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BLACK-WHITE DISCRIMINATION PERFORMANCE IN FRONTAL RATS

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In a previous paper (Dąbrowska 1968) it was shown that the initial learning of a black-white discrimination task by rats with frontal lesions is better than by normal rats. Normal Ss showed more spatial preferences in both original and reversal learning which suggests that even if the only way to solve a task is to use visual cues, normal rats showed a strong tendency to utilize kinesthetic stimuli. In those experiments food reward was used and Ss were deprived of food for 22 hr before testing. It was observed that adaptation of the frontal animals to such a schedule was excellent and no loss of body weight was observed. Body weight was maintained just like normal animals of the same age with ad libitum feeding.

Experiments of Brutkowski and Dąbrowska (1963, 1966) performed on dogs in which different parts of prefrontal cortex were removed showed that the animals after lesions of the medial prefrontal cortex displayed marked food oriented behavior characterized by sniffing, searching, and licking movements around the food cup through the testing session. A similar phenomenon was observed in dogs with lesions of the lateral surface of prefrontal cortex. We suggested that the loss of differential inhibition arising from lesions of the medial prefrontal cortex reflected the release of drive functions from cortical inhibitory control. This suggestion leads us to suppose that since the frontal lesion in the rats included all of the poles and probably an area corresponding to the medial prefrontal cortex of the dogs, rats with such lesions may be more

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strongly motivated than normals. Such hypothesis suggests that better and faster learning of a black-white discrimination in the frontal rats is due to the stronger food directed motivation.

To verify this hypothesis the present experiments were performed in which a different type of reinforcement was used (defensive reflexes). This type of experiment may show whether an improvements in performance of a black-white discrimination test by frontal rats is due to increased food motivation or rather is it related to impairment of cortical control of kinesthetic cues, which probably plays a very important role in normal behavior of rats.

METHOD

Subjects and apparatus. The Ss were 16 albino Wistar rats, 3 month old. The Thompson apparatus (Thompson and Bryant 1955) was used for avoidance training. This consists of a rectangular box divided into two compartments (A and B) by a wall in which doors opened in one direction (from A to B). The floor of the apparatus was a stainless steel grid through which an intermittent foot shock of 40—60 v was delivered from a shock source.

Procedure. One month prior to training the Ss were divided into two groups: group I (8 Ss) normal controls and Group II (8 Ss) frontals. Animals of group II were subjected to an operation in which the rostro-dorsal part of the cortex in front of the motor area was removed by suction under chloral hydrate anesthesia. Post-operative recovery was uneventful. One month after operation all Ss ware subjected to the following training schedule.

On day I (preliminary training) both doors were colored grey and both were unlocked. Ss were placed on the grid follor in compartment A and were allowed to wander freely in the compartment until they passed through one of the doors. When this occurred the S was left in the compartment B for 60 sec after which he was replaced in compartment A. During the second trial a very weak foot shock was used which increased the animal's running speed from compartment A to B. This procedure was repeated for 10 trials for each animal.

Days 2—11 (discrimination training). One door was black and the other white, The position of the doors was varied randomly. The black door was always locked and the white door was always unlocked. The Ss were placed in compartment A and 5 sec elapsed before the first of a series of intermittent foot shock was given. The foot shock was repeated until S opened the white door and passed into compartment B. Intertrial intervals were 60 sec, and during this time the animals remained in compartment B. Each S was given 10 trials a day for 10 days. A successful avoidance was scored when S passed from compartment A to B within 5 sec.

Days 12—21 (reversal training). The same procedure was used except that the white door was locked and the black door was unlocked.

The folowing parameters were taken into consideration as a measure of accuracy of the learning: the number of errors (attempts to open the incorrect door), number of avoidance responses, and time of response.

Experimental data were divided into trial blocks which were subjected to the statistical analyses. Each block consisted of mean number of measures taken from 20 consecutive trials for each animal.

After the termination of the reversal learning the animals were sacrificed, the brains were removed, fixed in 10% formalin, embedded in parafine and cut serially. The sections were stained with Nissl technique and reconstructions (Fig. 1) of the cortical lesions were done as described by Lashley (1931).

