown that neither subtotal nor total extirpation of the cerebellum interferes with the acquisition and performance of the classical defensive CR reinforced by an electric shock, although it leads to a decrease of the speed of the acquisition of the tonic CRs, that is, such reflexes in which the flexion of the animal's leg is maintained over a relatively long period of time. It has been demonstrated that dogs with the extirpation of the cerebellum, in which one forelimb and one hindlimb had been amputated prior to the extirpation were unable to walk using the two remaining legs.

Prior to 1942 the cerebellum has been treated as exclusively proprioceptive. However, from present knowledge it is obvious that the cerebellum also receives somesthetic, visual, auditory and interoceptive inputs (Snider and Stowell 1942, 1944, Snider 1950, Kullanda 1957, Firsov 1958). The cerebellum is thus recognized as an essential component of the external and internal analyzers, in the first place, of the motor analyzer (Gambariam 1959, 1963), in which the elaboration and synthesis of afferent inputs occur. The elimination of this component results in a disruption of the interaction between the alpha- and gamma-efferent systems (Granit 1955). Thus animals with lesions of the cerebellum are impaired in their utilizing the mechanism regulating the sensitivity of the proprioceptors. When this mechanism is affected the regulation of the muscle tonus appears to be defective.

All these facts and conclusions permit certain alterations in the diagrams illustrating the structural organization of the motor analyzer. Fig. 4 shows a diagram summarizing the above mentioned morphologic and physiologic achievements. It can be seen that the motor analyzer comprises fibres which come from both the classical (posterior column and medial lemniscus system) and supplementary proprioceptive pathways contained within the lateral and ventral parts of the spinal cord as well as in the brain stem and cerebellum. The duplication of the proprioceptive pathways and a wide distribution of the proprioceptive (kinesthetic) cells in the cortex are the best guarantees for a maximum precision in the functioning of the motor analyzer (Pavlov 1951). To summarize, the proprioceptive impulses travel up to the cortex in which the final analysis and synthesis occur; the cortex, in turn, gives rise to outgoing impulses which descend along efferent pathways to effect a given reaction.

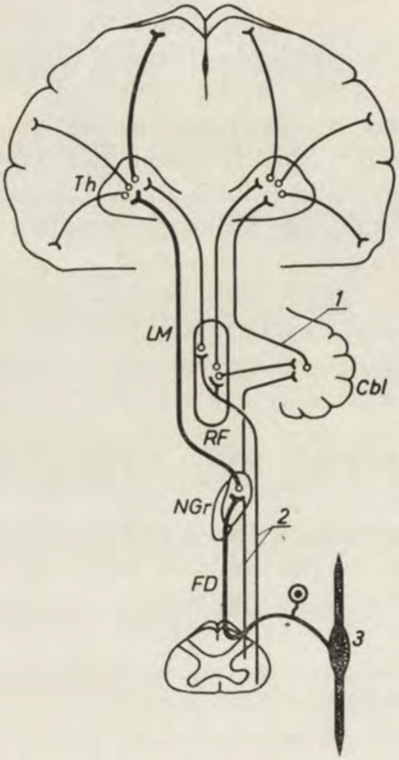

Fig. 4. Schematic illustration of structural relationships within the motor analyzer made according to the recent physiologic and morphologic findings. FD = dorsal columns of the spinal cord, NGr = nucleus gracilis, LM = medial lemniscus, Th = thalamus, Cbl = cerebellum, RF = brain-stem reticular formation. 1, the cerebellar pathway of the proprioceptive signalization; 2, the proprioceptive pathways of the lateral and ventral columns of the spinal cord; 3, muscle receptor

In contradistinction to the Pavlovian teaching, some investigators (Kukuev 1955, Kononova 1957) include the corticospinal tract in the motor analyzer. For example, Kononova, in considering the pathways of the motor analyzer, says: *"Efferent fibres of the motor analyzer (areas 4 and 6), connecting the cerebral cortex with the motoneurons of the ventral horns of the spinal cord, that is, the pyramidal or corticospinal tract, arise from the cells of the cortical part of the motor analyzer"*. Such interpretation is misleading since the pyramidal tract cannot be considered a structural component of the motor analyzer. The pyramidal tract is a part of the efferent system, whereas the motor analyzer refers to reception and perception (Pavlov 1951). According to Sherrington (1906), the pyramidal tract is an internuncial common path for numerous reflexes which are elicited by the stimulation of a great variety of receptors.

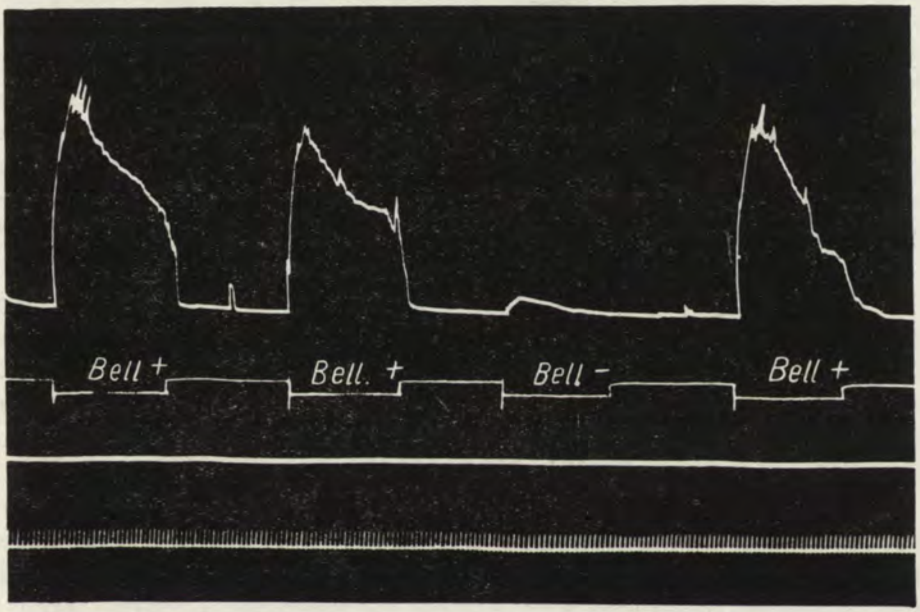

Fig. 5. Conditioned flexor reflexes of a dog, reinforced with electric shock administered to the foot, trained after a bilateral transection of the medullary pyramids. Denotations as in Fig. 1

Using microelectrodes, it has recently been shown (Buser and Imbert 1961, Patton et al. 1962) that the pyramidal cells of the cortical portion of the motor analyzer may be activated not only by somatic but also by acoustic and visual stimuli. Consequently, the giant Betz cells are identified as "polysensory" neurons (Buser and Imbert 1961) to emphasize that they respond to stimuli of different modalities. In view of these considerations, the pyramidal tract is considered a movement--producing agent and not a part of an analyzer.

A centrally integrated complex of motor responses built up on the basis of afferent synthesis (Anokhin 1963) is transmitted along the pyramidal tract to the motoneurons of the spinal cord. However, the pyramidal tract is not the sole pathway of motor function.

Recent experiments on dogs (Gambarian et al. 1964) have provided evidence, showing that surgical sectioning of the pyramids at the level of the medulla oblongata results in a surprisingly slight disturbance in the function of the motor apparatus. During the immediate postoperative period, a minimal deficit of the locomotor activity occurs which is clearly associated with a negligible paresis and ataxia of the limbs. However, these changes disappear very rapidly. The retention of conditioned reflexes is not lost except that the force of the reflexes is deficient (asthenia) within the first postoperative days. During the recovery period, it is possible to train a skilled tonic conditioned response (Fig. 5). After the amputation of a forelimb together with a heterolateral hindlimb, a dog with the previously sectioned pyramids is able to walk on the two remaining limbs. Also Górska (1966) has recently showed that the abolition of instrumental reflexes in dogs is not a consequence of the bilateral pyramidal interruption. On the other hand, Tower (1940) demonstrated that a section of the medullary pyramids in monkeys produces a definite impairment of volitional skilled movement.

In summary, the pyramidal tracts cannot be considered the sole servants of voluntary activity. Other efferent pythways are also implicated in the skilled voluntary movements. The conclusion is that the motor function seems to be greatly served by the extrapyramidal system, through which the supraspinal structures exert a control over the gamma efferent system that participates in the regulation of the muscle spindle function (Granit 1955).

The kinesthetic or motor analyzer contributes fundamentally to the performance of voluntary movements. However, the central integration of movements is mediated by a polyanlyzer action (Gambarian 1959, 1963, Garibian and Gambarian 1963). Thus a condition for establishment and performance of movements is that various analyzers interact; each analyzer is involved in a stage of the motor reaction.

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THE ROLE OF VISUAL CUES IN PERSEVERATIVE BEHAVIOUR OF THE RAT

Irena ŁUKASZEWSKA

Department of Neurophysiology, The Nencki Institute of Experimental Biology,
Warsaw 22, Poland

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In most maze experiments, rats are trained to run from the starting point to the goal, that is, a place where they are fed. Recently, it has been shown that rats may be trained to bring the food from the goal to the starting point and eat it there (Łukaszewska 1961). This type of behaviour has been called a "return reaction".

Our previous experiments (Łukaszewska 1963) have indicated that the return reaction is guided by the memory of kinaesthetic stimuli from the approach reaction. This guidance in rats is developed to such a degree that in about 90 per cent of the trials they correctly return to the starting platform. However, the return reaction, when investigated with variable starting platforms and a fixed feeding place, is strongly influenced by the return reaction performed in the preceding trial. When the animals started from the same platform as in the preceding trial, an increase in the number of correct responses was found. On the other hand, when the starting platform was changed, a strong tendency was observed in rats to return by the same route they took in the previous trial (Łukaszewska 1962).

The aim of this investigation was to determine the role of visual cues in the perseveration on the return reaction.

MATERIAL AND METHODS

Experiments were carried out in an elevated T maze (Fig. 1). Thirty six albino rats were divided into three groups. *Group 1* consisted of animals which were deprived of vision by electrocoagulation of the eyes; *Group 2* were normal rats which could make use of extra-maze visual cues; and *Group 3* were normal rats which, in addition to the extra-maze visual cues could make use of the intra-maze cues, that is, they were tested in a maze, one arm of which was white and another black. The animals were required to leave the cage which was placed on one of two starting platforms, reach the cup on the maze stem, grasp the food from it and return to the cage where they were allowed to eat.

Experiments were preceded by the preliminary training during which the animals of all groups were accustomed to the experimental conditions. In each group a series of 10 experimental sessions was given; each session consisted of 5 trials. In trials I and II, the animals started from the same platform (e.g., S_1). Thereafter the cage containing the rat was taken to another platform (S_2) from which trials III, IV and V were started. On the next day, for trials I and II the cage was placed on the same platform as in the last trials of the day before. When the animal entered the wrong arm half-way it was considered an error. The intertrial intervals were from 1/2 to 1 minute. The correction method was used, i.e., the animals were permitted to correct an error in the same trial.

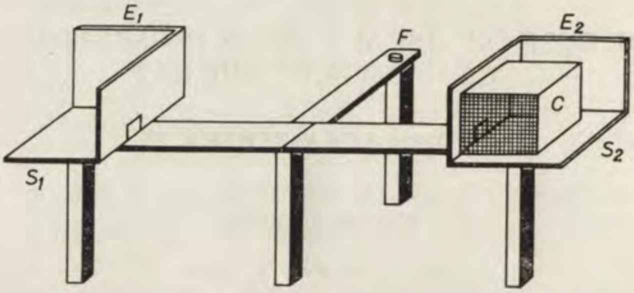

Fig. 1. Elevated T maze. S_1, S_2, starting platforms; C, cage; E_1, E_2, wooden screens; F, cup with food

RESULTS

The following course of performance was noticed in animals of all groups. In each experimental session, in trials I and II animals achieved a high level of performance but, after the change in the starting platform (trial III), the number of correct return reactions considerably decreased. In trials IV and V, the rats improved their performance (Fig. 2). This course did not change in the successive sessions of the series.

In the results, shown in Fig. 2, the most striking differences between groups occurred in trial III in which a competition was manifested between the return reaction and the perseverative tendency. The best performance, amounting to 80 per cent correct, was obtained in the blind rats. The rats put in the white-black maze chose on this trial a correct return route only 16 per cent of the time. The correct responses in seeing rats, put in the normal maze, were at a middle level, that is, about 50 per cent. For comparison of the groups a multiple comparison nonparametric test suggested by Ryan (Munn 1950) was used. This analysis shows that all groups significantly differ from each other when "the rate of error per experiment" equals $p < .05$.

Fig. 3 represents the histograms of errors in trial III in the three groups. One can see that most animals on the white-black maze committed 8-9 errors during the 10 day series. On the other hand, the blind animals reacted almost errorless (5 rats — O errors; 2 rats — 1 error). However, there were two blind rats committing as many as 7 and 9 errors. Seeing animals on the normal maze committed from 3 to 8 errors.

