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# EFFECTS OF PREFRONTAL LESIONS ON LEFT LEG-RIGHT LEG DIFFERENTIATION IN DOGS

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*Abstract.* Twenty five animals trained in the left leg–right leg differentiation were given orbital, proreal or medial precruciate lesions. Pure cortical ablations did not affect the task whereas these deep lesions involving the bundle of fibers inside the prefrontal region caused severe deficit. The medial lesions (superficial and deep) produced disinhibition of the intertrial reactions. The nature of the deficit in the differentiation and the relation between this deficit and the disinhibition is discussed.

Among a number of tests concerned with the discriminatory responses in animals to various stimuli one of the most popular is the go left-go right differentiation. In fact, while in the standard CR experiments the Pavlovian go-no go differentiation was ordinarily used for tests concerning discrimination of cues of various modalities, in the behavioristic procedures the go left–go right differentiation was applied for this purpose. A special version of this test, adjusted to the standard CR experiments in dogs, consists in training the animal to place the left or right foreleg on an elevated platform to two different stimuli. We shall call this test the left leg–right leg defferentiation.

An interesting property of the go left–go right differentiation was found by Ławicka (1964, 1969). She observed that whereas this differentiation is very easy when the directional cues are used (the tones from above and from below, for example), it is on the contrary very difficult when cues differing in quality, originate from the same course. The same rule has been discovered by Dobrzecka and Konorski (1967, 1968) with regard to the left leg-right leg differentiation.

The present paper deals with the problem of whether the prefrontal cortex is, or is not, involved in left leg–right leg differentiation and if it is, what is the area involved in this task.

As far as monkeys are concerned, Goldman and Rosvold found recently (1970) that ablations of arcuate and peri-arcuate cortex produce a severe deficit of the go left–go right differentiation to directional auditory stimuli (up-down).

## MATERIAL AND EXPERIMENTAL PROCEDURE

Twenty five naive, male mongrel dogs were used in this series of experiments. The testing was conducted in the usual CR chamber, the dog on the stand, in front of him the food-tray. Two loudspeakers were located on the left and the right side of the stand at a distance of 35 cm from its midline, on the level of the dog's head.

The method of passive movements was applied until the dog began to respond with active movement to the stimuli. The animals were trained to put their left foreleg on the feeder in response to one stimulus and the right foreleg in response to another stimulus. Each correct response was reinforced by food. The stimuli differed from each other not in quality but in location. The same tone of 1000 cycle/sec, delivered from an acoustic generator, was presented through the left or the right loudspeaker. The stimuli were given in random order, 17 times each, at intervals of 1 min. The tone lasted 5 sec in the absence of response but was discontinued when the dog performed the instrumental movement. A movement performed with the wrong foreleg or the absence of instrumental reaction was considered an error and therefore was not reinforced by food. No correction trials were given.

The training lasted until, in a 100 consecutive trials, the animal had attained the criterion of 45 correct responses to the left stimulus and 45 to the right. On completion of the training the dog was given seven days rest and afterwards retention testing was carried out. Usually we found that our animals retained the task at the criterion level. Only one or two dogs needed some additional training. The retention sessions were followed by surgery in which a certain part of the prefrontal region was bilaterally removed. The testing was resumed 7 days after operation and lasted until the original criterion was reached. When the experiment was completed the animals were sacrificed and the extent of brain damage checked.

A group of 20 dogs was trained in the following task. On presentation of the tone from the left side the animal was required to place his left foreleg on the feeder. To the tone from the right side he had to respond with his right foreleg (L-L, R-R). Five other dogs were presented with a task in which the required movement had to be performed with the leg opposite to the direction of the tone; the left tone — right foreleg, the right tone — left foreleg (L-R, R-L). Since no significant difference was observed between those two groups in the course of the pre-operative and post-operative training all animals will, therefore, be considered together as one group as far as the task is concerned. They will be subdivided, however, into several groups according to the character of lesions which were made in accordance with the subdivisions of the prefrontal cortex of dog described by Kreiner (1966) (*see* Fig. 1). In some animals the lesions covered the orbital area, situated on