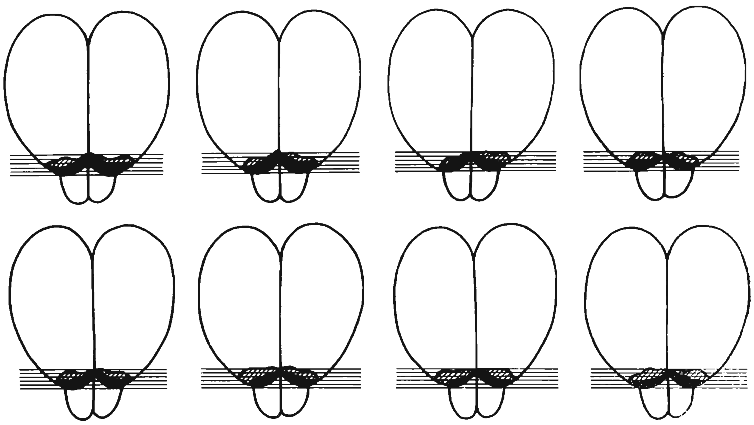

Fig. 1. Brains of the rats with lesions in frontal area. Black areas denote the parts of the brain in which both gray and white matter were removed. Striped parts show the parts in which only gray matter was removed

RESULTS

The number of correct discrimination responses in the course of both initial learning and reversal training were analysed using analyse of variance, mixed design, Type VI (Lindquist 1953) with the following factors: normal versus operated animals, learning versus reversal training, and blocks during the trainings. Fig. 2 shows per cent of correct responses made by normal and frontal Ss in separate blocks of initial and reversal learning. Initial learning curves for both groups of animals are almost the same. Reversal learning curves for these animals differs from learning curves and this difference is statistically significant ($p < 0.01$). Both groups made consecutively more and more correct responses in initial as well as in reversal learning. The differences between separate blocks of initial and reversal learning taking together both groups (normal and frontal) are significant ($p < 0.01$), and interaction between separate blocks and normal and frontal groups on both trainings combined is not significant. There is no difference between total number of correct responses made by frontal and control groups during the both trainings.

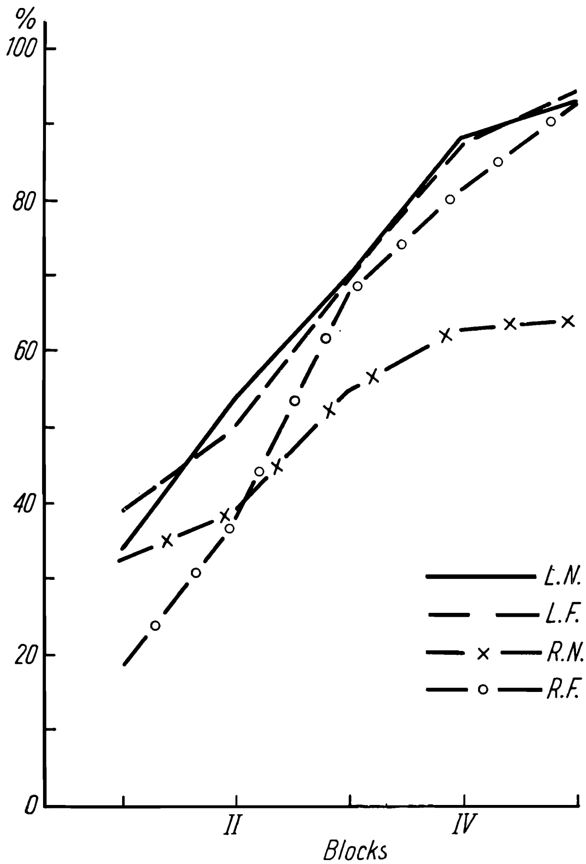

Fig. 2. Per cent of correct responses in initial and reversal learning. L. N., the course of learning in the normal group; L. F., the course of learning in the frontal group; R. N., the course of reversal learning in the normal group; R. F., the course of reversal learning in the frontal group