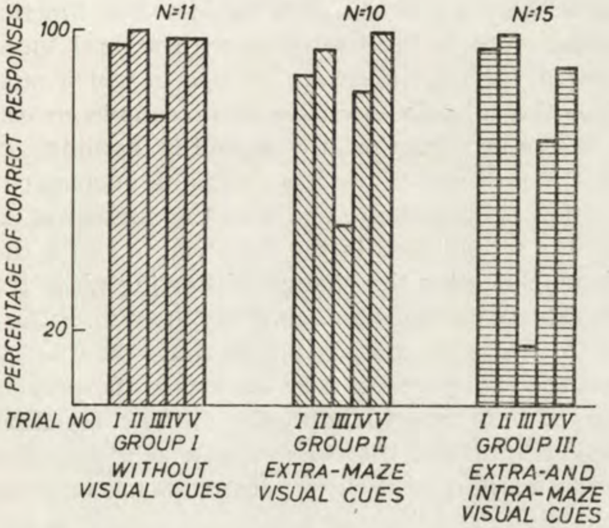

Fig. 2. The relation between return reaction and the amount of visual cues. I ... V, successive trials of experimental sessions. Each column represents the percentage of correct return reactions in the respective trial

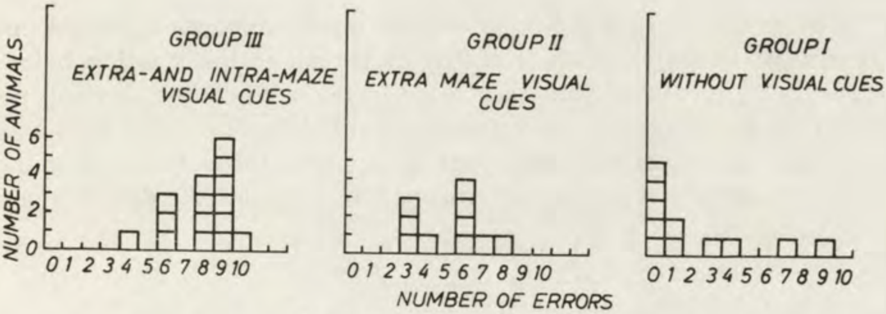

Fig. 3. Histogram of errors

The differences between groups in the remaining trials were not so remarkable. In general, the blind animals performed best. As far as the rats on the white-black maze were concerned, it should be stressed that they improved considerably in the last trials (trial IV — 70 per cent, trial V — 90 per cent).

DISCUSSION

As was previously demonstrated (Łukaszewska 1963) the return reaction is based on proprioceptive cues; i.e., to make a correct choice in the return route the rat must turn in the opposite direction to the turn performed in the route to the food. But with several successive runs in the same direction, the conditions are created in which rats learn the return route. Thus the animals now have two means in choosing the return route : one is the return reaction, the second is learning.

As long as the position of the cage remains unchanged learning and the return reaction act in alliance and thus the number of correct responses is higher in the second than in the first trial in which the return reaction works alone. But after the change of starting place the relation between the two factors becomes antagonistic. In spite of the fact that rats are quite able to choose the proper return route they have a strong tendency to repeat the choice which they learned in the previous trials.

The findings of the present study point to the correlation between the amount of visual stimuli and the perseverative tendency. Since the perseveration is due to learning of the preceding response our result is in agreement with the literature in which ample evidence is given (Munn's review of the literature, 1950) that visual stimuli exert a favorable influence on learning of the elevated maze.

SUMMARY

Three groups of rats provided with different amounts of visual information were tested as to their ability to return to the starting point by a route they previously took to reach the food. When the starting point was shifted, perseveration errors were recorded in all groups. Rats helped by visual cues committed much more errors than those deprived of them. It was concluded that the perseverative behaviour in rats depends on visual stimulation.

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CHANGES OF THE BACKGROUND NOISE INTENSITY AND THE BAR-PRESSING RESPONSE RATE[1]

K. ZIELIŃSKI[2]

Department of Psychology, McMaster University, Hamilton, Ont., Canada

(*Received July 1, 1965*)

The aim of the present experiment was to investigate the effect of changes of the background noise intensity on the performance of a learned behavior. The operant conditioning method seems to be more appropriate for this purpose than methods in which response is performed to the conditioned stimulus interspersed with long intertrial intervals. In the operant conditioning method the experimental situation is an eliciting stimulus, and under a variable interval schedule of food reinforcement a given response, e.g. bar-pressing, is performed with a stable rate. Obviously, any change in the experimental situation evokes at first an orientation response, which interferes with other responses. It was shown that the onset and the offset of an external stimulus produce very similar orientation responses (Sokolov 1957). Thus, a depressing effect of the change of the background noise intensity on the bar-pressing rate may be expected independent of the direction of the change (increase or decrease of the background noise intensity).

Orientation reactions usually undergo rapid habituation and then another effect of the change of the background noise intensity may be expected. It is generally accepted that, other things being equal, there

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[2] Now at the Department of Neurophysiology, the Nencki Institute of Experimental Biology, Warsaw 22, Poland.

exists a direct correspondence between the intensity of the external stimulation and the organism's activation level (Duffy 1962). We expected that a similar relation will be observed when the rate of the bar-pressing response instead of physiological measures are used as an index of the organism's activation level. Thus, when the orientation reaction undergoes habituation, an increase of the background noise intensity should produce a higher rate of responding, whereas a decrease of the noise intensity should produce a lower rate of responding.

Some information concerning this problem was obtained in previous studies. In a number of experiments the effect of the to-be conditioned stimulus on the on-going bar-pressing response rate was investigated during the so-called Pretest Day. It was noticed that the first presentation of a white noise stimulus interferes with the bar-pressing behavior (Kamin and Brimer 1963); however, this effect was very shortlasting and full habituation occurred within 3 mins. of the stimulus presentation (Zieliński 1965a). The same effect was observed also in the case when the external stimulus consisted in an increase of the background noise intensity, whereas the effect of a decrease of the background noise intensity was hardly visible (Zieliński 1965b). It was also shown that on the remaining trials during the Pretest Day the acoustic stimuli presented under the increase procedure begin to increase the response rate, whereas the stimuli presented under the decrease procedure continue to depress the response rate (Hilton 1964).

It was shown on monkeys that after lateral frontal and, especially, orbital frontal lesions, the habituation of responses to novel stimuli is much delayed in comparison with intact animals (Butter 1964). On the other hand, there is evidence showing that in conditions of an increased level of external stimulation prefrontal-lobectomized monkeys exhibit more hyperactivity than nonoperated controls (Isaac and DeVito 1958). Thus, the second question investigated in our experiment was whether or not lesions in frontal pole of the brain in rats have a similar effect on habituation of the orientation reaction and on the stimulating effect of the increased level of external stimulation as observed in monkeys.

MATERIAL AND METHOD

The experiment was performed on 24 male hooded rats from McMaster Univ. colony, approximately 7 mo. of age. The apparatus consisted of 4 standard Grason-Stadler operant conditioning units with equipment for automatic programming and recording. Rats with lesions in the frontal pole of the cortex (anterior part of Krieg's area 10, Krieg 1946), in motor cortex (posterior part of Krieg's area 10 and area 6), and nonoperated, constitute three experimental groups, 8 subjects each. The places and extent of lesions in typical animals are presented in Fig. 1.

The preliminary training began 10 days after operation. The Ss were reduced to 75% of ad lib. body weight and maintained at that weight during the experiment, daily portions being given 1 hour after the experimental session. An initial presentation of 40 "free" .045 g Noyes pellets on a 1-min variable interval (VI) schedule ("magazine training") was immediatelly followed by a period with a continuous reinforcement schedule until 120 food pellets were delivered in a single session. Then followed six daily 1-hr. training sessions of bar pressing under a 2.5 minute VI food-reinforcement schedule, resulting in acquisition of stable on-going bar-pressing behavior for food. Finally two test sessions were given.

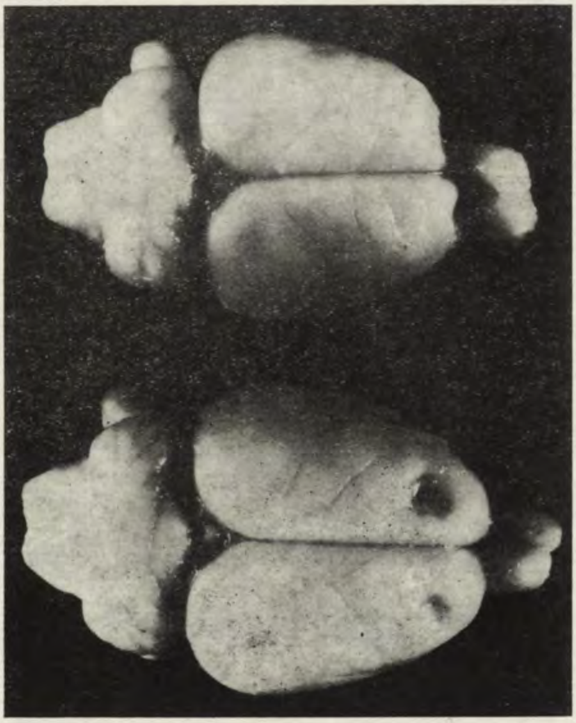

Fig. 1. The places and extent of lesions in typical animals of the frontal group (upper picture) and those of the motor group (lower picture)

Except for the first training session, the 60 db white noise from a Grason-Stadler Model 601A noise generator was delivered to the experimental space all the time. During the two test sessions the test consisting of a change of the 60 db background noise intensity to 80 db (increase procedure) or 40 db (decrease procedure) was applied. The test white noise intensity was applied 4 times daily for 30 secs. in regular 15 min. intervals. Half of the Ss from any experimental group were tested under the increase procedure, and the others under the decrease procedure.

The number of bar-pressing responses were counted independently for the three 30 secs. periods just before, during, and after each change of the background noise intensity. Numbers of responses emitted during these periods will be denoted as A, B, and C respectively.

RESULTS

Comparison of the experimental groups. As an index of the effect of the changes in background noise intensity on the bar-pressing response the $\frac{B}{A+B}$ ratio was used. If changes of the noise intensity do not produce any change in response rate, the ratios equal .5. Ratios more and less than .5 indicate increase and decrease of the response rate during the test noise intensity, respectively.

Ratios were calculated for the 1st, the 2nd-4th (pooled), the 5th, and the 6th-8th (pooled) test noise intensity applications for each S independently. Then the analysis of variance with three experimental groups and two testing procedures as main effects was done to estimate the data obtained. As seen from Table, this analysis shows that only one main effect — the testing procedure, was statistically significant in the 1st, and the 6th-8th test noise intensity applications.

Table

Analysis of variance of the $\frac{B}{A+B}$ ratios

Test applications:		The 1st testing day				The 2nd testing day			
		1st		2nd - 4th		5th		6th - 8th	
Source of variation	df	MS	F	MS	F	MS	F	MS	F
Groups	2	.0270	<1	.0041	<1	.0372	2.50	.0080	1.00
Procedures	1	.1736	5.83*	.0068	1.11	.0494	3.32	.1770	22.13**
Interaction	2	.0015	<1	.0025	<1	.0192	1.29	.0031	<1
Error	18	.0298	—	.0061	—	.0149	—	.0080	—

* denotes the effect significant at the $p < .05$ level, and ** denotes the effect significant at the $p < .001$ level.

As no effect of the lesions was discovered, the data will be presented with the experimental groups pooled and only the effect of the testing procedure will be discussed. The median numbers of bar-presses in the 30 secs. periods before, during and after the test noise intensities are presented in Fig. 2.

The effect of the 1st test noise application. As seen from Fig. 2, the first change of the 60 db noise intensity to 80 db resulted in a marked decrease of the bar-pressing response rate. This effect was significant at the $p < .01$ level, as estimated by comparing the number of responses emitted before and during the first application of the 80 db noise (Wilcoxon matched-pairs signed-ranks test, two tailed).

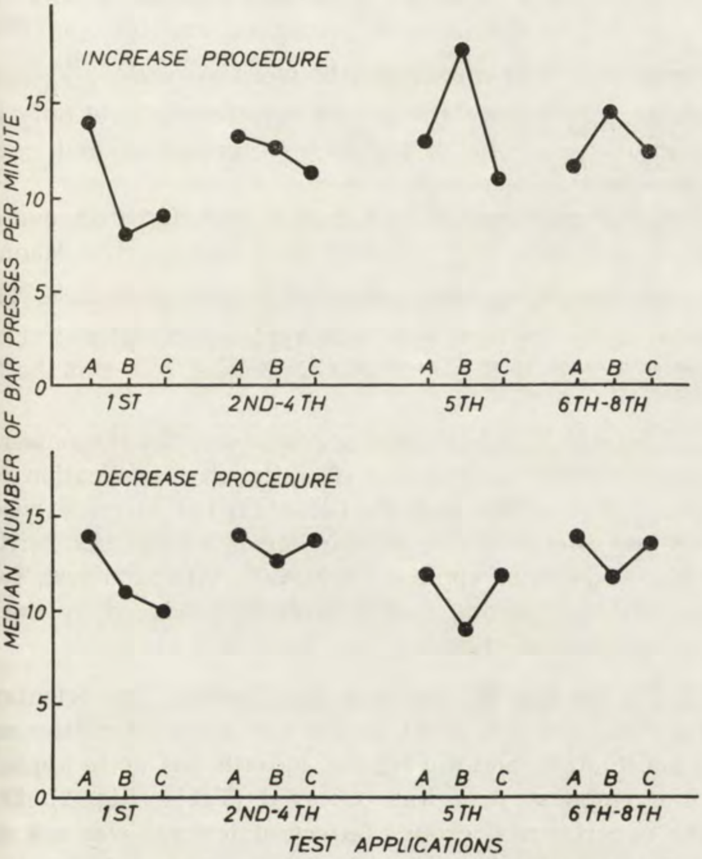

Fig. 2. Median numbers of bar-presses per minute emitted during the 30 secs. periods just before the onset of the test noise intensity (A), during the test noise intensity (B), and after the offset of the test noise intensity (C). In the increase procedure the intensity of the background noise was changed for 30 secs. from 60 db to 80 db, in the decrease procedure the intensity of the background noise was changed from 60 db to 40 db, also for 30 secs

In the "decrease" procedure the first change of the noise level from 60 db to 40 db resulted also in a decrease of the bar-pressing response rate ; however, this effect was smaller and statistically not significant (Wilcoxon test). Actually, in the few animals with a low level of the ongoing bar-pressing behavior, the application of the 40 db test stimulus increased (instead of decreased) the level of responding. The correlation between level of the on-going bar-pressing behavior and the depressing effect of the test noise intensities was observed under both testing procedures. The Spearman rank order correlation coefficient between A and A-B terms equals .87 ($p < .01$) for the increase procedure, and .60 ($p < .05$) for the decrease procedure. The correlation between A and $\frac{B}{A+B}$ ratios had a negative sign, but reached the $p = .05$ significance level only in the decrease procedure ($r_s = -.49$ for the increase procedure and $-.59$ for the decrease procedure).