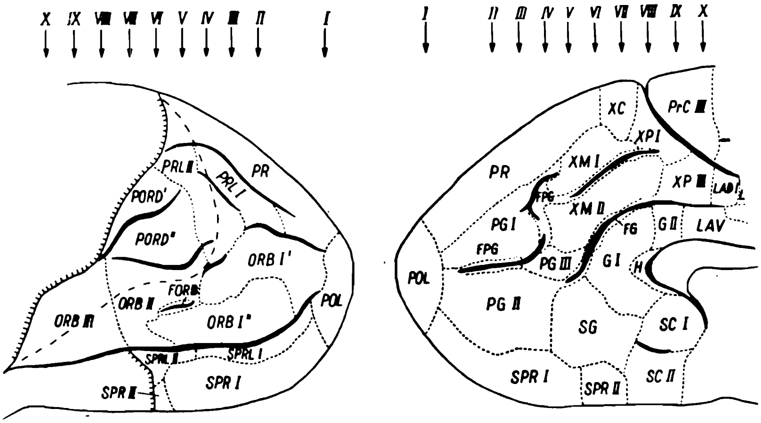


Fig. 1. Lateral and medial aspect of prefrontal area in dog. ORB, orbital area; PR, proreal area; PG, pregenual area; XM, XC, XP, precruciate areas. The arrows indicate the plane of section. From Kreiner, 1966.

the lateral aspect of the hemisphere in dog; in the others the proreal or medial region was removed. The extent of ablations will be described separately for each group of animals.

## RESULTS

### *Cortical ablations*

Cortical ablations were performed on 12 dogs. For location of these ablations *see* Table I, for the extent of lesions in the representative animals *see* Fig. 2.

Following the partial cortical removals all the dogs were able to solve the task. The results are presented in Fig. 3. The animals with orbital, proreal and some with the medial ablations worked at the