Although, the trend of changes in both groups is similar, the damage of frontal zone effects on the course of training, because the interaction between normal and frontal groups, initial and reversal learning during the course of trainings is significant ($p < 0.01$). Much more perseverative responses is observed in frontal group than in normal one in the first two blocks of reversal learning ($p < 0.05$, Mann Whitney U-test, two tailed). The last two blocks of reversal learning shows opposite differences. Frontal animals made much more correct responses than normal Ss ($p < 0.01$, Mann Whitney U-test, two tailed).

Fig. 3 shows average response time (in seconds) for normal and frontal animals in consecutive blocks of acquisition and reversal training. These results were analysed by Analyse of variance (type as before). The time of responses for frontal group in initial learning and reversal one was longer than for normal group but the difference statistically insignificant. The response time during initial learning for both groups is longer than

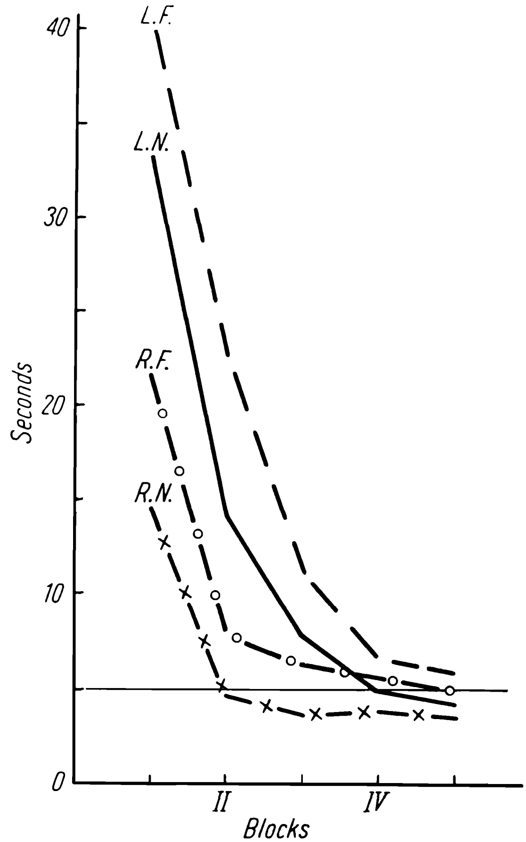

Fig. 3. Average response time in separate blocks, L. N., learning in normal group; L. F., learning in frontal group; R. N., reversal learning in normal group; R. F., reversal learning in frontal group

in reversal learning ($p < 0.01$). Taking under consideration the course of training for initial and reversal learning together for both groups, the response time is shorter in every consecutive block, the difference is $p < 0.01$. The interaction between the course of initial and reversal learning is also significant ($p < 0.01$). But the difference between the course of training in frontal Ss and normal rats is not significant, and the difference between the response time for normal and frontal Ss in initial and reversal learning is nearly significant ($p < 0.10$). Normal group differs from frontal one only in three last blocks of reversal learning ($p < 0.05$, Mann Whitney U-test, two tailed). Latencies of normal group were shorter than frontal one in the last three blocks of reversal learning.

The number of avoidance responses in the course of both initial and reversal training were analysed using analyse of variance (type as before). Fig. 4 shows per cent of avoidance responses made by 8 rats in each group in blocks consisting of 20 consecutive trials in initial and reversal learning. Curves for initial and reversal learning of normal rats reach