The difference between the two testing procedures discovered by the analysis of variance was confirmed by the nonparametric Mann-Whitney test with experimental groups pooled over each procedure. The $\frac{B}{A+B}$ ratios calculated for the first test noise application differed at the $p < .02$ level (two-tailed test), with a stronger depressing effect of the 80 db test stimulus.

As seen from Fig. 2, in both testing procedures the response rates were decreased not only during, but also after the first application of the test noise intensity. This effect was significant in the increase procedure as estimated by the comparison of the number of bar-presses emitted before and after the 80 db noise application ($p < .05$, Wilcoxon test, two-tailed). Thus an orientation reaction was apparently produced by the offset as well as onset of the test stimuli.

The effect of the 2nd-4th test noise applications. The orientation reactions to the onset and the offset of the test noise intensities underwent very rapid habituation, and during the 2nd-4th test noise applications no effect on the response rate was observed (Table, Fig. 2). Differences between the experimental groups (effect of lesions) was not discovered even when the analysis of variance was done for each test noise application independently.

The effect of the test noise applications during the second testing day. It is seen from Fig. 2 that the 80 db stimulus produces during the second testing day quite different changes of the rate of the bar-pressing response to those observed at the first application. During the second testing session applications of the 80 db noise intensity resulted in an increase of the response rate, and this effect for the 6th-8th test applications was significant ($p < .01$, Wilcoxon test, two tailed). For the 5th application of the 80 db test stimulus the increase of the response rate does not reach significance because two rats with lesions of the frontal pole showed a marked decrease of the response rate. Note that the variance related to the groups differences was greater during the 5th test intensities application than during other applications (Table).

The 40 db test stimulus in any application had the tendency to decrease the rate of responding ; however, only in the 6th-8th applications the numbers of responses emitted before and during test noise intensity differed significantly ($p<.01$, Wilcoxon test, two tailed). One has the impression that depressing properties of the 40 db noise intensity on the bar-pressing rate increased over consecutive applications.

During the second testing day no effect of the test stimuli offsets was observed and the rates of responses before and after the test noise intensities were nearly the same.

DISCUSSION

In our experiment the first change of the background noise intensity produces decrease of the bar-pressing response rate. Then this pattern of responding produced by the orientation reaction, was changed to another pattern, in which the bar-pressing rate directly corresponds to the noise intensity level. In previous studies reporting the effect of an acoustic stimulus on on-going bar-pressing behavior, usually a single $\frac{B}{A+B}$ ratio was computed for the whole Pretest Day and the median walues for each experimental group were presented (e.g. Kamin and Brimer 1963). These data were interpreted as evidence that the CS had no systematic effect on the bar-pressing response rate until the CS was related to the reinforcing stimulus. Computation of the single daily ratio obscures two different effects of the change of the background noise intensity level on the on-going bar-pressing behavior.

The phenomena described here show a striking similarity to those described for other sensory modalities by Sokolov (1957) and discussed further by Berlyne (1960). According to Sokolov, the application of an external stimulus produces two basic kinds of changes in the activity of sense organs and the central nervous system, which be calls orientation and adaptation reactions. The orientation reactions observed are neither specific to the modality of the external stimulus nor to its onset or offset. Orientation reactions undergo a rapid habituation and are followed by adaptation reactions which are specific for the sensory modality of the external stimulus. Adaptation reactions produced by the onset of the stimulus have an opposite sign to those produced by the offset of the stimulus, and they do not undergo extinction or habituation (Sokolov 1957).

In our experiment it was not the orientation reaction itself, but rather its effect on the on-going bar-pressing response which was measured.

Although the orientation reaction is nonspecific with regard to the intensity of the stimulus, in our experiment the effect of the orientation response on the bar-pressing rate was stronger under the increase procedure (80 db test noise intensity) than under the decrease procedure (40 db test noise intensity). A similar difference between the two procedures was also observed with other intensities of the test stimuli (Zieliński 1965b). It is interesting to note that with the same amount of change (measured in decibels) from the background noise intensity, stimuli presented under an increase procedure in CER technique results in more rapid conditioning and better performance than those presented under a decrease procedure (Kamin 1963, Hilton 1964, Zieliński 1965b).

The direct relation between the noise intensity and the bar-pressing response rate observed during the second testing day corresponds to the adaptation reaction by Sokolov, and may be due to the "nonspecific activating role" of the amount of external stimulation, as postulated by the arousal theory. However, the white noise in this experiment was a stable element of the experimental situation, to which the bar-pressing behavior was conditioned. Thus, the effect of the changes of the white noise intensity during the second testing day may also be covered by the law of strength of the CS (Pavlov 1927, Konorski 1948), or stimulus intensity dynamism theory (Hull 1949).

It was expected that frontal lesions will have different effect depending on the stage of testing. On the basis of theories explaining the frontal animals' deficit in terms of an "inertia of the excitatory process" (Konorski 1957), "disinhibition of perseverative errors" (Ławicka and Konorski 1959), "difficulty in overcoming strong response tendencies" (Rosvold and Mishkin 1961), or "perseveration of central sets" (Mishkin 1964), a smaller disruptive effect of the first test noise application on the bar-pressing response in frontal than in normal Ss may be expected. Although perseveration of responses in rats after frontal lesions has been reported (Morgan and Wood 1943, Bourke 1954, Maher 1955, Łukaszewska 1964), no increase of the perseveration of the bar-pressing response in frontal rats tested in the present experiment was noticed and the first test noise application had similar disruptive effect in normal and operated Ss.

Slow habituation of the disruptive effect of the novel stimuli on the on-going bar-pressing behavior after frontal lesions has been reported in monkeys (Butter 1964). An effect of frontal cortex ablation on the process of habituation was also found in rats (Glaser and Griffin 1962). Such an effect was not observed in rats tested in the present experiment. However, it should be noted that in Butter's experiment the novel stimulus consisted in change of the 60 db white noise to a tape recording of repetitive drum beats (70 db above threshold) and flashing red and green light instead of normal white illumination. This compound stimulus resulted in a very pronounced decrement in rate of bar pressing (about 20 per cent of the normal rate). In our experiment the only aspect of the external stimulation which evoked the orientation response was the change of white noise intensity. The orientation response had a rather weak effect on the bar-pressing behavior (response rate dropped no more than to 50 per cent) and habituation was rapid in all Ss.

Frontal lesions may effect also the correspondence between the bar-pressing rate and the white noise intensity observed during the second testing day. It was suggested that the frontal cortex exerts an important regulating influence on brain stem mechanisms and thus, on the sensory input (Livingston 1957), and the hyperreactivity exhibited by prefrontal-lobectomized animals presumably reflects the removal of this regulating influences (Isaac and DeVito 1958). However, in the present experiment the relation between the bar-pressing rate and white noise intensity was not disturbed by frontal lesions.

SUMMARY

An experiment was performed on 8 normal rats, 8 rats with lesions in the frontal pole of the cortex (anterior part of Krieg's area 10), and on 8 rats with lesions in the motor cortex (posterior part of Krieg's area 10 and area 6). After acquisition of a stable on-going bar-pressing response for food, the background white noise of 60 db intensity was changed either to 80 db or to the 40 db eight times for 30 secs. Half of the Ss from any experimental group were tested under the increase procedure, and others — under the decrease procedure.

1. The first change of the background noise resulted in a decrease of the bar-pressing response rate, the 80 db test intensity having a stronger effect than the 40 db test intensity. This effect of the orientation response was observed both to the onset and to the offset of the test noise intensities.

2. This effect became quickly habituated, and no changes of the bar-pressing response rate were observed during the 2th-4th applications of the test noise intensities.

3. During the next applications, a direct correspondence between the noise intensity and the bar-pressing response rate was observed: the 80 db test noise intensity produced an increase while the 40 db noise produced a decrease in the bar-pressing response rate.

4. No significant effect of the lesions in either the frontal or a motor part of the cortex was found on either the effect of the orientation res-

ponse, its habituation, or on the relation between the bar-pressing response rate and the noise intensity.

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EXPERIMENTAL 'PETIT MAL' EPILEPSY PRODUCED WITH CHLORAMBUCIL[1]

Allan F. MIRSKY, Susana BLOCH-ROJAS[2] and William F. McNARY

Division of Psychiatry, Department of Anatomy, Boston University Medical Center, Boston, Massachusetts, U.S.A.

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The production of experimental epilepsy has long been of interest to students of the nervous system. Convulsive agents such as acetylcholine (Ajmone Marsan and Fuortes 1949), pentylenetetrazol (Bircher et al. 1962), penicillin (Ajmone Marsan 1963), alumina cream (Kopeloff et al. 1950) and tungstic acid (Blum and Liban 1960) have been used to study the origin, mechanisms and propagation of seizure activity. In addition, however, such agents have been used in neuropsychological experiments (Stamm and Pribram 1960, 1961) to investigate the behavioral concomitants of epileptic discharges. For the most part these studies have been concerned with experimental focal epileptic disorders, and relatively little success has been achieved in producing an experimental analog of a "nonfocal" disorder such as petit mal epilepsy. Aside from the studies of Jasper and associates (Jasper and Droogleever-Fortuyn 1947, Hunter and Jasper 1949, Pollen, Perot and Reid 1963) in which low frequency electrical stimulation of midline thalamic structures was employed, chemical and pharmacological methods have been infrequently used in the production of experimental petit mal epilepsy. An exception is the study of Guer-

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[1] Some of these results were presented at the Eastern EEG Society in March 1964. This work was supported by NIH grant K3-MH-14,915, NSF grant G-21382, grant 61-241 from the Foundations Fund for Research in Psychiatry, and by the NIH General Research Support funds of the Boston University School of Medicine. Chlorambucil was supplied by the Burroughs-Wellcome Co., Tuckahoe, N.Y.

[2] Prof. Rojas was on leave from the Institute of Physiology of the University of Chile, Santiago, Chile.

rero-Figueroa et al. (1963) in which subcortical implantation of crystalline alumina powder in cats produced EEG patterns suggestive of the slow-wave discharges of petit mal. Recently, however, chlorambucil (p-(N,N-dichlorethyl) amino-phenyl-butyric acid), a nitrogen-mustard derivative, has been reported by Pradhan and Ajmone Marsan (1963) to produce EEG changes in cats and rabbits virtually identical to the bilaterally synchronous and symmetrical spike-and-wave patterns of petit mal epilepsy. These effects were produced by lethal doses of the drug administered to cerveau isolé, flaxedilized or anesthetized preparations.

The question arises as to whether or not this drug is capable of producing similar EEG patterns in the monkey, and further, whether or not the effects can be produced by non-lethal doses in chronic preparations. The latter would provide a means of studying the behavioral accompaniments of the chlorambucil-induced EEG patterns. Such a model disease state might have wide usefulness in physiological and behavioral investigations of petit mal epilepsy and would thus supplement the information provided by the electrical stimulation studies.

MATERIALS AND METHODS

Subjects. Nine adolescent female Macaca mulatta monkeys were used, five in investigating the acute effects of the drug and four in studying the chronic effects.

Acute effects of the drug. The animals were anesthetized with 40 mg/kg of sodium pentobarbital which was supplemented as needed in 30 mg amounts. Electrodes for recording cortical and subcortical EEG were located stereotaxically by means of a Kopf instrument. The cortical electrodes, which recorded activity from the dura mater over frontal, central and occipital areas bilaterally, consisted of small (2—3 mm) coils of stainless steel wire or of stainless steel screws of 4 mm. diam. The concentric bipolar depth electrodes were 22 ga. stainless steel hypodermic tubing which contained a teflon-coated .0104 in. diam. stainless steel wire insulated except for the tip. The depth recording was between the 1—2 mm. uninsulated tips of the wire and the tubing which were separated by 1—2 mm. distance. Recordings were made (Grass Model III EEG machine) from such areas as midline thalamus, midbrain reticular formation, hippocampus, fornix, medial and lateral geniculate, inferior colliculus, internal capsule and caudate nucleus. Chlorambucil was prepared for intravenous administration immediately before injection by dissolving it in 1—2 cc. of absolute alcohol and then diluting it with water to a total volume of 5 cc. Heparin was used to keep the cannula patent. The usual dose schedule involved an initial injection of 10 or 20 mg. This was repeated at 30 min. intervals until the convulsive effect was observed.

At the conclusion of the experiment, the animals were perfused percardially with saline and 10% formalin. The block of brain tissue containing the electrode tracks was frozen and sectioned at 40μ for histological verification of the placements. The sections were stained with Sudan black B.

Chronic effects of the drug. All chronic animals were trained in the performance of a rapidly and continuously presented successive color-discrimination task designed to elicit sustained attentive behavior. A similar task, the Continuous Performance Test or C.P.T., has been used extensively to study attention in man (Mirsky and Kornetsky 1964). In the monkey version of the C.P.T. the animals were required to press a response lever for a red light but not for a green or blue light. The stimuli were presented as a 2.6 cm. diam. circular patch of color on a black background. Stimuli appeared for 1 sec. every 2—3 sec., and the animal had 0.75 to 1.0 sec. in which to respond. A test consisted of the presentation of 100 stimuli, of which 25—40% were "positive" (red); the test duration was approximately 5 min. The apparatus for presenting and controlling stimuli was constructed of standard operant-conditioning type modular units. Two animals (L and F) were trained to perform the discrimination to avoid an electric shock delivered through a belt worn about the abdomen; both failure to press for red within the allowed time and pressing for green and blue were punished. Two other animals (J and M), maintained on a chronic water deprivation schedule, were trained to perform a similar task for the reward of a 0.2 cc. sip of water; one sip was delivered through a tube near the animal's mouth for every four lever presses to the red stimulus (i.e., a fixed ratio schedule of 1:4). A lever-press to a negative stimulus resulted in the presentation of 5 more negative stimuli and thus delayed the opportunity to receive a sip of water. The animals were tested in primate restraining chairs; at other times, they were housed in standard primate cages.

