EFFECTS OF PREFRONTAL LESIONS ON LEFT LEG–RIGHT LEG DIFFERENTIATION TO NONDIRECTIONAL ACOUSTIC CUES IN DOGS

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Abstract. Twenty five dogs were trained preoperatively in left leg–right leg differentiation to nondirectional acoustic cues. Removal of the medial precruciate cortex as well as the proreal or orbital cortex together with underlying fibers did not affect performance of the task, whereas lesions which involved the fibers underlying the medial precruciate cortex produced more or less pronounced, yet moderate impairment. Comparison between impairment described in this paper and that obtained following similar lesions in earlier experiment with directional cues indicates that fibers underlying the medial precruciate cortex are of greater importance when directional cues are involved in task.

INTRODUCTION

In a previous paper (7) it has been shown that the bundle of fibers underlying the medial precruciate cortex in dogs is essential for left leg–right leg differentiation to acoustic directional cues. Prefrontal cortical lesions with no or only very slight damage to fibers did not affect performance of this task. On the other hand, it is known that cortical prefrontal lesions produce a severe impairment in the go left–go right differentiation to acoustic directional cues (3). It is also known that there is a distinct difference in the acquisition rates of left leg–right leg as well as go left–go right differentiation to directional and nondirectional cues (1, 2, 5, 6). The tasks including the nondirec-
tional stimuli appeared to be much more difficult than those with directional cues.

This paper concerns the problem of whether the prefrontal cortex and/or underlying fibers are involved in left leg–right leg differentiation to nondirectional cues.

MATERIAL AND METHODS

Twenty-five experimentally naive mongrel dogs were trained in left leg–right leg differentiation to acoustic cues in alimentary situation. The training was conducted in a standard CR chamber. The speaker was situated in front of the feeder on the level of the dog's head. Tones of 500 cycle/sec and 1000 cycle/sec were used as cues. Experimental sessions consisted of 34 trials, with each tone presented 17 times according to the Gellerman series.

Preoperative training consisted of three phases: shaping, acquisition and retention. First, the animal learned to approach the feeder when food was presented and to take it from the bowl. During the second phase the tones were introduced and a method of passive movements applied. The dog was forced to place his left foreleg on the feeder when the tone of 500 cycle/sec was presented and to place his right foreleg after the 1000 cycle/sec tone was given. When the dog began to respond to the tones with foreleg movements, the forced movements were no longer used. During this period of testing, food was presented only when the dog responded to the tone by performing the instrumental reaction with the correct foreleg. Food was not presented when an instrumental reaction was performed with an incorrect foreleg or in the absence of a reaction. No correction trials were given. The training was conducted until the animal attained the criterion of at least 90 correct responses in 100 consecutive trials, 45 to each tone. When criterion was reached the dog was given 7 days of rest and afterwards retention testing was carried out. When the animals had retained the task at the criterion level, the retention sessions were followed by surgery. The testing was resumed 7 days after the operation and lasted until the original criterion was reached. At the conclusion of testing the animals were anesthetized with an overdose of Nembutal and perfused through the heart with saline followed by 10% neutral formalin. The brain was dehydrated, embedded in paraffin and sectioned at 20 μm. Every 20th section was stained alternatively according to the Nissl an Klüver-Barrera technique. Every 40th frontal section was projected on the medial, lateral or horizontal surface of the hemisphere, depending on the place of damage, for analysis of extent of lesion.
RESULTS

Anatomical findings

All dogs were divided into five groups according to the type of lesions which were made in accordance with the subdivisions of the prefrontal cortex in dogs by Kreiner (4) (Fig. 1).

**Group \(Pcr\) \((n=5)\):** The medial precruciate cortex was removed in dogs \(Pcr1-5\). The ablations covered the entire medial precruciate cortex and included little of the underlying fibers, and also small portions of the proreal and cingular cortex. Lesions were very similar to each other and are represented by dog \(Pcr\ 1\) (Fig. 2).

**Group \(Fb\) \((n=5)\):** The fibers underlying the medial precruciate cortex were damaged in dogs \(Fb1-5\) together with a narrow strip of the proreal cortex through which a sucker was inserted into the brain. In this group the lesions were less consistent. In dogs \(Fb3-5\) damage
Fig. 2. Reconstructions of representative lesions. Cross-sections show histological verification of damage. Numbers indicate placement of the particular section. Pcr, precruciate; Pr, proreal; Orb, orbital; Fb, fibers.
to the fibers was more extensive than that in Fbl and 2. The lesions are represented by Fbl and 5 (Fig. 2).