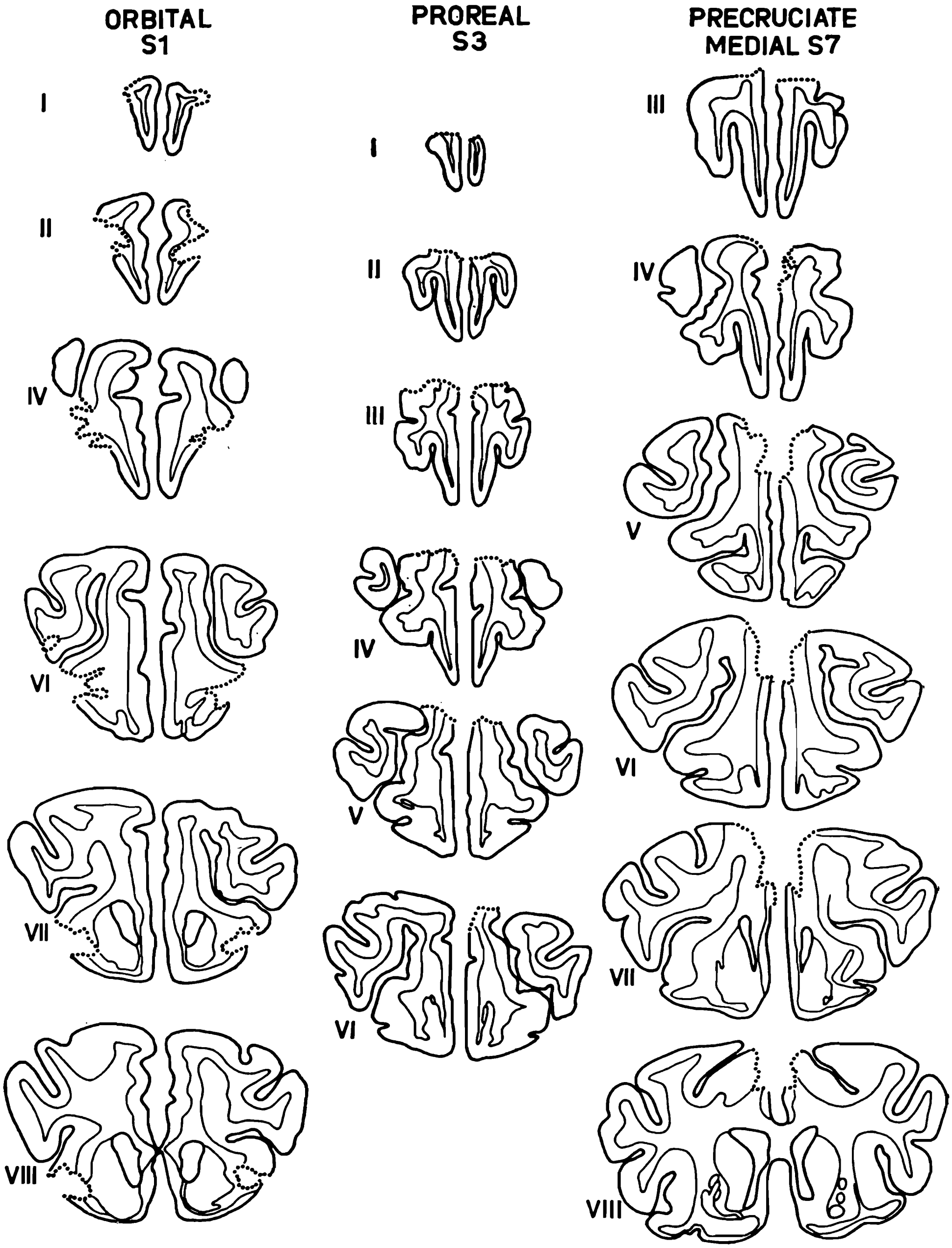


Fig. 2. Selected cross sections in representative dogs after cortical ablations. Dotted line indicates the border of lesion. The planes of sections are indicated (*see* Fig. 1).

TABLE I

Superficial lesions

| Area | Orbital | Proreal | Medial | | | Total prefrontal |
|---|---|---|---|---|---|---|
| | | | Pregenual and polar | Precruciate | Precruciate and pregenual | |
| Dog | S1, S2 | S3, S4 | S5, S6 | S7, S8, S9 | S10, S11 | S12 |

criterion level from the very beginning of the post-operative testing. Only three dogs with medial ablations (S8, S9, S11) showed a slight impairment (14, 19, 21 errors respectively). However, they improved rapidly and attained the criterion in the second block of a 100 trials. The histological examination showed that in dogs S9 and S11 some subcortical white matter was injured and only in S8 was the damage confined to the cortex. Thus, we see that all dogs with partial cortical ablations were very good in performing the left leg–right leg differentiation. However, to make sure that cortical prefrontal ablations did not affect the animal's ability to perform the task, the entire prefrontal cortex was removed in dog S12. Although the post-operative performance of the test by this animal was more impaired than in any dog with partial lesions (48 errors, Fig. 3) improvement followed as rapidly as in the other animals and the criterion was also reached in the second hundred trials.

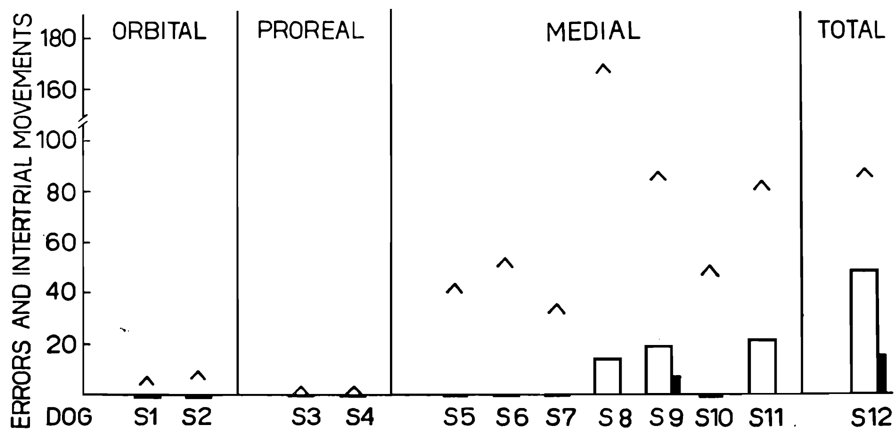


Fig. 3. Number of total and omission post-operative errors and intertrial movements after cortical ablations. White bars denote the number of total errors and black, omission errors. Dashes denote the number of the intertrial movements in the first block of a 100 trials.

As far as behavior during the intertrial intervals is concerned, the animals with medial lesions differed from all the others. Whereas, the medial dogs performed numerous left and right foreleg movements in the intervals the animal with orbital or proreal ablations either did not perform any such movements or only very few.