After completion of training, the animals were prepared surgically in the same fashion as the acute animals except that sterile technique was employed, all electrodes were wired to a miniature plug (Amphenol type 126—173) on the occiput, and the entire array covered with dental acrylic. The skin was closed in anatomical layers over the plastic. During the testing from this point on, it was possible to record EEG and behavior on the attention test simultaneously. Two channels of a Grass Model 7 polygraph were used to record stimuli, responses and reinforcements; 5 or 6 EEG channels were recorded concurrently. (See Figs. 4, 5 and 6). The brain areas surveyed, and the histological procedures, were similar to those of the acute experiments.

After several weeks had been allowed for recovery, the animals were retested on their "attention" tasks. When the preoperative level was reattained (usually within one or two sessions) chlorambucil treatment was started. The drug was prepared as described in the acute study and administered intraperitoneally once daily at doses of 3.0 mg./kg. for periods of 3 to 7 days. Drug administration was stopped when overt tonic-clonic convulsions were observed. Animals were tested daily prior to and at 1/2 hr. and 1 hr. intervals post administration. Occasionally, additional post-administration drug tests were given.

RESULTS

Acute study. Within 20 min. of injection of an effective dose (18 mg./kg. or more) multiple spikes appeared with increasing frequency in all EEG leads. This was followed by periods in which regular and rhythmic patterns suggestive of the spike-and-wave activity of petit mal were recorded and was almost invariably accompanied by tonic-clonic convulsive motor activity. Flattening of the record in all leads was regularly observed after this. This sequence was repeated a number of times until the death of the animal (within 2—3 hrs). Fig. 1 illustrates spike-and-wave-like patterns observed in two of the acute preparations. The discharges were bilaterally symmetrical and synchronous across the cortical leads and tended to occur simultaneously in the cortical and depth derivations. Although the frequency of the repetitive spike-wave patterns was usually between 3—4 cycles/sec., it could range from 2—7 cycles/sec. These observations are quite similar to those of Pradhan and Ajmone Marsan with the exception, possibly, that no subcortical discharges were observed independently of or antecedent to cortical discharges.

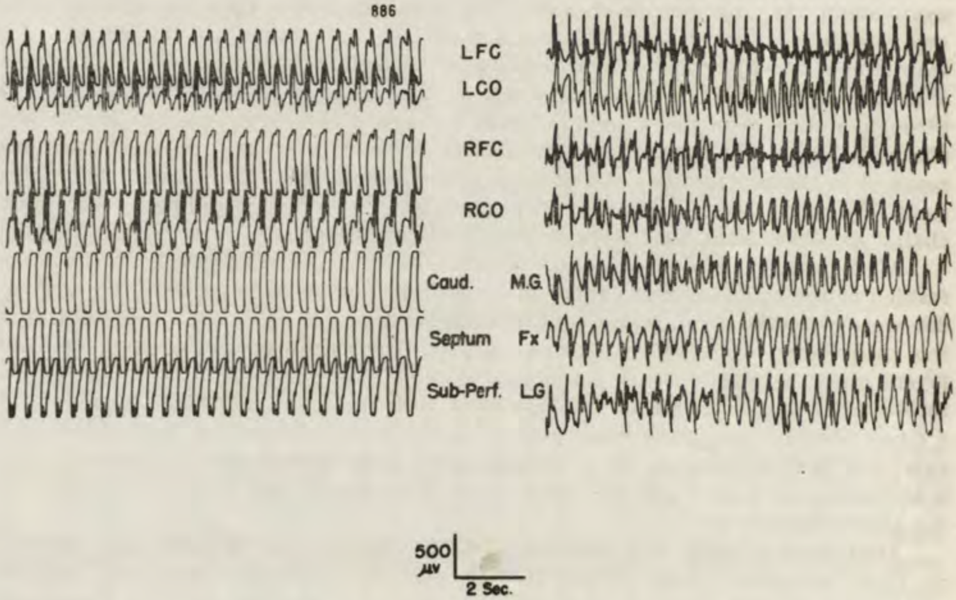

Fig. 1. Spike-and-wave activity seen following administration of 18 mg/kg (or more) of chlorambucil in two acute monkey preparations. The abbreviations used in this and subsequent figures are as follows: LFC = left frontal to left central cortex; LCO = left central to left occipital cortex; LP = left parietal cortex; LO = left occipital cortex; LF = left frontal cortex; LC = left central cortex; Cz. = central midline cortex. Similar abbreviations were used to designate the right cortical placements. Caud. = caudate nucleus; Corp. Call. = corpus callosum; Sub-Perf. = = sustantia perforata; M.G. = medial geniculate; Fx = fornix; Inf. Coll. = inferior colliculus; Int. Caps. = internal capsule; L.G. = lateral geniculate; Midbr. Tegm. = = tegmentum of midbrain; N. Reun. = nucleus reuniens; Hippo. = hippocampus; Pretect. = pretectal region. All cortical tracings used a "bipolar" derivation; some "unipolar" recordings were made against an indifferent or ground electrode which consisted of a screw anchored to the skull. Note the bilateral symmetry of the discharges from the cortical placements and the synchrony of the discharges from all placements

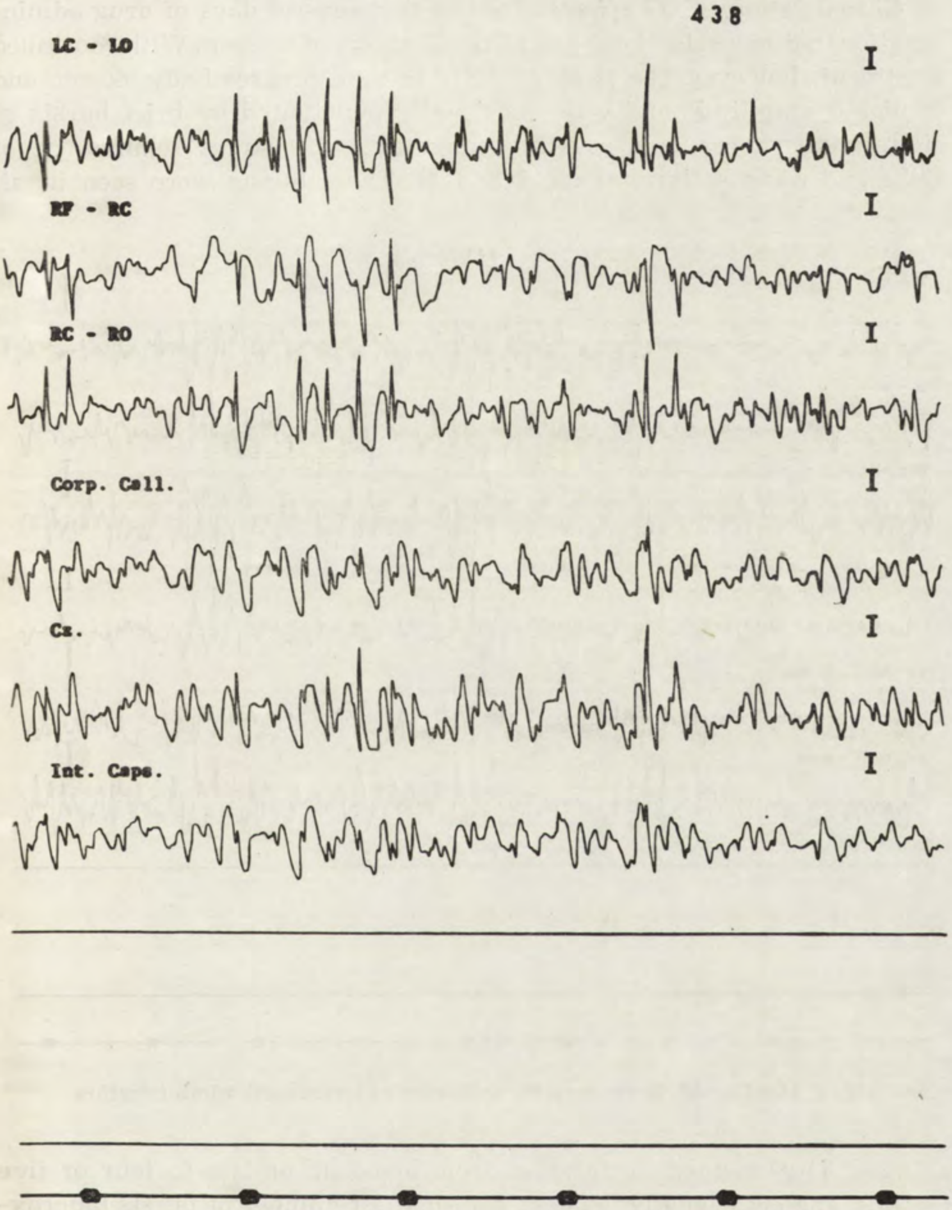

Fig. 2. Monkey J. Burst activity seen following several days of chlorambucil administration. Bottom channel shows one-second intervals; 100 µV calibration signal is shown at right above each channel. Time and calibration signals are also depicted in this manner in Figs. 3—6

Chronic study. EEG effects. For the first several days of drug administration, neither behavioral nor EEG effects could be seen. With continued treatment, however, the baseline EEG became progressively slower and of higher amplitude and was occasionally punctuated by brief bursts of bilaterally synchronous, usually symmetrical discharges reminiscent of spike-and-wave activity (Figs. 2 and 3). These bursts were seen in all animals. They ranged in duration from a second or less to four or five seconds, and occasionally, longer. The smallest number of bursts (approximately 20) were seen in monkey L; in monkey M there were approximately 80, whereas for F and J there were well in excess of 300 during the drug and immediate postdrug periods. The activity was invariably present simultaneously in all leads, cortical and subcortical. All animals were observed to have one or more tonic-clonic convulsions during this period (i.e., days 3—7 on drug); however, the burst activity was seen both before

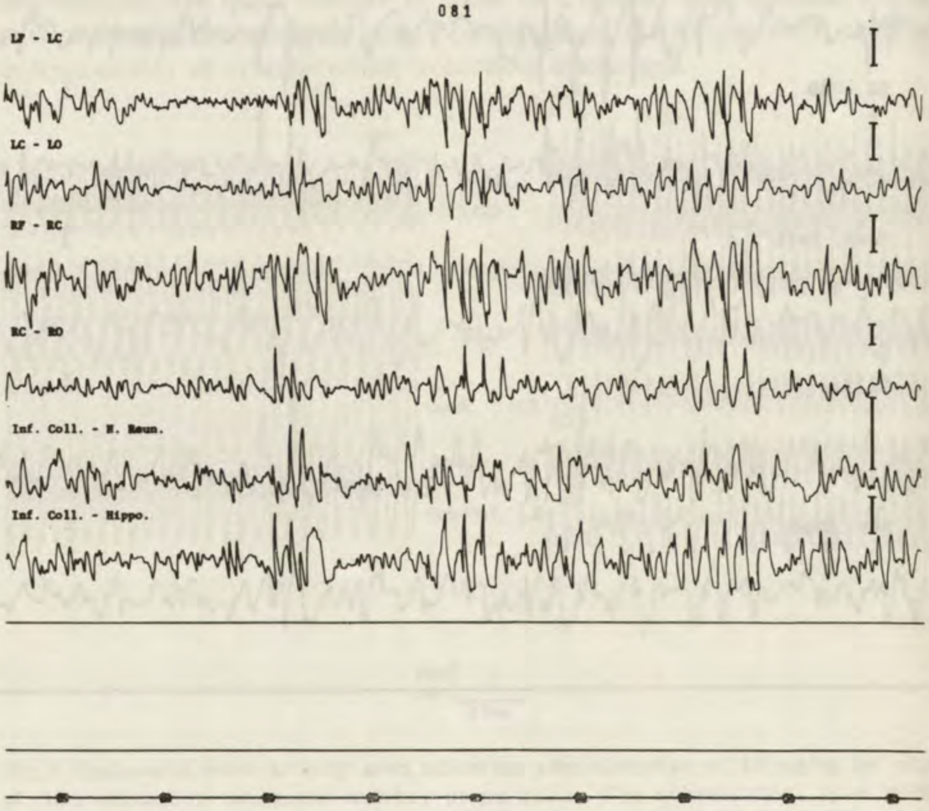

Fig. 3. Monkey M. Burst activity following chlorambucil administration

and after the periods when seizures were observed, and it tended to persist for several days after the drug was stopped.

Behavioral effects. During the period of maximum EEG change, the test behavior of all animals was markedly impaired. Some of the animals appeared to be in an odd stuporous state: their eyes were open, and they responded to touch, to sounds, or to the sight of the experimenter, but they were unable to execute the well-practiced test responses satisfactorily. Concequently, there was a great increase in omission errors during the drug period. One animal (monkey J) exhibited severe motor effects characterized by generalized tremor, jerky movements and weakness. This effect disappeared shortly after the drung was stopped.

Table I

Mean C. P. T. Scores (% Correct Responses to Positive Stimulus) During Chronic Chlorambucil Experiment[1]

		Mean[2]	Range of Scores	
Predrug	1	84	36[3] — 100	
	2	85	57 — 97	
	3	89	65 — 100	
Drug	1	82	66 — 97	
2nd from	last	39[4]	17 — 79	Period of maximum EEG change
	last	42[5]	24 — 56	
Postdrug	1	41[4]	7 — 69	
	2	60	15 — 89	
	3	94	90 — 98	← Bursts no longer appear
	4	90	79 — 100	
	5	85	68 — 97	

[1] The test in the predrug period were all obtained postoperatively and within one to three weeks prior to chlorambucil administration. The drug period lasted between three and nine days; all postdrug tests were conducted within seven days of the last drug administration.

[2] Based on N = 4.

[3] Each score is itself the mean of 3 tests.

[4] Differs from Predrug 3 at $p < .05$ (t test).

[5] Differs from Predrug 3 at $p < .01$ (t test).

The behavioral deficit was seen to carry over from one day to the next, so that it was noted even on the preadministration tests (i.e., roughly 20—24 hours after the previous injection). The effect was similar in the shock and water animals even though the beseline level of performance in the water animals tended to be lower than that of the shock animals.