**Group PcrFb** (n = 5): The medial precruciate cortex together with the underlying fibers were removed in dogs PcrFbl-5. Cortical removals were very similar to each other in all dogs. They included the entire medial precruciate cortex with some injuries in proreal and cingular cortex. Damage to the fibers, however, was less consistent, and was more extensive in PcrFb4 and 5 than in PcrFb1–3. The lesions in this group are represented by PcrFb1 and 5 (Fig. 2).

**Group PrFb** (n = 5): The proreal cortex and the underlying fibers were removed in dogs PrFbl-5. In two of them (PrFbl and 2), damage was confined to the proreal gyrus while in three others some fibers underlying the presylvian cortex were involved (Fig. 2).

**Group OrbFb** (n = 5): The orbital cortex and the underlying fibers were removed in dogs OrbFbl-5. The lesions were consistent including beside orbital gyrus some fibers underlying the presylvian cortex (Fig. 2).

**Behavioral results**


Figure 3 shows each animal’s errors to criterion performed during the postoperative retention testing.

![Fig. 3. Performance of left leg-right leg differentiation following partial prefrontal lesions. Bars indicate errors-to-criterion. Denotations as in Fig. 2.](image)

**Group Pcr:** Removal of the medial precruciate cortex had no effect on performance of the task. All five dogs worked at the criterion level from the very beginning of the postoperative testing.

**Group Fb:** Damage to the fibers underlying the medial precruciate cortex together with a strip of the proreal cortex produced some impairment. Two dogs (Fb1 and 2) retained the task near the criterion level,
performing 15 and 18 errors. The remaining animals (Fb3–5) showed greater, yet moderate, impairment: 37, 39, 43 errors respectively. All errors consisted of performing the instrumental response with the incorrect foreleg.

**Group PcrFb:** Damage to the medial precruciate cortex together with the underlying fibers moderately affected performance of the task. Both dogs in which damage to fibers was smaller (Pcr1 and 2) worked at or near the criterion level performing 10 and 20 errors. Three other dogs in which damage to the fibers was more radical (PcrFb3–5) performed 27, 66 and 77 errors, respectively. All errors consisted of movements performed with the incorrect foreleg, similarly to Group Fb.

**Group PrFb:** Removal of the proreal cortex and underlying fibers did not impaired performance of the task. All animals worked at the criterion level from the very beginning of the postoperative retention test.

**Group OrbFb:** Similarly, removal of the orbital cortex and underlying fibers did not affect performance of the task.

**DISCUSSION**

The results demonstrate that left leg–right leg differentiation to two tones of different frequencies may be impaired by some ablations within the prefrontal region, but not by others.

Impairment of performance of the task was observed only following those lesions which included the fibers underlying the medial precruciate cortex (subcruciate fibers). They are: damage to those fibers themselves together with a strip of the proreal cortex or damage to the medial precruciate cortex together with the underlying fibers. Impairment was not observed following either removal of the precruciate cortex itself or after removal of the proreal or orbital cortex together with the underlying fibers when the subcruciate fibers were left. This finding shows that the fibers underlying the medial precruciate cortex in dogs seem to be of some importance for left leg–right leg differentiation to nondirectional cues.

The impairment found in the present experiment, however, was moderate and shortlasting. Postoperative errors varied from 10 to 77, whereas errors performed during the original learning varied from 178 to 600. On the other hand, a very pronounced deficit in left leg–right leg differentiation after damage of the fibers underlying the precruciate cortex was found when directional cues were used (7). The numbers of postoperative errors were similar to those performed during acquisition. Differentiation of location of the cues in space, seems to make the task
very difficult for dogs deprived of the fibers underlying the medial pre-cruciate cortex.

The wide range of impairment in the present study, as measured by the number of postoperative errors-to-criterion, may be due to both, the extent and/or the placement of damage to the fibers in a particular animal. Although this cannot be confirmed by the results of this study, it nevertheless seems possible that either the extent or the particular site of damage is responsible for a degree of the postoperative impairment of function.

The exact role of the subcruciate fibers in left leg-right leg differentiation, however, is not fully understood since it is not known what other brain structures are connected to the prefrontal cortex through these particular fibers.

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REFERENCES


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