*Deep lesions*

As already mentioned, in two dogs in which a slight impairment of the differentiation was observed, the damage encroached into the white matter. This seemed to indicate then when fibers lying deeper under the medial cortex are damaged together with the cortex, it causes a defi-

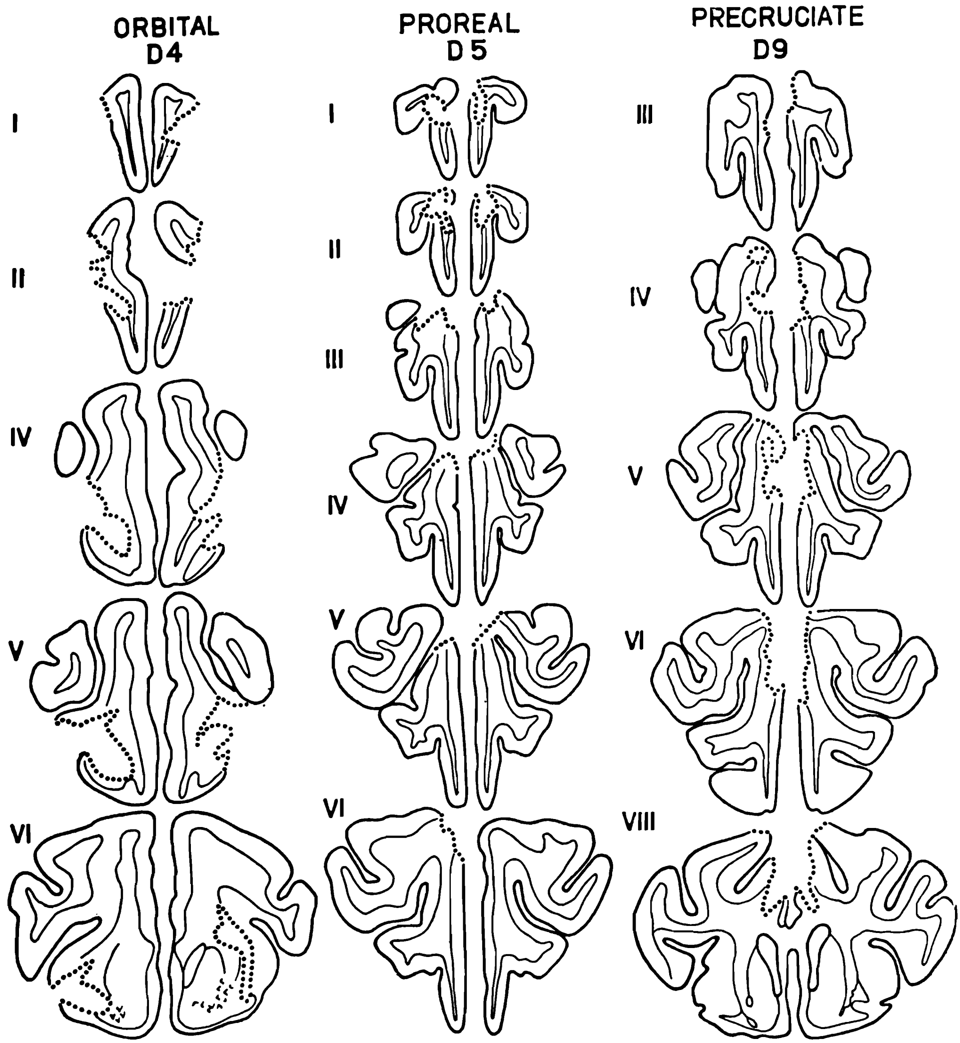


Fig. 4. Selected cross sections in representative dogs after deep ablations. For explanation *see* Fig. 2.

cit in the performance of the test. To check this supposition, deep lesions including the cortex and underlying white matter were made in 10 other dogs (Table II). The lesions in representative animals are shown in Fig. 4. The results of the removals are presented in Fig. 5.

TABLE II

Deep lesions

| Area | Orbital | Proreal | Medial precruciate | Bundle of fibers |
|---|---|---|---|---|
| Dog | D1, D2, D3, D4 | D5, D6 | D7, D8, D9, D10 | D11, D12, D13 |

In dogs with orbital or proreal ablations no change in the performance of the left leg-right leg differentiation, nor in intertrial intervals behavior was observed. The only exception was the orbital dog D4 who made 24 errors and showed disinhibition of intertrial reactions. But in this particular case, as the histological examination showed, the lesion was exceptionally deep and, what seems more important, it encroached the medial part of the prefrontal area (Fig. 4 *II–V*).