The predrug, drug and postdrug scores are summarized in Table I. Each of these scores is based on 12 observations: 4 animals X 3 tests per day (one test preceding and two following drug administration). On pre- and postdrug days, the three tests were spaced at intervals similar to those used during drug days. As seen in the Table, there was a significant drop in performance in the last two drug days, and in the first postdrug day. After this time, the performance returned rapidly to the predrug

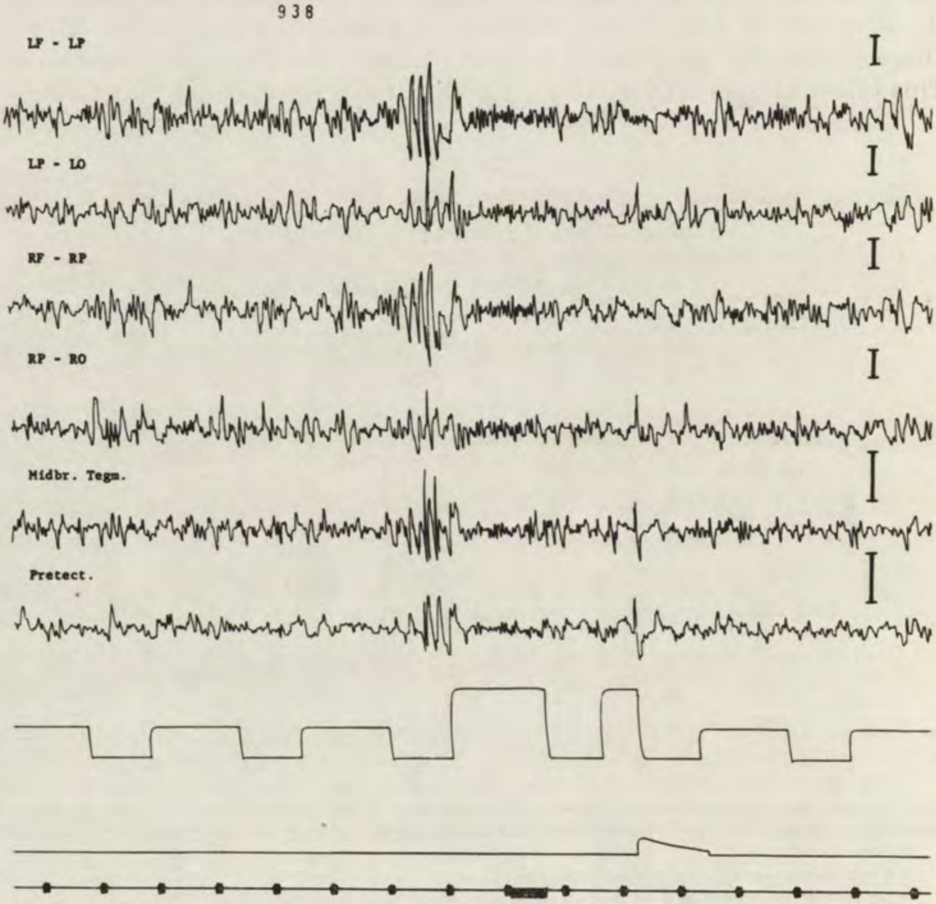

Fig. 4. Monkey F. Channel 7 represents stimuli shown to animal: low level deflection is negative signal (green or blue light); higher deflection is positive signal (red light). Bar press occurrence and duration are shown below this (channel 8) and reinforcements (shock for omission errors) are superimposed on time signal channel. In this sequence, the animal failed to press for the first positive signal and received a shock; she pressed quickly for the second positive signal and avoided a shock. The bar press terminated the positive signal. The first positive signal was preceded and partly accompanied in time by a spike-and-wave burst in all EEG channels

condition. Burst activity disappeared at about this time, but the EEG background frequency and amplitude did not revert completely to the normal state for approximately two weeks.

Specific relation between EEG and behavioral effects. The question arises as to whether or not omission errors and the bursts of spike-and-wave-like activity occurred coincidentally in time. The existence of such

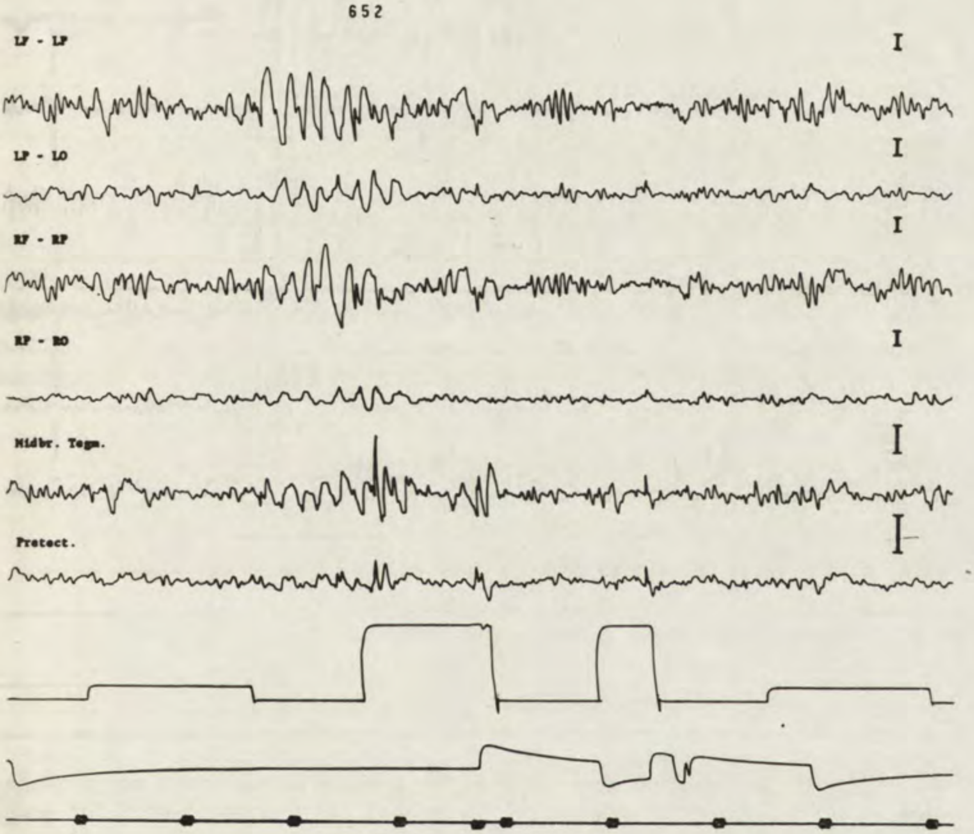

Fig. 5. Monkey F. The sequence of behavior and EEG events in almost identical to that shown in Fig. 4, except that the animal pressed the bar to the first positive signal after shock had begun (escape response). Note brief shock on time signal channel. She pressed rapidly to the second positive signal and then immediately afterwards once again

coincidences would strengthen the case for the similarity between the chlorambucil-induced state and the naturally-occurring petit mal; it is wellknown (e.g., Mirsky and Van Buren 1965) that momentary lapses in performance may accompany spike-and-wave bursts in man. There were in fact numerous instances of this phenomenon during the study (Figs. 4, 5 and 6). Table II summarizes for all animals each instance in which a burst and a correct stimulus occurred simultaneously. For the purposes of this analysis, extra tests were run in addition to those at 1/2 hour and 1 hour postdrug. No test was included in this analysis in which

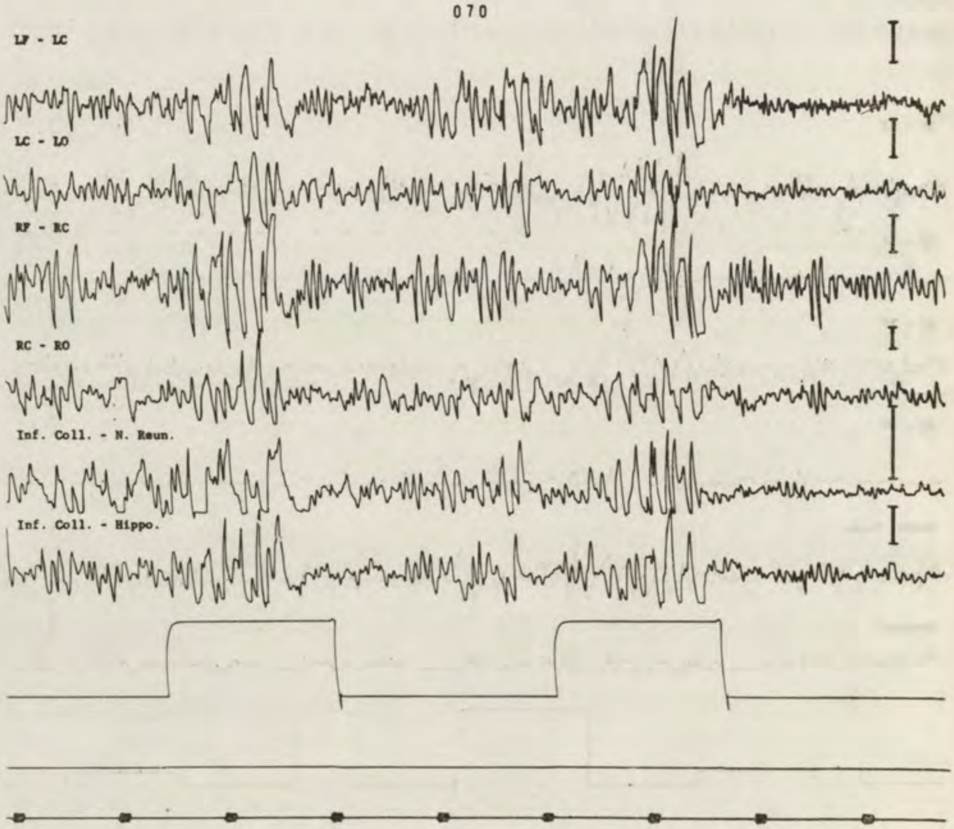

Fig. 6. Monkey M. Omission of response to two positive signals which are accompanied by spike-and-wave bursts. Since this animal was trained to work for water reward, no positive reinforcements were delivered in this period. They would have appeared on the time signal channel, as shown in Figs. 4 and 5 for shock

the animal did not make at least one response; 10% of the drug period tests were eliminated for this reason. Included are 10 tests from the postdrug period in which spike-and-wave-like bursts continued to appear.

For the three animals in which it was possible to make this analysis, it is clear that the percentage of correct responses was much lower in the presence of bursts than in their absence. For the group as a whole the percentage of correct responses during bursts was 13.6%; in their absence the percentage was 44.6%. This difference was highly significant

Table II

Summary of Performance on All Tests Including One or More Bursts Coinciding With a Correct Stimulus; Excluding Tests With No Responses

		MONKEY				
		L	F	J	M	TOTAL
Percent correct Responses	Burst	—[1]	16.1	17.1	0	13.6
	Nonburst	—	72.4	38.4	14.8	44.6
N (correct stimuli)		—	256	248	188	692
p (χ^2)		—	$<.0005$	$<.01$	$<.15$	$<.0005$

[1] No burst occurred during a test in which L made any responses.

($p<.0005$). Clearly, however, the animals exhibit significant behavioral impairment even in the absence of burst activity. In Table III, which summarizes performance on all tests excluding bursts, it is seen that each animal individually, and the group collectively, is markedly impaired during the drug administration period.

Table III

Summary of Performance on All Tests Excluding Bursts, Pre vs. During Drug

		MONKEY				
		L	F	J	M	TOTAL[2]
Percent Correct Responses	Predrug[1]	97.3	96.0	82.8	66.8	84.6
	Drug	74.1	77.7	66.0	46.7	64.5
N (correct stimuli)		513	862	574	921	2870

[1] Predrug — Drug differences are significant (χ^2) at $p < .0005$ throughout.

[2] A discrepancy can be noted between the nonburst performance during drug in Table III and the nonburst performance in Table II (e.g., 64.5% vs 44.6% for Total). This is due to the fact that Table III summarizes all drug tests including the early ones in which performance was unimpaired, whereas Table II includes only the later tests in which bursts were occurring.

Additional drug tests. Well after complete recovery from the effects of chlorambucil had been achieved, other centrally-acting drugs (chlorpromazine, secobarbital, d-amphetamine) and another nitrogen mustard derivative reported by Jones et al. (1958) to have marked convulsant side effects (chloroquine mustard hydrochloride) were administered to one or more of the animals in amounts sufficient to produce behavioral impairment. Although changes in EEG frequency and/or amplitude were often observed, the specific spike-and-wave-like effects of chlorambucil were never seen.

DISCUSSION

The present results confirm the earlier studies of Pradhan and Ajmone Marsan (1963) with cats and rabbits and extend them in a significant way. Chlorambucil is capable of producing spike-and-wave--like EEG effects in the chronic monkey preparation which have behavioral accompaniments similar to those seen in human petit mal epilepsy. Perhaps the most noticeable difference between the spike-wave forms of petit mal as seen in man and those induced by chlorambucil lies in the frequency of the repetitive pattern. In man, the pattern repeats usually between the frequency of 3—4 cycles/sec.; in the monkey, the range observed was more like 2—7, with the preponderance of bursts occurring at the higher frequency. Although it is true that chlorambucil-induced bursts longer than 4—5 sec. in duration were rare, many human patients with petit mal have bursts which are predominantly of short duration (Mirsky and Van Buren 1965).

In addition to the specific association between the spike-wave patterns and the impaired performance on the attention task, there was evidence that the animals are more generally impaired (as compared with the predrug measures) even in the absence of the spike-wave patterns (see Table III). This raises the question as to whether the drug was producing simply a general toxic effect which was to some extent independent of spike-and-wave EEG changes. As noted in Table I, however, the significant behavioral effect is more or less coincident in time with the period of maximum EEG change (i.e., spike-and-wave patterns) and is reversed after the bursts no longer appear. Therefore, any toxic effect which is reflected in behavior must be closely related to the central effect which gives rise to the spike-wave patterns in the EEG. Mirsky and Van Buren (1965) have noted a similar relationship between the performance errors and electrographic signs in human petit mal; i.e., the impaired attention of petit mal is not explained in terms of the spike-wave EEG changes; they are related but independent symptoms of the disease. Other drugs can produce behavioral deficit; the significance of chlorambucil is that it may produce both behavioral *and* EEG changes of the petit-mal type.

