

Cortical area in the rat that mediates visual pattern discrimination

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Abstract. In Experiment I, bilateral ablations of the caudolateral cortex involving Krieg's area 36 impaired discrimination of visual patterns but not delayed alternation. In Experiment II, the same type of lesions retarded postoperative learning to discriminate embedded visual patterns. In rats from the Experiment II tracers of axonal transport gave no signs of damage of the connections of the primary visual cortex. In agreement with this, Nissl stain of the dorsal lateral geniculate nuclei showed no neuronal loss or gliosis. These results suggest that caudo-lateral cortex in rats corresponds to the inferotemporal cortex of primates.

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INTRODUCTION

"Although the rat's detail vision is abolished by complete destruction of the striate areas of the cerebral cortex, the capacity for discrimination of simple geometrical figures is little affected by extensive lesions within these areas, so long as some part of the cortical projection of the binocular field remains intact" (Lashley 1939).

It is not known whether the rat has a cortical area which corresponds to the inferotemporal visual association cortex in primates. In monkeys this cortex is localized in the temporal lobe (Iwai and Mishkin 1969, Mishkin 1982) and is characterized by afferents from the pulvinar (Benevento and Rezak 1976, Trojanowski and Jacobson 1976), from peristriate cortical areas (Desimone et al. 1980); and by relatively few neurones with projections to the pontine nuclei (Glickstein et al. 1985). The neurobehavioural approach revealed that the primate inferotemporal cortex is involved in shape perception (Yaginuma et al. 1982) and visual recognition (Mishkin 1982) but not crucially in mediation of delayed response-type behaviour (Rosvold and Szwarcbart 1964, Dean 1981).

These properties may guide the search for a counterpart to the primate inferotemporal cortex in nonprimate mammals. We reviewed the available evidence for the existence of such an area in the rat and found that the caudolateral cortex, labelled "area 36" by Krieg (1946) and "Te2" and "Oc2L" by Zilles et al. (1980) has some resemblance to the inferotemporal cortex in the macaque monkey. Thus, considering the curvatures of the rodent and primate hemispheres, the caudolateral cortex in rats is found in a position similar to that of the inferotemporal cortex in monkeys. Moreover, this area in rats is interconnected with the thalamic caudolateral nuclei (Mason and Gross 1981, Deacon et al. 1983) and with the cortical areas known to be involved in vision (Miller and Vogt 1984, Sanderson et al. 1991) and contains relatively few neurones with projections to the pontine nuclei (Wiesendanger and Wiesendanger 1982, Legg et al. 1989). The inferotemporal areas in the monkey and the caudolateral

cortex in the rat receive direct innervation from the entorhinal cortex (Kosel et al. 1982).

Lashley (1931) in his study of mechanisms underlying pattern vision in the rat concluded that the cortex along the lateral border of the striate area is crucially involved in pattern vision. His inference was based on only one positive case (No. 27) with lesion restricted to the posterolateral cortex. That brain had a herniation of the hippocampus and consequently could have had damaged visual connections.

In the present study we have attempted to establish (1) whether the caudolateral cortex in the rat mediates visual pattern discrimination and delayed alternation and (2) whether caudolateral cortex of the rat is essential for a difficult visual pattern discrimination in animals with preserved connections between lateral geniculate and the striate cortex. A part of this work has been reported (Williams et al. 1986). In all studies described here the surgical procedures were carried out in total anaesthesia. No aversive stimuli were used.

EXPERIMENT I

The aim of this experiment was to find out whether ablation of the caudolateral cortex would mimic the effects of destruction of the inferotemporal area in primates: an impairment of visual pattern discrimination along with virtually intact delayed alternation.

Methods

SUBJECTS

Eight male Wistar rats, weighing 180-200 g at the beginning of the experiment, were used. The animals lived individually in cages where water was always available. Rat chow mashed with water was used as reward. Supplementary chow, if needed, was given shortly after daily training. Using food deprivation we reduced body weight of the rats to 90% of the initial value. This deprivation level was kept throughout the experiments, with a correction for normal growth of the animals.