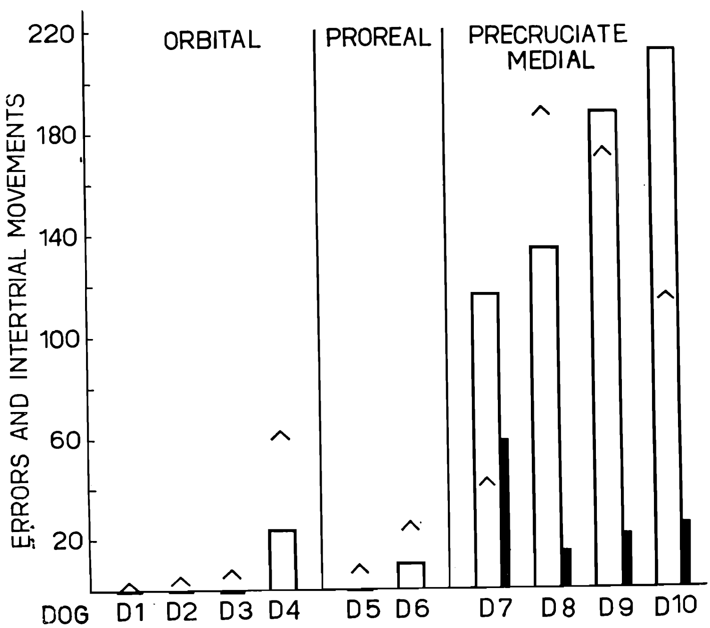


Fig. 5. Number of total and omission post-operative errors and intertrial movements after deep ablations. For explanation *see* Fig. 3.

On the other hand, a severe deficit in the left leg–right leg differentiation and a considerable disinhibition of intertrial reactions was observed in all dogs with medial removals. The number of errors ranged from 120 to 212. The incorrect responses decreased gradually in the course of post-operative experimentation and extensive retraining of 500 to 900 trials was necessary before the animals again attained the criterion.

The animals committed either commision errors (movement with the wrong foreleg) or omission (no movement to the CS). In three dogs the commission errors considerably outnumbered the omission errors while in one dog both kinds of errors were equally frequent.

The number of intertrial movements in animals with deep lesions was similar or even stronger than that observed after medial cortical lesions.

The fact that the deficit in the left leg-right leg differentiation was found only after deep medial removals but not after other lesions, raised the following question. Is the deficit due to the combined damage to the medial prefrontal cortex and the bundle of fibers lying parallel to this cortex, or rather due to the injury to the bundles themselves? To answer this question the bundle of fibers below the proreal cortex (Fig. 6) was removed bilaterally in three dogs: D11, D12 and D13.

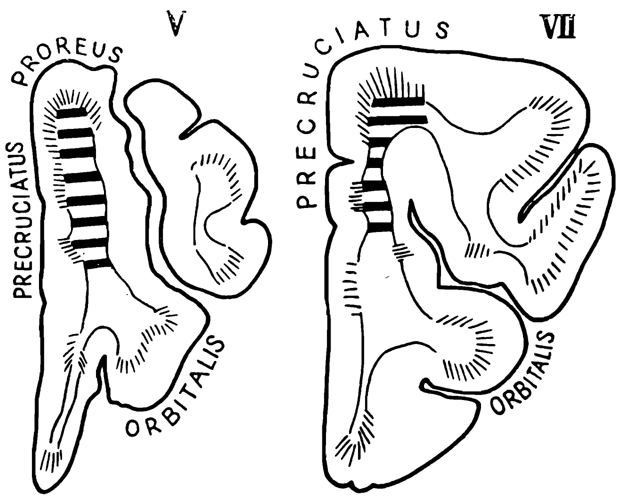


Fig. 6. Frontal sections of dog's brain. Modified from Kreiner 1966. The site of "bundle" lesion shown.

Together with the bundle some part of the proreal gyrus was also damaged while approaching the fibers. The representative damage is shown in Fig. 7 and the results of the lesions are presented in Fig. 8.