The ultimate value of this drug-induced model disease will depend on the extent to which the mechanism and/or locus of its action resembles that which underlies the human disorder. Penfield and Jasper (1954) have argued that there is a subcortical pacemaker in this disease, located probably within the midline thalamic or upper brain stem structures that are included within the centrencephalic system. Moreover, in the absence of convincing evidence of structural subcortical pathology, they have suggested that the "lesion" might be fundamentally biochemical in nature. Although the previous workers (Pradhan and Ajmone Marsan 1963) found evidence that the chlorambucil-induced EEG discharges might originate subcortically and be propagated to cortical areas, there was little suggestion of this in the present study. The propagation may have been so rapid as to be undetectable with our technique; or, it may be that we did not survey the appropriate subcortical areas.

With respect to the hypothesis of biochemical changes in petit-mal, there is an extensive literature (Alexander and Stacey 1958) on the profound effects upon DNA synthesis produced by chlorambucil and other alkylating agents. These effects are reflected in anatomical changes in the rapidly-dividing cells of the lymphatic system, bone marrow and intestinal lining; although the convulsive liability of nitrogen-mustard drugs is well known, structural changes have not been described in the central nervous system. The existence of such changes is problematical, moreover, since mitosis or cell division is not generally regarded as taking place in the cells of the central nervous system of a mature animal. No gross alterations were detected in the brains of the animals used in the present study; however, our histological methods were designed only to locate electrode tracks. If there are central neural changes, however, they may be secondary to some systemic effect and are likely to be subtle (and transitory) in nature since the behavioral and electrographic effects of chlorambucil are reversible. Possibly, prolonged administration of chlorambucil might produce permanent effects, which would then be more likely to be acompanied by some obvious cellular alteration.

Studies of this sort may eventually shed light on the fundamental pathophysiological mechanism of petit mal epilepsy. In the meantime, the present results suggest that chlorambucil (and possibly other related compounds) may have wide usefulness in simulating both electrographic and behavioral effects of this disease.

SUMMARY

1. The behavioral and electrographic effects of acute and chronic administration of the nitrogen-mustard derivative, chlorambucil, were investigated in nine Macaca mulatta monkeys.

2. Acute administration of the drug in lethal doses (in excess of 18 mg./kg.) produced repetitive convulsions; these were accompanied by prolonged EEG bursts of spike-„and-wave activity resembling that seen in petit mal epilepsy.

3. Chronic daily administration of the drug in trained monkeys produced EEG burst patterns resembling the spike-and-wave discharges of

petit mal epilepsy; profound impairment on tests designed to measure sustained attentive behavior was also noted. Many instances were observed of the simultaneous occurrence of errors on the tests and bursts of epileptiform activity.

4. The similarity between the effects of the drug and the manifestation of petit mal epilepsy in man were noted; also discussed was the relationship between the known central changes produced by the drug and the presumed pathophysiology of petit mal epilepsy.

5. Chlorambucil (and possibly other related compounds) may provide a useful model for simulating and investigating the behavioral and EEG effects seen in petit mal epilepsy.

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CONTRIBUTION TO THE ETHOLOGY OF *LEPTOTHORAX ACERVORUM* (HYMENOPTERA: FORMICIDAE)

Jan DOBRZAŃSKI

Department of Biology, The Nencki Institute of Experimental Biology,
Warsaw 22, Poland

(*Received March 3, 1965*)

Little has been done in regard to the behavior and ethology of *L. acervorum*. A considerable part of the knowledge of this species we owe to Forel (1920) who, however, did not investigate the ethology of this species under natural conditions. Finding small working capabilities of all species of *Leptothorax*, Forel draws attention to the similarity of behavior of workers and female ants. A very interesting phenomenon, never met with in other ants, has been discovered by him during the investigation of the *L. acervorum's* intraspecific fights under artificial conditions: the defeated adversaries were seized, carried to a distance of a few centimeters and then, abandoned without being done any harm. Forel does not comment on this peculiar phenomenon.

It is commonly accepted (Koehler 1951, Bondroit 1918, Bernard 1951) that the colonies of this species are very few. In investigating the spacial distribution of *L. acervorum*, Begdon (1953) maintains that, in contradistinction to the opinions, predominating thus far, this is not a species, living only in the symbiosis with other ants. He considers the neighborhood of other species to be a matter of pure chance.

L. acervorum has also been pointed out as a host of social parasites. According to Adlerz (1896), Wheeler (1910) and Skwarra (1929), this species is a parasitifer of *Harpagoxenus sublevis* and, according to Kutter (1950) — also of *Doronomyrmex pacis*.

MATERIAL AND METHOD

The problem of a durable marking of ants, indispensable in ethological investigations, has not so far been solved in practice. The dye stays on a large ant (for instance, *Formica rufa*) for a few weeks and maximum for 2 months. On smaller species such as, *Tetramorium*, *Leptothorax* and species of *Lasius*, of small size, it is mostly a matter of a few hours and, less frequently, a few days. Apparently, a definite area that is necessary for the durable adherence of the dye.

It was necessary, therefore, to develop new methods of marking, more durable and suitable to small ants. The method of tying colored silk threads around the petiole, we applied, was good enough only in the case of certain *Lasius* species, while it was unsuitable to the smallest species. A double knot in which the thread must be tied is too large for *Leptothorax* or *Tetramorium*, distinctly hampering them. In addition, the fact that the ends of the thread, of necessity cut short, may, after some time, come untied and then, the loop slips off, is a general disadvantage of this method. Thus, this method is, for mediumsized ants (as, *Lasius* or *Myrmica*), undoubtedly better than the dye but this mark is seldom worn by the ants for a longer period than 6 to 7 weeks.

In search for a better method of marking small ants, we used very thin copper wires, the same as those of which the electric litz wires are twisted.

At first, a loop should be tied halfway the length of a few centimeter long wire and tightened around a needle whose shape allows one to adjust the size of the loop to the dimensions of the abdomen of a given ant. Holding the end of the wire in one hand, thus prepared loop should be slipped, through the abdomen, on the petiole of the ant, held with the other hand. Then, by gentle pulling both ends of the wire, the loop should be tightened to such an extent that the petiole might be loosely encircled and, at the same time, that the loop could not slip off over the abdomen. The ends of the wire should be cut off as short as possible by means of very thin high precision (ophthalmologic) scissors. Attention should be paid lest the limbs be cut off with which the ant tries to break free. It is commendable, therefore, to carry out this operation under a magnifying glass.

It should be emphasized that the smaller the diameter of the original loop, tightened around the needle, the lesser is the deformation of this loop when, in turn, tightened around the ant's body. The flattening of the ring, thus formed, is a negative phenomenon which may be avoided, at least to a certain extent, by preparing as small a loop as possible which, of course, is determined by an ant's abdomen circumference.

It is already after a few minutes that thus marked ants resume their normal activities. It has been shown by several weeks of field observations that they seek food like any other, unmarked individuals and the small copper ring does not encumber their movements, even when they are fighting their enemies.

The *Leptothorax acervorum* workers, marked in the manner, described above, have survived through the winter in the artificial breeding and, set free in the spring, they normally started seeking food, in the same way as unmarked ants. This is the first case, I know so far, of a mark which lasted through the winter until the next year. This method gives, therefore, the opportunity for ethological investigations, particularly in the field of the division of work.

The difficulties in distinguishing individual specimens make up a disadvantage of this method which, in part, may be avoided, at least in such not numerous species as Leptothorax which, in addition, have a rather not too extensive feeding ground, by observing — under the magnifying glass — the shape of their rings and, in particular, the shape of the cutout. However, it would be only the use of varicolored wires, made of different materials, that could be considered a perfect method.

OBSERVATIONS AND EXPERIMENTS

All field observations and experiments were carried out under natural conditions, that is, in a mixed forest with much light, penetrating through the tree crowns. The ant nests built in dry sticks, found in great numbers in this forest, were used for experiments.

1. Controlling the Feeding Ground

Experiment 1: Throwing over of the stick with the L. acervorum nest to a new place. Sometimes, such a phenomenon may occur in a quite natural way since the small (10 to 15 cm in length) stick, containing the nest, may be accidentally knocked by a man or an animal. In the case of this species, whose feeding ground radius seldom exceeds some scores of centimeters, such knocking the stick constitutes a complete change in the environment.

The behavior of ants in the new place is as follows. After a shock, caused by the fall of the stick, a few workers run out of the nest. Then, they return and, after 1 to 2 minutes; a few pairs of workers get out of the nest. In each pair, one ant follows the other, keeping so close that its antennae always touch the abdomen of the foregoer. Sometimes, the second ant walks away for a moment, exploring the ground in a place 2 to 4 cm distant. When the first ant does not feel the touch of its antennae on the abdomen, it stops instantly and waits for the return of its companion. The latter, returning, touches its foregoer with its antennae and the pair sets out again. Mostly, such a pair, after 10 to 15 minutes of the ground reconnaissance, returns in the same order to the nest. Sometimes. after a few minutes of such a team work, the ants part company with each other and each worker walks separately. I also happened to observe a female as the second ant in a pair.

Such running in single file was also observed in *Cardiocondyla emeryi* and *C. venustula* by Wilson (1959) who called this phenomenon "tandem running". According to Wilson, the aim of such "tandem running" is to lay a scent-trail towards the source of the food.

Since, in *Leptothorax acervorum,* I never succeeded in observing tandem running of pairs after they found the food or under any other normal conditions, I have a reason to believe that, in this species, the phenomenon described has a different biological character than that ascribed to it by Wilson. It may be assumed that this is a form of a joint exploration of a new area. Observations, collected in the course of the second experiment speak in favor of this assumption.

Experiment 2: Putting the stick with the L. acervorum nest on the previously explored feeding ground of another nest of the same species (hereafter called, "the nest of natives"). The stick, containing the transferred nest (reffered to as "the nest of intruders"), was broken in halves which we put near each other 20 cm from the native nest. After a moment, pairs started to leave the intruder nest. (Here, we draw the attention to the difference as compared with the previous experiment. Then, the pairs started to go out of the nest only when, after the stick was knocked, the fact was discovered by single workers of the nest being placed in a new area. In experiment 2, it was evidently the breaking of the stick that became a stimulus which induced the pairs to leave the nest).

The movements of intruders caused the appearance of single natives. Fights arose in several places and it was observed that the pairs were mostly fighting jointly which, in ants, is a rare phenomenon. After a few minutes, pairs of ants were also getting out of the native nest.

On the basis of these observations the previous statement may thus be supplemented: this is not only a new area, but also every new, so far unknown situation that are jointly recennoitered by the pairs.

Soon, several bitter battles were fought on the entire area of the feeding ground of the native nest and it were not only the pairs that fought jointly. When the *L. acervorum* worker met other ants fighting each other, at first, it palpated them and then, joined forces with its companion. In *Lasius fuliginosus, Formica rufa, F. sanguinea* and *Polyergus rufescens,* it may be often observed that, under similar circumstances, the worker seizes any of the fighting ants which, sometimes, happens to be its fellow ant from the same nest.

Although the experiments of this type were repeated many times and although we observed many battles, both on the first and on the next days of experiments we never noticed even a single dead or wounded ant. Each duel was terminated in the following manner: the defeated ant was seized, in any position, by its victorious adversary who carried it some scores of centimeters from his own nest and then, threw it over without doing any harm to it, which is in full conformity with Forel's observations. The fight of any two representatives of *Leptothorax* seems to consist exclusively in efforts to seize the adversary and to apply such a grip as to disable him to such an extent as to carry him perhaps outside the boundaries of the feeding ground of the conqueror's nest.

In one case, an intruder worker climbed the stick with the native nest and was jointly attacked by four natives. However, even in this instance of an absolute supremacy, no bloody issue of the battle was observed. After a brief struggle, one of the natives seized the intruder and carried him, uninjured, outside the territory of the nest.

This was a seesaw combat in which both the natives and the intruders happened to be defeated and carried out, sometimes, as far as to the distance of 1 m. or more. Some intruders, despite of being carried out to a completely unknown area, after a prolonged running about, returned to their nest and once more took part in the fight.

This carrying the adversary to a place outside ones own territory may be elucidated in the following way. In nature, it is a rather rare occurrence that the entire nest might at once appear in another nest's area. On the other hand, it happens frequently that a strange female or a few strange ants come to found a new nest. Persistent carrying such intruders to a place outside the territory of the native nest has probably the effect of the discouraged intruders giving up this territory and looking for some other area to found their new nest.

Thus, in my opinion, the biological importance of carrying intruders outside ones own territory consists in preventing from the foundation of a strange "competitive" nest on ones own territory.

It is easy to understand, therefore, why such a keen observer as Forel could not succeed in grasping the sense of such a behavior of the ants. His observations were carried out under artificial conditions and his formicary limited the area of the activity of ants which thus were unable to carry their adversaries outside the boundaries of their territory. This was precisely the reason why their behavior could not be logically explained.

In our experiment, not all the workers were engaged in combat. At the same time, in the intruder nest, all the property was carried from one broken part of the stick to the other. Other workers were plugging up a too wide an opening which was formed by breaking the stick.

Here, we may observe, therefore, the three simultaneous operations: the reconnaissance of the new area and the battle; transferring the progeniture from the damaged nest; the repair of the nest.

Thus, even the battle fought, under so unusual circumstances, against the unexpected enemy, did not involve all the inhabitants of the nest which indicates the division of work in *L. acervorum*. We have not studied this problem in a more profound manner but certain doubts arose if this division of work in this species is permanent. We noticed, for instance, a larva carrying worker which, after some time, got out of the nest as the second ant of a pair and reconnoitered the terrain which might testify against the permanent division of work.