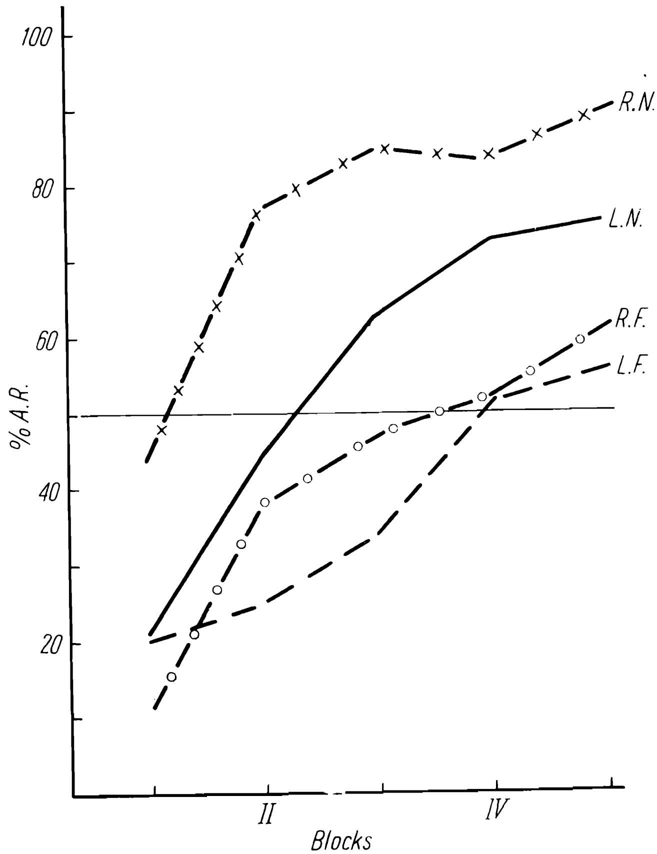

Fig. 4. Per cent of avoidance responses in frontal and normal animals in separate blocks. A. R., avoidance responses

higher level of performance than curves for frontal Ss. Total number of avoidance responses made by frontal rats was smaller than by normal animals and this difference is statistically significant ($p < 0.05$). Both groups (normal and frontal) made more avoidance responses in reversal learning than in initial one ($p < 0.05$). The number of avoidance responses for both groups (taken together) is bigger in every consecutive block of reversal training in comparison with the corresponding blocks of original learning ($p < 0.01$). The course of learning is different than the course of reversal learning in both groups ($p < 0.05$) but this course does not differ frontal and normal groups. The frontal damage affects the number of avoidance responses during the learning and reversal learning phases in the black-white discrimination training.

In the present experiment avoidance responses and discrimination correct responses are not necessarily correlated. That is, according to the present procedure, it was possible for Ss to avoid shock without first making a correct choice, and it was also possible for him to make a correct choice without avoiding the shock. Table I shows the number of

Table I

The number of errors made by frontal and normal groups in avoidance trials

No. of animals	Blocks	Initial learning I	II	III	IV	V	Σ	Reversal learning I	II	III	IV	V	Σ
Frontals	1	0	1	0	0	0	1	0	0	0	0	0	0
	2	0	0	0	0	0	0	1	5	4	2	1	13
	3	0	0	2	0	0	2	2	14	9	5	2	32
	4	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	1	6	4	3	0	14
	6	0	0	0	3	0	3	0	2	2	0	0	4
	7	0	0	0	0	0	0	3	4	0	0	0	7
	8	0	0	0	0	0	0	0	1	1	2	0	4
	Σ	0	1	2	3	0	6	7	32	20	12	3	74
Normals	1	0	1	0	0	0	1	0	6	8	3	2	19
	2	0	4	4	3	3	14	3	9	4	9	8	33
	3	0	1	0	1	0	2	4	10	9	9	8	40
	4	0	0	2	2	1	5	7	8	9	5	8	37
	5	0	0	0	0	0	0	0	6	3	0	0	9
	6	0	3	6	1	0	10	6	11	8	8	6	39
	7	0	4	0	0	0	4	2	10	6	6	3	27
	8	0	2	3	2	0	7	6	12	9	5	4	36
	Σ	0	15	15	9	4	43	28	72	56	45	39	240

errors in discrimination made by both groups of rats in initial and reversal learning, only in avoidance trials. And Table II shows number of errors made only in escape trials. For avoidance trials the difference between both groups is significant in initial learning ($p < 0.002$, Mann Whitney U-test, two tailed). Frontal Ss made much less discrimination errors in avoidance trials than the normal rats in initial as well as in reversal training. However, in escape trials this difference during the initial learning is not significant; it means that if the animals made choice under schock the frontal rats made as many errors as normal Ss.