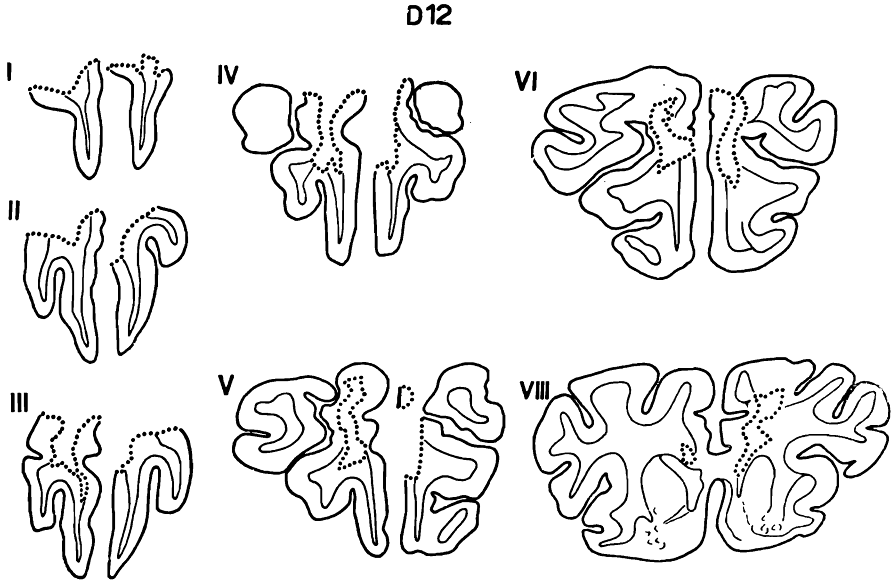


Fig. 7. Selected cross sections after damage to the bundle of fibers in dog D12. Explanations as in Fig. 2.

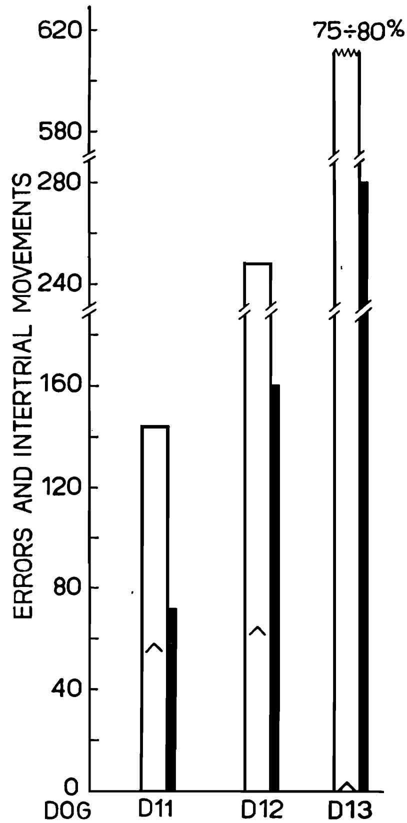


Fig. 8. Number of total and omission post--operative errors and intertrial movements after injury to the bundle of fibers. Explanations as in Fig. 3.

A considerable impairment in the left leg–right leg differentiation was found in all three animals. In dogs D11 and D12 the deficit was more or less the same as that observed after deep medial ablations. The dogs re-attained the criterion after post-operative training of 400 and 500 trials and 144 and 241 errors respectively. A much greater impairment was found in dog D13. This animal continued to perform at the chance level in 800 trials and still made many errors throughout further hundreds of trials. Even after extensive retraining of 1400 trials and 611 errors, he worked at the level of 75 to 80% of correct responses.

TABLE III

Summary of results

| Lesion | | Impairment of left leg-right leg differentiation | Intertrial movements |
|---|---|---|---|
| Orbital | Superficial | — | — |
| | Deep | — | — |
| Proreal | Superficial | — | — |
| | Deep | — | — |
| Precruciate medial | Superficial | — | + |
| | Deep | + | + |
| Bundle of fibers | | + | ? |

Characteristic for these dogs was the high rate of omission errors amounting to about 50% of total errors. In dogs D11 and D12 these errors were observed mainly in the early post-operative period while in D13 only some time after operation.

As far as the intertrial movements are concerned the situation is not clear. Two dogs showed a considerable disinhibition, similar to that observed after medial lesions. The dog D13 however, whose deficit in the left leg–right leg differentiation was the greatest, did not show any such disinhibition.

A short summary of all our results is given in Table III.

## DISCUSSION

In spite of a careful examination of the prefrontal cortex, we could not find any cortical area responsible for the left leg–right leg differentiation. Perhaps other cortical lesions, outside the prefrontal region (the premotor or motor cortex for example) could have produced the deficit in the differentiation. However, the results of an experiment performed in our laboratory by C. Dobrzecka, L. Stępień and J. Konorski (unpublished data) show that bilateral removals of either premotor or motor cortex do not impair the left leg–right leg differentiation. It seems therefore that the cortical ablations do not affect this task.