MAZES

The rats learned delayed alternation in a T-maze (Mogensen and Divac 1984) and visual discrimination in a modified Grice box (a shorter version of that used by Divac 1971). The discriminanda were made with black tape, 1.9 cm wide, on white cardboard. The positive patterns, a "plus sign" and an "X", were made of two stripes each 14.5 cm long, and the negative patterns, a square and a diamond, had each side 8.7 cm long (peripherally). All patterns were mounted with their centres 8.0 cm above the lower cardboard edge. Each cardboard was attached to the back surface of the transparent plastic door (17 cm wide and 19 cm high). The total area of the black surface of the discriminanda was the same for each pair, in order to avoid discrimination on the basis of flux. The front surfaces of the plastic doors were frequently wiped with wet cloth.

TRAINING

On two consecutive days each animal was left individually for 10 min in each of the mazes. Mashed chow was offered at each end of both mazes. In this phase of training the doors were removed from the Grice box. Following habituation to the two apparatuses, the rats were shaped to run in the T-maze: an animal was placed in the start box, the guillotine door was lifted and the rat was allowed 5 s to reach a goal box. Runs with 5 s or shorter latency were rewarded with 7 s access to the food. Thereafter the rat was transferred for 10 s to the holding box and then placed in the start box again. If the rat had not reached the goal box within 5 s, it was transferred to the holding box to wait for 15 s before the next trial. The shaping continued until the animal ran with a latency of 2 s or less in each of the 20 daily trials. The same number of daily trials was given for each task throughout the experiments. On the day following completion of shaping, delayed alternation training began: only alternations from the preceding runs were rewarded. The first run was always rewarded and was not counted. Training continued daily until a subject made less than four

errors in one day and less than seven errors in three consecutive days (for details see Öberg and Divac 1975).

When the criterion on delayed alternation was reached, the rats were first shaped to run in the Grice box without the doors. Following the first day the doors were introduced. They were first fully open (horizontal) and then on each successive day lowered first to cover 1/2, then 3/4, then 7/8, and finally the entire space from the bottom of the box to the bar from which the door was hanging.

When the rats learned to push under the swinging doors, the plus and square patterns were introduced. The door with the square was always blocked and its position was changed according to Fellow's (1967) series. The choice of the door bearing the plus sign was rewarded with 7 s of access to the mashed food. The animals were trained to the same criterion as in delayed alternation. As soon as the criterion was reached in the plus-square discrimination, the rat began training on X-diamond discrimination with diamond as the negative stimulus, to the criterion of less than 3 errors in one day. Finally, the rats were given 20 trials in delayed alternation and 20 trials of visual discrimination, ten trials with each pair of the discriminanda. Half of the subjects began with delayed alternation and the other half with visual discrimination. The order was reversed on each successive day. The training continued until the rat made less than 4 errors in one day and less than 13 errors in six days in either maze (10% of errors). On the last day of training the subject was operated. After the recovery period and food deprivation in the last two days of the recovery period the rats were given another run of six days with both tasks under the same conditions as preoperatively.

SURGERY AND HISTOLOGY

Ablations were performed under Equithesin (3.3 ml/kg) anaesthesia with addition of 1 mg/kg atropin. The cortex was removed bilaterally by subpial aspiration (for details of surgical procedures see Mogensen and Divac 1984). The animals were