In reversal learning normal rats made much less errors than frontals and this difference is highly significant ($p < 0.008$).

Table II

Number of errors made by frontal and normal groups in escape trials

No. of animals \ Blocks		Initial learning I	II	III	IV	V	Σ	Reversal learning I	II	III	IV	V	Σ
Frontals	1	15	10	4	2	0	31	16	12	3	0	0	31
	2	10	11	4	3	1	29	16	8	7	3	2	36
	3	10	10	4	2	1	27	12	4	0	5	1	22
	4	16	14	12	2	3	47	16	9	6	4	1	36
	5	12	6	9	6	3	36	17	8	6	2	4	37
	6	13	10	8	1	1	33	18	13	6	1	1	39
	7	8	6	0	1	0	15	12	4	1	1	1	19
	8	14	12	5	1	0	32	16	10	3	2	0	31
	Σ	98	79	46	18	9	250	123	68	32	18	10	251
Normals	1	11	12	10	3	3	39	11	4	2	3	2	22
	2	15	6	2	3	0	26	17	6	3	2	1	29
	3	12	8	4	0	3	27	5	2	0	2	1	10
	4	11	8	4	0	0	23	5	4	0	0	0	9
	5	15	3	0	1	0	19	16	5	5	1	0	27
	6	14	9	5	0	0	28	6	0	0	1	0	7
	7	15	6	3	1	1	26	12	4	5	5	3	29
	8	13	7	5	2	0	27	8	2	1	0	0	11
	Σ	106	59	33	10	7	215	80	27	16	14	7	144

Fig. 5 shows inter-relations between number of correct responses in black-white discrimination and number of avoidance responses made by normal and frontal animals in two last blocks of initial and reversal learning. First point on the X-axis represents initial learning. Second one shows reversal learning. Number of avoidance responses or correct responses in discrimination is shown on the Y-axis. Continual line represents increase of number of avoidance responses made by normal rats from initial to reversal learning. This increase is greater in comparison with the line (interrupted) corresponding to the avoidance responses made by frontal rats. Nuber of avoidance responses made in two blocks of learning does not differ between two groups of animals. The difference in reversal learning is statistically significant ($p < 0.03$, Mann Whitney

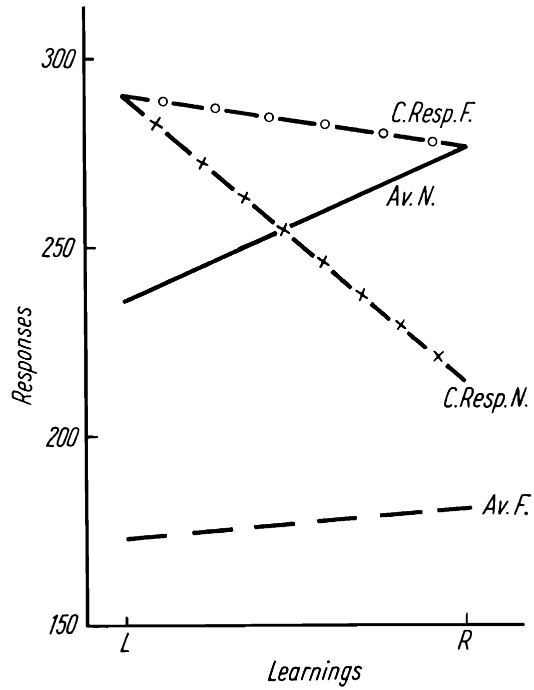

Fig. 5. Inter-relations between number of correct responses and the number of avoidance responses in initial and reversal learning. C. Resp. F., the number of correct responses in frontal group; C. Resp. N., the number of correct responses in normal group; Av. N., the number of avoidance responses in normal group; Av. F., the number of avoidance responses in frontal group; L., initial learning; R., reversal learning

U-test, two tailed). Number of correct responses in discrimination made in two last blocks of initial and reversal learning is represented by interrupted line with circles for frontal rats, and interrupted line with crosses for normal Ss. Number of correct responses is the same in initial learning for both groups, but in reversal learning these groups differ from each other ($p < 0.02$). These data show that if the increase in number of avoidance responses is greater the greater is the decrease in number of correct discrimination responses. The number of avoidance responses in normal rats increases much more in frontal Ss, and the number of correct responses decreases also more than in frontal rats.