On the other hand, severe impairment was observed when the bundles of fibers inside the prefrontal region were injured — the effect produced either by deep medial lesions, or by damage to the bundle of fibers together with the proreal gyrus. The question arises whether the deficit in the left leg–right leg differentiation was the result of the combined damage to the cortex and bundle of fibers, or of the interruption of the fibers themselves? We are not yet ready to answer this question but our guess is, that the fibers forming the bundle inside the prefrontal region might be essential for the left leg–right leg differentiation. Injury to those fibers may interrupt the connections between various cortical or cortico-subcortical structures engaged in the performance of the task. Unfortunately, we do not know what are the points of departure and termination of the fibers included in the prefrontal bundle in dog. This will be the subject of future research.

Another problem is the nature of the deficit in the left leg–right leg differentiation produced by these lesions. The great number of omission errors, observed in all three dogs with lesions in the bundle of fibers plus the proreal gyrus and in one animal with deep medial ablation, might suggest that injury to the fibers could somehow cause "technical" difficulty in performing the instrumental movements. Two observations, however, show that this is not so. In the same experimental sessions in which the instrumental responses were absent, dogs D7, D11 and D12 used to perform many movements with either left or right foreleg during the intertrial intervals. The number of such movements greatly surpassed the number of omission errors. On the other hand, dog D13 who did not exhibit any disinhibition of the intertrial reactions, commited no omission error at all in the first stage of the post-operative testing. The omission errors, which appeared in considerable numbers in the further course of the experiment, were due to the frequent non-reinforcement of the incorrect movements.

Thus, we see that the deficit in the left leg–right leg differentiation was not caused by "technical" difficulties, but was rather due to difficulty of choosing the correct foreleg to respond to a given stimulus.

As all dogs improved and all, but one, re-attained the criterion, the question arose whether the improvement was the result of post-operative training. Two facts seem to indicate that the retraining was an essential factor. The number of errors decreased gradually and the post-operative training took as long or even longer that the original training. Some dogs were given a 2–3 weeks break in post-operative training which did not seem to have any effect on the performance.

Another point which requires comment is the relation between the two symptoms: impairment of the left leg-right leg differentiation and disinhibition of the intertrial movements. It should be recalled that such movements do appear in the original training due to generalization of the instrumental reflex to the experimental situation. The movements not reinforced by food become inhibited. From many experimental studies we know that the re-appearance of these movements is an indicator of the disinhibitory syndrome, observed after removals of the medial part of the prefrontal cortex in dogs and of the orbito-frontal cortex in monkeys. So, the fact that this syndrome appeared in the present experiments after medial lesions is quite understandable.

Now an interesting question arises as to whether the same lesion is responsible for the disinhibitory symptom and the impairment of the left leg-right leg differentiation. Our experiments show that this is not the case. The disinhibitory symptom was manifested after pure cortical lesions, while the left leg–right leg differentiation was not affected. On the other hand, at least in one dog a dramatic impairment of the left leg–right leg differentiation was not accompanied by disinhibition of the intertrial responses.

The independence of these two symptoms is to be expected on the basis of theoretical considerations. In fact, the re-appearance of the intertrial movements is the effect of the hunger drive disinhibition whereas the impairment of the left leg-right leg differentiation is not due to this factor, since here both reactions were reinforced and the task consisted in the choice of correct movement to the given stimulus.

It would be interesting to consider the possible relation between the impairment of the left leg–right leg differentiation with another behavioral disorder manifested after similar lesions, called by us "magnetoreaction" (I. Stępień and L. Stępień 1965). The latter disorder consists in a strong tendency to approach the source of the positive CS. This is particularly pronounced when the location of the stimulus is spatially separated from that of the food. It should be noted that there is a great difference between the procedure in which the magnetoreaction was exhibited and the procedure used in our present experiment. In the previous experiments the training occurred in a big room and locomotor responses were used. On the other hand in the present experiments the dog was on the stand and his locomotor responses were partially restricted. Accordingly, there was no possibility to observe properly the magnetoreaction even if it was present. The elucidation of the relationship between the two disturbances requires further experimentation.

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