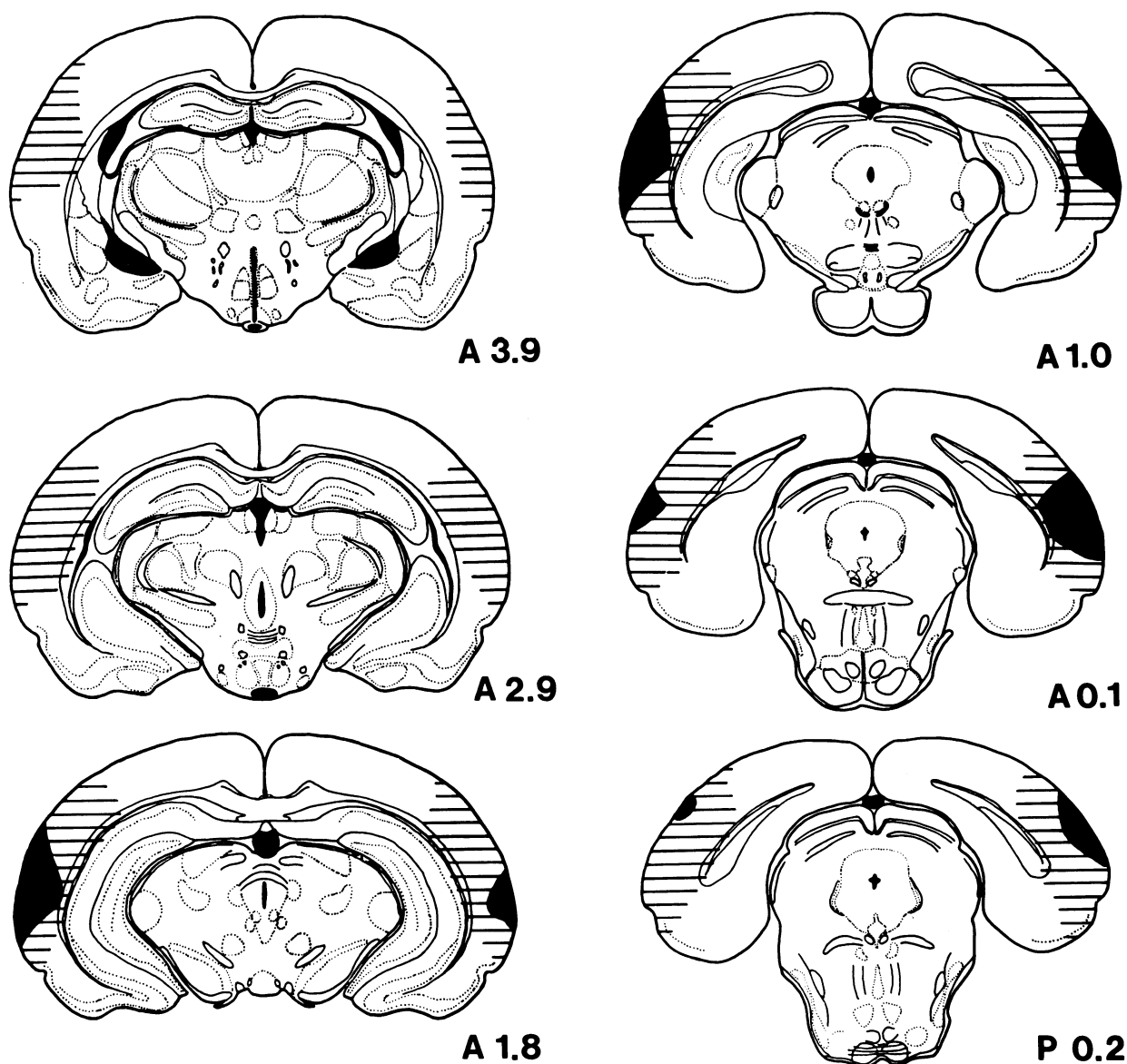


Fig. 1. Lesions in Experiment I. Black: the tissue removed in all animals. Horizontal stripes: the tissue removed in at least one rat.

given 10 days to recover with food *ad libitum* during the first 8 days. Food deprivation was resumed from the last two days of the recovery period. On the last day of the postoperative test each rat was anaesthetized and perfused with saline and formalin. The brains were cut frozen at 20 μ m. One series was stained with cresyl violet and used for reconstruction of lesions.

Results

HISTOLOGY

The posterior cortical lesions damaged variable amounts of area Te2 and Te1 and Te3 (the auditory cortex) as well as the area OC2L (terminology of Zilles 1985). In no instance did we remove the ro-

stroventral portion of Te2 (Fig. 1). Microscopic examination of the dorsal lateral geniculate nucleus (LGNd) revealed a moderate degeneration in one

animal, and barely noticeable degeneration in two other animals. Five other brains showed no signs (in Nissl stain) of degeneration in this nucleus (Fig. 2).

BEHAVIOUR

The results are shown in Table I. Comparison of preoperative and postoperative performance revealed a significant impairment in retention of visual discrimination (Mann-Whitney U-test, $P=0.01$), while retention of delayed alternation was not impaired (Mann-Whitney U-test, $P=0.5645$).