The direct correlation between number of avoidance responses and discrimination errors in two last blocks of initial and reversal learning was examined in both groups by Spearman's test. This correlation is statistically significant only for reversal learning of both groups ($r = 0.46$, $p < 0.05$).

DISCUSSION

Results of the present experiments show that there is no difference between normal and frontal animals in original learning of the black--white discrimination if a defensive reflexes (avoidance procedure) is used. There is instead a difference in reversal learning between these animals. At the beginning of reversal lerning rats with frontal lesions make many more errors in the first block of 20 trials than the normal subjects, but the number of these errors decreases very quickly in the next 20 trials (block II) and reach the level of errors observed in normal animals in the same block. In the next consecutive blocks the number of errors decreases in both groups, but in frontal animals this decrease is quicker than in normal animals and difference in the course of reversal learning between two groups gradually increases.

This result is not due to the slower process of inhibition in normal animals because they exhibited many less perseverative errors than frontal subjects. The response to the previously correct stimulus is much more difficult to extinguish in rats with frontal lesions than in normal animals. Nevertheless, reversal training in frontal Ss is quicker and better than in normal rats. Similar results were obtained in a previous paper (Dąbrowska 1968) in which a food reward was used. It has been shown that the course of both initial and reversal learning of the black-white discrimination problem is faster in frontal rats than in normals. But if the animals were trained in a black-white discrimination using a defensive (avoidance) method there was no difference between normal and frontal animals in learning whereas in reversal learning the normal animals were much worse than frontals and the difference between these groups increases during the course of reversal learning.

Unfortunately, an explanation of these results is difficult and we consider several possible hypotheses. There are in the literature two contradictory suggestions: the first implies that damage to the frontal lobes influences feeding, fear and aggressive behavior which is normally suppressed. Fulton et al. (1932), Watts and Fulton (1934) showed that partial or complete ablation of the frontal lobes caused an increase in food intake. The same was shown by Langworthy and Richter (1939). Anand et al. (1958) reported a decrease in food intake after frontal damage restricted to the posterior orbital cortex, whereas when the lesion spared the posterior orbital cortex increase of the food intake was observed. Brutkowski and Dąbrowska (1963, 1966) showed that the instrumental response elaborated before operation to the positive stimulus (reinforced by food) and inhibited to the negative stimulus (not reinforced) was disinhibited after ablation of the prefrontal cortex. During this disinhibition there were observed movements directed to food.

Similarly, there are data showing changes of behavior associated with anxiety states or fear and aggressiveness. Kennard (1945) demonstrated rage responses after removal of the entire frontal lobes or in some instances after selective lesions of the orbital cortex. These findings have been confirmed by Aleksandrov (1949), Bond et al. (1957), Bykov (1957) and Auleytner and Brutkowski (1960). Brutkowski and Mempel (1961) have reported that violent rage and anger are released in dogs following ablations of the genual and subgenual gyri on the medial surface of the frontal cortex.