During one of the experiments of such type, a marked worker from the intruder nest returned, after a brief reconnaissance of the ground, to its nest and started to carry the progeniture out of it. It carried the larvae in a direction opposite to that of the native nest and hid them in the moss

20 cm further. After some time, other ants started to follow its example and general carrying out of all the property from the stick to a hiding place in the moss was soon in progress.

We carried out an experiment to check if it was the damage we have done by breaking the stick, or the eagerness to leave the native nest the neighborhood of which was too troublesome that caused all this removal.

Experiment 3: Putting the stick with the intruder nest in the place where the progeniture, carried out of it, is hidden in the moss. At the first moment, the scared workers tried to hide among the forest litter but, after a few minutes, they noticed the stick and instantly started to bring to it once more the progeniture and the property. Since that moment, not a single case has been recorded of carrying the progeniture out of the stick[1].

One of the workers which previously carried the progeniture out of the stick and hid them in the moss and, at the moment when the stick was moved, was on its way towards it, circled about for quite a long time, looking for the stick in its previous place. We took it, together with a leaf on which it happened to sit at this moment, and put it on the stick with the nest in its new place. At once, it walked into the entrance opening and, afterwards, several times went out and came back to the nest, never getting down to the earth and never carrying out the progeniture.

These facts testify to an exceptionally efficient mutual communication capabilities of *L. acervorum*. In other species, for instance, in those of the *Formica*, much discrepancy was for a longer time observed, under similar circumstances, in the activities of particular worker ants. The latter case shows that it is indeed the mutual communication in *L. acervorum*. A worker ant was returning to its nest, not knowing that the stick was moved once more and that, in view of a new situation, the progeniture is once more brought inside the nest. It was only the meeting with its fellows in the nest, without any reconnaissance by this ant, that was quite enough to change its behavior.

It may well be that the communication is facilitated in this species by a small number of workers which take part in every operation (as a consequence of a small number of all individuals in a colony).

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[1] There was the following order of bringing once more the progeniture and the property to the stick: puppae, young and old workers, winged individuals, eggs and, finally, some unidentified small particles, probably, the food reserve. The workers and winged individuals were carried in various positions but mostly they were seized halfway their body length and carried in any posture, sometimes, even with their heads downwards.

2. Problem of Feeding

Forel maintains that *L. acervorum*, bred by him, ate only the honey and refused to eat insects he gave them. In our case, they also did not pay attention to adult insects but eagerly collected the larvae of flies and brought them to the nest.

During the field studies, however, we have never succeeded to observe this species attacking insects longer than 0.5 mm or their larvae. On the other hand, it was more than once that we observed the worker ants of this species as they carried so tiny *Apterygota* that, without the use of the magnifying glass, we could not recognize them to be insects. Thus, *L. acervorum* are predatory ants but, in contradistinction to *Tetramorium* which are also small, they usually do not attack any adversary larger than themselves.

In view of the existence of many species of small noxious insects which live in forests and are not paid any attention by larger species of predatory ants, *Leptothorax* may probably play a positive role in forest protection.

3. Interspecific Relations

In general, larger species of ants do not pay attention to *L. acervorum*. When, for instance, a worker ant of *Lasius fuliginosus* stepped on a worker of *L. acervorum* without paying any attention to it, the latter pretended to be dead (which is in conformity with Jakubisiak's observation, 1948) until the larger ant walked away. When, during the field trials, two *Lasius brunneus* workers approached the honey, which was just eaten by a female and a few workers of *L. acervorum*, the latter with drew at first. The *Lasius* ants were indifferent and did not pay any attention to them and then, *Leptothorax* returned to their food. It was only the female ant of *L. acervorum* that remained unperturbed by the appearance of *Lasius* and continued eating.

A source of food (honey) at which several very different species of ants are crowded represents a rather unnatural situation. In nature, under normal conditions, a food, interesting to the species of ants, so different in the manner of feeding and in their dimensions, is rather hard to come by. In my opinion, *L. acervorum* have nothing to do with larger species of ants and, therefore, I agree with Begdon's statement that the near neighborhood of the nests of *L. acervorum* and of larger species is a matter of pure chance. I think that their biocenosis is so different that *L. acervorum* simply does not disturb them and, hence, their indifference to this species. Since, in the forest it is difficult to find an area which would not already be controlled by any ant nest, *L. acervorum* frequently settles in the neighborhood of larger species, doing this on the basis of a mutual indifference.

CONCLUSIONS

1. Tandem running occurs in *L. acervorum* only under new, unknown circumstances and serves for a team reconnaissance of the area in the case of danger.

2. The purpose of carrying the defeated strange ants outside the feeding ground of the native nest is to prevent them from the foundation of the intruder nest in such an area.

3. An accurate mutual communication may be observed in *L. acervorum.*

4. *L. acervorum* feeds on the smallest forest insects, mostly on *Apterygota.* In this connection, the question of a possible usefulness of this fairly widespread species, is an interesting problem which should be elucidated.

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RESEARCH ON ANIMAL BEHAVIOR AT THE NENCKI INSTITUTE OF EXPERIMENTAL BIOLOGY

J. A. CHMURZYŃSKI

Department of Biology, The Nencki Institute of Experimental Biology,
Warsaw 22, Poland

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The Department of General Biology of the Warsaw Scientific Society, established in 1918, was the first scientific institution in Warsaw at which the research on animal behavior was undertaken. It was not long before it was affiliated with the newly founded Marceli Nencki Institute of Experimental Biology of the Warsaw Scientific Society. After World War II, this Institute was taken over by the Polish Academy of Sciences. At present, in addition to the Department of Animal Psychology and Ethology, Jagiellonian University in Cracow, and the ethological group at the Institute of Ecology of the Polish Academy of Sciences in Warsaw, the Nencki Institute is the third Polish institution concerned with animal behavior research.

Thus the research on animal behavior, carried out at the Nencki Institute, was started at the very beginning of the Institute's existence, and is incessantly continued until the present-day time. It has always been closely related with other biological problems dealt with at the Institute, covering most of the fundamental ethological and zoopsychological problems.

During the prewar period, this research was conducted primarily at the Department of General Biology and, for a short time, also at the Department of Experimental Morphology.

Although, as we have mentioned above, the first of these departments was founded in 1918, the origins of our ethological traditions may be traced as early as almost sixty years ago since the work, taken up at this Department, reflected the scientific interests of its founder and director, Professor Romuald Minkiewicz whose first papers on the experimental ethology were published in 1906. The publications which appeared up to 1918, may, therefore, be treated as a sort of a "prehistory" of the ethological trends, predominating at the Department.

The work of Dr. Jan Dembowski, another eminent scientist of this Department, who, between 1927 and 1934, as a docent of the Warsaw University, was the head of the Department of Experimental Morphology of the Nencki Institute, constituted an additional source of the scientific inspiration in this field. As a matter of fact, Dembowski's interests were undoubtedly influenced by Minkiewicz's personality.

After World War II, the traditions of the ethological research have been continued at the Nencki Institute by the Department of Biology which inherited them from both prewar departments. This has been observed during the period of Professor Dembowski's direction, from the Institute's reëstablishment in 1947 up to 1960 (cf. Dembowski 1952, 1956a), as well as most recently, that is, since 1961, under the direction of Docent Stanisław Dryl. The ethological problems are frequently dealt with by the members of the sections on protozoology which investigate ciliates and makes up the fundamental research project of the Animal Behavior Research Group of the Department of Biology. It is noteworthy that the ethological investigations are given their physiological basis by the research work on the physiology of higher nervous activity, done at the Department of Neurophysiology.

The fact that at the Department of General Biology of the Nencki Institute the ethological and zoopsychological investigations have been treated as inseparable from other biological problems, has been emphatically illustrated by the following opinion, expressed probably by Minkiewicz and published in the Institute's report for the years 1920-1927[1] (pp. 28-29): "The analysis of the relation of the organism, as an entirety, to its environment and, therefore, the analysis of its (1) morphological (shape, color, dimensions, etc.), (2) physiological (movements, internal rhythms, metabolic, secretory, excretory, etc. processes) and (3) ethological or psychophysiological (instincts, habits, memory, spatial orientation, relations with other organisms such as, symbiosis, imitation, etc.) active adaptations is the general aim of investigations carried out at the Department". The program, to which Minkiewicz was devoted from the beginning of his scientific career, was fulfilled by the two prewar departments of the Institute, mentioned above, and, nowadays, it is continued by the Department of Biology.

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[1] "The Nencki Institute of the Warsaw Scientific Society, 1920—1927: Organization, Activities, Means." Warsaw, 1928, published by the Institute; pp. 76 (in Polish).

So far, the achievements of the Nencki Institute's workers are related to almost all basic problems of animal behavior, that is, (1) perception, (2) movement, (3) taxes, (4) learning and memory, (5) spatial orientation, (6) instincts and (7) habits. In view of the fact that currently the Animal Behavior Research Group consists only of three workers, holding the title of an adjunct (which corresponds roughly to Senior Research Associate), that is, Dr. Jerzy Chmurzyński (acting chief of the Group), Dr. Janina Dobrzańska and Dr. Jan Dobrzański, it is of course impossible to continue research on all subjects, previously studied. It was decided, therefore, that the problems elaborated should meet the following criteria: (1) they should take in the phenomena which are, biologically, interesting from the point of view of adaptation, traditional at the Institute and, at the same time, important to human economy; (2) they must not waste the previous achievements but, on the contrary, must explicitly refer to them; (3) they should fill out a gap in the research of the other Polish scientific institutions which deal with animal behavior and, on the other hand, avoid investigations of the already elaborated problems.

The following problems are currently investigated by the Animal Behavior Research Group: (1) color preference, (2) spatial orientation in flying *Hymenoptera-Aculeata*, (3) ethology of ants and (4) behavioral types ("temperaments") in various species and individual differences in behavior.

Over the past 45 years of research, the animals investigated were mostly invertebrates, such as, protozoans (ciliates) nemerteans (*Lineus ruber*), annelids (earthworms) many forms of arthropods as, crustaceans of the class *Malacostraca (Amphipoda, Decapoda)*, *Arachnoidea* (spiders), winged insects, *Pterygota* of different orders as, caddis flies, *Diptera*, *Hymenoptera* (*Mutillidae, Formicidae, Sphegidae, Psammocharidae*). Of vertebrates, fishes, amphibians (frogs), birds (chicken) and mammals (bats, albino rats) were studied. Thus, most attention has for a long time been paid to the animals in which the behavior patterns of instinct predominate. At present, such animals also are investigated. These are insects of the suborder *Hymenoptera-Aculeata*. For an increasingly progressing correlation of the basic research with the economic practice, considerable emphasis has been put on the Institute's traditional (for the last 30 years) subject of interest, that is, ants with all their unquestionable importance to the forestry (Jan Dobrzański and Janina Dobrzańska), as well as on bumblebees and honeybees, the allies of farmers and fruit farmers (Jerzy A. Chmurzyński). Theoretical aspects of the studies on the latter are also elaborated in another traditional (cf. Minkiewicz 1931c, d, 1932, 1933, 1934a) species, that is, the digger wasps. In addition to these insects, mostly elaborated during field studies, laboratory investigations are carried out on the blowfly, *Calliphora erythrocephala (Diptera, Cyclorrapha)* and on the Siamese fighting fish, *Betta splendens (Teleostei, Anabantidae).*

REVIEW OF RESEARCH TOPICS

(1) Perception. In many reports, the animals' perceptive capabilities appear a more general and complex biological phenomenon (for instance, in Minkiewicz's studies on the protective coloring or camouflage, depending on the character and color of the environment, of such decapod crustaceans as *Hippolyte varians* (*Caridea*) (Minkiewicz 1908b, c) and *Maia squinado* (*Brachyura, Brachygnata, Oxyrhyncha*) (Minkiewicz 1907d, 1909a) or of hermit crabs, *Eupagurus* (*Anomura*). Likewise, the information, concerning the color discrimination (Chmurzyński 1957, 1960), visual acuity (Chmurzyński 1960, 1964c) and pattern discrimination by digger wasps *Bembex rostrata* (*Aculeata, Sphegidae*) was collected in connection with the studies on the spatial orientation of these wasps (cf. Chmurzyński 1953, 1959, 1960, 1963, 1964a, b). In 1913, Minkiewicz dealt with the capability to discriminate colors in fish. A long series of studies by Minkiewicz (1927) and his associates (Salomea Biederman 1927, Salomea Razwiłowska 1927 and others) on the memory and the capability to develop conditioned reflexes in the frog, considerably contributed to the knowledge on the visual perception of these animals. Olga Krauze (1929) reported on pattern discrimination in the earthworm.

"Gestalt" in perception was a subject of Dembowski's (1932, 1935, 1946a, 1955b, 1959b) interest, while *Bembex's* capability of seeing and discriminating shapes, as well as the role of shapes in this wasp's spatial orientation was experimentally analyzed by Chmurzyński (1960, cf. 1964b). Dembowski (1959a) was also interested in the problem of the compensation of the sense organ function.

(2) *Movements.* The studies on what is called a peripheral reaction in *Paramecium caudatum* and on the angle of reflection, occurring together with it (Dembowski 1923a, cf. 1924, Grębecki et al. 1955, 1956, Krystyna Golińska 1963), that is, phenomena bordering on kineses and taxes (for instance, the klinotaxis), may serve as an interesting example of a behavioral and, at the same time, physiological analysis of an animal's movement.

Wiktoria Stanisława Dembowska's (1925a) studies on the movements of the internal antennae of the crab *Dromia vulgaris* (*Brachyura, Brachygnatha*) make up an instance of a research on the phenomena by which the internal excitation of an animal is manifested. A detailed anatomical analysis of the motor apparatus and of the movements of the limbs and the body of the same crab, trying to extricate from a loop, was taken up by Dembowski. Since that period Dembowski revealed his interest in the problem of the functional compensation of extremities which has particularly been reflected in his later research on the larva of caddis fly *Molanna angustata* (Dembowski 1933b, 1955a, 1957).

(3) *Taxes*. The problem of taxes was directly or indirectly dealt with in many papers. The simplest behavior patterns of *Paramecium caudatum* (*Ciliata, Holotricha*) were investigated in all their aspects (these investigations are continued by the protozoological group of the Biology Department) which was clearly the influence of Professor Dembowski's (1938, 1945) interests.

The galvanotaxis (a) has been dealt with by Dryl (1962, 1963a, c) and Grębecki (1963a, b, c, d, 1964). Dryl (1952, 1959a, b, 1961a, b, 1963b, cf. 1963d) has also been concerned with the chemotaxis and chemokinesis (b). The geotaxis (c) of the *Paramecium* was investigated by several authors (Dembowski 1928, 1929a, b, c, 1931a, b, Barbara Fedecka 1956, Zofia Śmiechowska-Martyna 1956). The geotaxis of *Drosophila melanogaster* was dealt with by Jadwiga Krieger-Kuźnicka (1955) and the phototaxis (d) of *Drosophilia melanogaster* by Aniela Krupińska (1956). This problem was also a subject of Grębecki's (1955) studies on the larva of the caddis fly *Molanna angustata*.

The chromotaxis (e), closely related with the phototaxis, was an object of a lively interest of Minkiewicz (1906a, b, 1907a, 1912) in his studies on the nemertean *Lineus ruber* and the crustaceans as, hermit crabs *Eupagurus* (*Decapoda, Anomura*) (Minkiewicz 1908d, e) and *Maia squinado* (*Decapoda Brachyura, Brachygnatha, Oxyrhyncha*) (Minkiewicz 1906a, b, 1907a) which, to a certain extent, were carried out in connection with the camouflage behavior (Minkiewicz 1907b, 1908b-e, cf. 1936). Minkiewicz showed that approaching the colored light may be a symptom of a taxis which is distinct from the photo-(=helio-) taxis and he introduced for it an excellent and up-to-mark term, "chromotaxis" (in original, "a chromotropism").

As a completion of these studies on the nature of the chromotaxis, Chmurzyński and Barbara Lipińska took up their work on the so-called hierarchy of colors (cf. Chmurzyński 1957) in the blowfly *Calliphora erythrocephala* (*Diptera*). The results, obtained thus far (Lipińska 1964), have, to a considerable extent, supported the hypothesis that the preference for the monochromatic lights by the blowfly is a *sui generis* phenomenon, that is, a chromotaxis which, according to Minkiewicz's terminology, is a purple-taxis and not an expression of a positive phototaxis, correlated with a different spectral sensibility of the visual system. The analysis of this extremely interesting problem will be continued. It should be stressed that the possibility to continue the research on marine organisms, started by Minkiewicz, would be very valuable.

The phenomenon of chromotaxis is closely associated with the hierarchy of colors, displayed by the animals and it frequently makes up its mechanism as is the case of the research, cited above. These papers are considered to be contributions to the analysis of the animals' psychobiological features. Various mechanisms of animal behavior display different conditioning either, in the case of group features, upon the ancient phylogeny, or, in the case of specific features, peculiar to particular species, upon the younger phylogeny, or finally, upon the living environment. In the latter case, the same psychobiological feature may be shared by different forms, unrelated to each other, but having common ecological requirements (for instance, *Myrmeleon and Vermileo*). At the same time, some of these features are identically manifested under different living conditions and some others are marked by a closer correlation with one or a few situations. "A hierarchy of impressions", so termed by the author (Chmurzyński, 1953, 1957), representing a series of impressions, preferred by an animal under given circumstances, and arranged in an evaluating manner is especially suitable to such an interesting analysis. It takes in "a hierarchy of senses (modalities)" and "a hierarchy of qualities" within the same analyzer because both elements, forming the hierarchy of impressions, are a permanent value characteristic of a given animal species and, in general, peculiar to a given biological situation and, therefore, as such, they may make up a specific ethological "measure" of a species. The hierarchy of colors is an instance of such a hierarchy of qualities. In his studies on *Bembex rostrata*, carried out as part of the investigations on the spatial orientation, Chmurzyński (1957) set up the hypothesis, in the field of the psychological evolution, that several colors, preferred by these insects, that is, the hierarchy of colors, are — even during these wasps' return to the nest — phylogenetically conditioned upon the color of flowers which make up their proper source of food, and he verified this hypothesis in a comparative manner. Thus, Wojtusiak's[2] theory on the correlation between the insects' sense of colors and the colors of flowers becomes extended and developed. It would be interesting to check if this phenomenon is also applicable to other insects. Maybe, with time,

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[2] R. J. Wojtusiak (1937), Color Discrimination in Animals and the Colors of Flowers. Kosmos B, 62, pp. 259—284 (in Polish).

an analysis will be effected, made by the chromotactic method in association with ecological observations.

The preference for shapes (f), studied by Chmurzyński (1953, 1960) also in *Bembex rostrata*, is related with the visual analyzer in much the same manner as the chromotaxis. Chmurzyński suggests that this preference in insects is an example of what he called "a marmarotaxis" or, moving in the direction of the source of a stimulus, giving the impression of a flashing light, like "a kinetotaxis" (g) which was investigated by Minkiewicz (1931a, b) in the dancing males of the fly *Fannia canicularis* and in the fish *Leucaspius delineatus* (the term "kinetotropism" was proposed by Minkiewicz).

(4) *Learning and Memory.* Learning and memory of animals make up another phenomenon, clearly adaptive in character, which is studied at the Institute. The following three types of learning have been investigated: (a) habituation — in the ciliate *Spirostomum ambiguum* (Kinastowski 1963a, b), in the common orb-webbed spider *Aranea diadema* (Rasza Szlep 1952) and in the Siamese fighting fish *Betta splendens* (Chmurzyński unpubl.); (b) imprinting — in chickens (Zieliński 1960a, b) and (c) conditioning — in the ciliates, *Stentor coeruleus, Spirostomum ambiguum* (Jadwiga Dąbrowska 1956) and *Paramecium caudatum* (Dembowski 1950, Jadwiga Dąbrowska 1956), and in the frog (Minkiewicz 1927, Salomea Biederman 1927, Salomea Razwiłowska 1927, Leonia Papierbuch 1928, Franciszka Gutglas 1936). The learning of the albino rat in the maze was investigated by Jadwiga Dąbrowska (1959a, b, c, 1960, 1961). The same method was applied by Ewa Horn (1963) who studied the earthworms' capability to perform a conditioned reflex.

The memory in *Paramecium caudatum* was studied by Dembowski (1922a, b) and the memory of fish was dealt with by Minkiewicz (1913).

(5) *Instinct.* The phenomenon of the food preference in *Paramecium caudatum,* investigated by Dembowski (1922a, b), which — in certain respect — is the simplest type of instinct, opens the next group of subjects, comprising the analysis of instinct in animals. Dembowski was particularly interested in the plasticity of the instinct to which he devoted a series of papers, describing the construction of cases by the larvae of caddis flies *Molanna angustata* (Dembowski 1923b, 1933a, b, 1937). As a matter of fact, Dembowski objected to the application of the term, an instinct, particularly so in his prewar papers (Dembowski 1937, 1946a). After World War II, his views became nearer the ideas, represented by the Lorenz-Tinbergen ethological school (Dembowski 1960, 1961). During that period, the construction of cases by the

Molanna larvae was dealt with by his associate, Rasza Szlep (1958b). Her papers on the common orb-webbed spider *Aranea diadema* (Rasza Szlep 1952, 1958a) were on related subjects since they also concerned the plasticity of the constructing instinct.

In the early stage of his studies, Minkiewicz was interested in the instinct and he published the results of his experimental work on the camouflage of *Maia squinado* (*Brachyura, Oxyrhyncha*) (Minkiewicz 1907b, c, d, 1908a, 1909a, 1910), as well as his conclusions and theoretical remarks on this subject (Minkiewicz 1905, 1907c, d, 1908a, 1909a).

(6) *Spatial Orientation.* The research on this problem has been carried out on *Aculeata*. Chmurzyński (1953, 1959, 1960, 1963, 1964a, b) has dealt with the spatial orientation of *Bembex rostrata* and with related problems (Chmurzyński 1957, 1964c). The materials have also been collected for the ecological conditioning of the spatial orientation (cf. Chmurzyński, 1965).

Recently, experiments were started on the distant orientation, that is, the so-called distance of the return of the honeybee (*Apis mellifica*) and bumblebees (*Bombinae*). It is intended to relate the distance of the return with the radius of the area known by these insects, that is of their life range which is an index of the motility of the species. In the case of these insects, which pollinate the economically important plants, the investigations may contribute to the determination of the optimum distribution of the nests of the insects investigated over agricultural areas.

(7) *Habits.* The research on the habits of animals, partially entering the field of the experimental ethology, has been carried out on forms with different degrees of the organism complexity, that is, from the earthworm (Olga Krauze 1929), through the arthropods such as, *Phronima sedentaria (Amphipoda, Hyperiidea)* (Minkiewicz 1909b), crabs as, *Dromia vulgaris* (*Decapoda, Brachyura, Notopoda*) (Stanisława Dembowska 1925b, 1926, Dembowski 1925a-c, 1926) and *Uca pugilator* (*Brachyura, Brachygnatha, Brachyrhyncha*) (Dembowski 1926), *Hymenoptera* as, ants (Minkiewicz 1939a-d, Janina Dobrzańska 1957, 1959, Dobrzańska and Dobrzański 1960, 1962, in press, Dobrzański 1956, 1959a, b, 1960, 1961), *Myrmosa brunnipes* (*Mutillidae*) (Minkiewicz 1935), *Pompilidae* (Minkiewicz 1934b), *Sphegidae* (Minkiewicz 1931c, d, 1932, 1933, 1934a, Chmurzyński 1960), larvae of caddis flies *Molanna angustata* (Dembowski 1923b, Sulamita Staropolska and Dembowski 1950) — up to the bats (Krzanowski 1958a-d, 1960).

The ethological analysis of the inter-specific relations from the point of view of the social parasitism was taken up by Dobrzański 1959a, b, 1960, 1961, 1965) with the coöperation of Janina Dobrzańska (1960, 1962). They discovered a group of worker ants which incite the rest of the group of *Polyergus rufescens* to robbing expeditions. They called them, "activists".

Like the bumblebees and honeybees in the agriculture and horticulture, the ants play an important role in forestry. Hence, the importance of the knowledge of their habits, life range, manner of exploiting the terrain and other closely related problems such as, the division of work in the nest, passing information to each other, etc. On the basis of her observations, Janina Dobrzańska (1957, 1958, 1959) has set up a hypothesis that in ants there are two forms of social feeding, which exclude each other, that is, either a division of the area between particular individuals of a given colony (in *Formica rufa s.l., F. pratensis, F. truncicola*), or a mutual notification on the food found (in *Myrmica scabrinodis, Tetramorium caespitum*). Most recently, this author discovered an intermediate form, *Lasius fuliginosus*, in which there is a division of the feeding ground and, although it is not very accurate, but certain forms of indirect notification (Janina Dobrzańska unpubl.) may be observed. The ant leaves a smell trace, leading from the source of food to the nearest path, frequented by other ants. A mutual communication of the crabs *Uca* was dealt with by Dembowski (1925d).

(8) *General Problems of Animal Behavior*. The interest in the individual differences in animal behavior is one of the characteristic features of the ethological investigations, distinguishing them from, for instance, ecological ones. This is well cared for by the myrmecological group (Janina Dobrzańska and Jan Dobrzański, in press). Recently, this research group has taken up the investigations on the response differences in the aggressive behavior of the male Siamese fighting fish, *Betta splendens*.

In the departments discussed, much attention has also been paid to the theoretical problems. This has been displayed mostly in Professor Dembowski's publications in the field of animal psychology (1926b, 1946a, b, 1949, 1955b, 1956b, 1959b) and cybernetics (1958).

I would like to express my sincere thanks to the Librarian of the Smithsonian Institution, Washington, D.C., for kind providing a paper by Professor R. Minkiewicz.

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Book review

On the joint and seperate function of the cerebral hemispheres (Materialy o parnoi i razdelnoi deetialnosti bolshikh polusharii golovnogo mozga). V. M. MOSIDZE. Edited by K. S. ABULADZE. Tbilisi: Izdatelstvo „Metsniereba", 1964. Pp. 152, illustrated.

This volume is an important contribution to the literature concerned with the interhemispheric transfer, which is one of the challenge problems of the modern physiology of the brain. Its author, Dr. Vakhtang Mikhailovich Mosidze is Professor and Head of the Laboratory of Higher Nervous Activity, Institute of Physiology, Academy of Sciences of the Georgian SSR, Tbilisi (Tiflis), Georgia, USSR.

Mosidze combined the conditioned-reflex method with regional cerebral ablation and stimulation of subcortical structures under circumstances of chronic implantation of intracerebral electrodes in dogs. He found that antagonistic processes, that is, either facilitation or inhibition, may occur at the same time in symmetric "points" of both cerebral hemispheres. A simulataneous tactile stimulation of the hindlimb and local acoustic stimulation applied to the ipsilateral ear may cause interference with some cerebral mechanisms and inhibit a conditioned reflex on one side and produce activation on the other side. The evidence was presented that hemidecortication impairs neither facilitation nor inhibition on the contralateral side. In another series of experiments, Mosidze has shown that stimulation of the caudate nucleus exerts an inhibitory influence on the conditioned salivary outflow from the ipsilateral parotid gland.

The above findings indicate that it is possible "to split" the functional integrity of the brain without transecting the commissural pathways.

On the basis of Mosidze's earlier studies, it is known that a large unilateral lesion of the auditory area in the cerebral cortex leaves both acoustic food-reinforced conditioned reflexes and differentiations unaffected. In this monograph, it is reported that the ability to spacially localize the source of an acoustic stimulus is lost with unilateral auditory area involvement. This result indicates that space localization has to do with an interaction of both hemispheres.

This is a stimulating book and of principal interest to the specialist.

L. S. Gambarian (Erevan, USSR)
Stefan Brutkowski (Warsaw, Poland)

Cena zł 24.—

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