The second suggestion is apparently quite opposite to the previous one that the fear and anxiety states are suppressed after frontal ablations. Streb and Smith (1955) discovered that the rats after bilateral lobotomy showed less responses indicative of anxiety than the sham operated controls. Kahn (1953) also showed that the damage of the frontal cortex caused a loss of responses based on the anxiety state. Stamm (1964) found that monkeys with prefrontal cortical ablations exhibited lower rates of "frustrative" responses than controls. Their behavior was thus less disrupted and their overall performance was consequently superior to the controls. Jeeves (1967) suported a suggestion of Amsel (1958) and Stamm (1964) and explained his results as a frustration elicited by non-reward after a number of prior rewards in consequence of several reversals. However, Maher et al. (1960) and Streb (1954) did not observe a decrease or reduction of anxiety after frontal ablation. On the other hand, Maher et al. (1960, 1962) claimed that impairment of the avoidance responses can be observed as a result of the hyperactivity after frontal damage. Zieliński (1966) found that prefrontal lobotomy resulted in lengthening of the latencies of the avoidance responses, shortening of the latencies of the escape responses and transient but definite impairment of the avoidance reflex performance. He claimed that "neither the hypothesis which assumes direct correspondence between the strength of the classically conditioned fear and the instrumental avoidance responses nor 'drive disinhibition' hypothesis explain deterioration of the avoidance reflexes trained with a warning stimulus after lesions in the frontal pole of the cortex".

As we may see from this short review all possible changes related to the anxiety state have been reported in animals after frontal lesions (in lower animals) and after prefrontal damages (in higher animals). It may be suggested that the effect of the lesion can be associated with the extent of damage, varying procedures of the experiments and the different kind of animals used in experiments.

After prefrontal damage in rats acquisition and reversal learning in a black-white discrimination test are better in operated rats than in normal subjects.

However, a comparison of the speed of both initial and reversal learning of the black-white discrimination with food reward varsus defensive (avoidance) method suggests the method of problem solving with rats. Previous experiments (Dąbrowska 1968) and the present one were carried on by the same person, using similar methods of making lesions. Other parameters during the course of experiments were the same or similar, except one — reinforcement (food versus shock). We may point out the following differences in the results of these experiments:

1. Generally speaking, the speed of learning in both experiments is different. The animals trained with food reinforcement required about 300 trials to reach the same level of learning which is obtained by animals trained in the defensive method after 100 trials.

2. Using food reward performance of the frontal animals in initial learning was better than in the normal group. Such differences were not observed in animals trained with shock reinforcement. The course of learning in these animals is the same.

3. The frontal animals trained with food reward were slightly superior to normal rats during the course of reversal learning and reached similar (slightly lower) levels of acquisition, while the normal animals trained by the defensive method eliminated the errors very slowly in comparison with frontal subjects.

According to point 1 and 3 it can be supposed that shock reinforcement is stronger than food reward and because of it learning with shock reward is faster in both groups (controls and frontals). Now, if the faster learning is due to the stronger reinforcement, according to point 2, food motivation increases after frontal lesion. Fear or anxiety, on which conditioning is based is not affected by this lesion because differences between the two groups were not observed in learning. Now, the question arises: why did the normal rats make so many errors in reversal learning and why was the process of solving the second task so slow?

One of the explanations of this phenomenon is that the process of learning in the defensive (avoidance) procedure includes two different aspects: the first, solving of the discrimination problem and the second.

avoiding the shock. If latencies of responses in frontal animals are longer than in normal Ss so that they could work on the basis of escape, but not avoidance, they should solve the discrimination problem to get the briefest shock. And if the latencies in normal animals are very short, then they may make both correct and incorrect choices during the free 5 sec and still avoid shock; in this case solving of the discrimination problem is not important for the animals. Results of the present experiments shown in the Fig. 5 supports and illustrates this explanation. Maybe the subtle differences in emotional reactivity between normal and frontal rats are also responsible for these results.

SUMMARY

Effect of frontal ablation on initial and reversal learning in black--white discrimination test with defensive reinforcement was investigated in albino (Wistar) rats. Frontal lesion was performed one month before the training. Initial learning was similar in two groups of animals (normal-control, and frontal). Significant differences between these groups were observed in reversal learning. During the first phase of reversal training frontal rats performed much more perseverative errors than normals, but in the last phase of reversal more discrimination errors were observed in normal Ss. Direct correlation between number of avoidance responses and discrimination errors was observed during the training in both groups. Results were discussed in terms of fear drive decrease effects of frontal ablation and special procedural conditions during the training.

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