Attempts to correlate lesion size, degeneration of the LGNd and the discrimination performance showed that: (1) the amount of invasion of the auditory cortex was without influence on the perfor-

TABLE I

Errors in the pre- and postoperative retention tests for each individual in the first experiment

	Visual decrimination			Delayed alternation		
	Preop.	Postop.	D	Preop.	Postop.	D
1	10	25	15	10	3	-7
2	5	5	0	10	9	-1
3	3	27	24	8	8	0
4	7	4	-3	8	11	3
5	2	22	20	12	21	9
6	4	19	15	6	11	5
7	3	18	15	8	7	-1
8	5	14	9	10	15	5
Mean	4.9	16.75	11.9	9.0	10.6	1.6

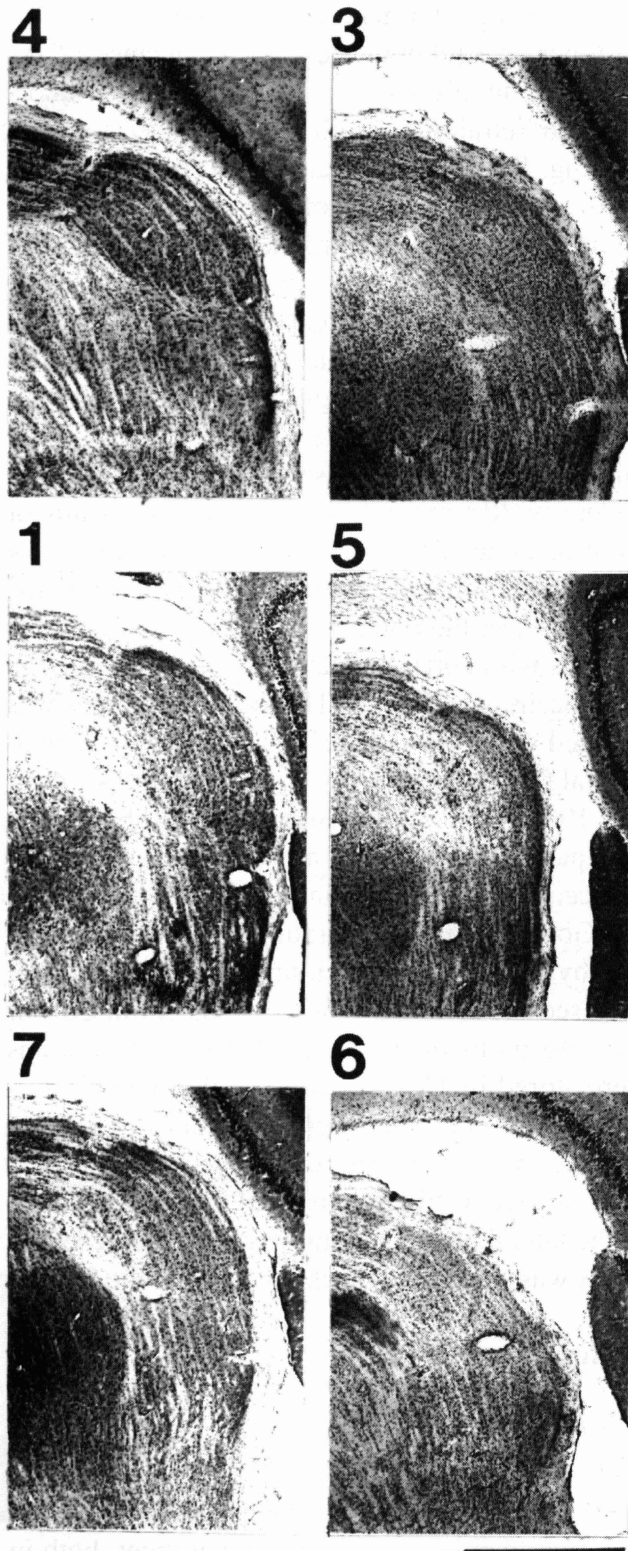


Fig. 2. The range of retrograde degeneration in Experiment I. Each photograph shows lateral geniculate nucleus from a representative coronal section. All pictures are oriented for convenience in the same way, regardless of the side in the brain. The geniculate bodies with the strongest degeneration are shown in the right column, and the comparable levels in animals with no obvious degeneration in the left column. The numbers above the upper left corner of each photograph identify the animal and should be used to compare this figure with Table I. The animal 4 had only a small and superficial cortical lesion on the side of the photographed geniculate body. Bar: 1 mm.

mance, and (2) the largest impairment was found in the animal (No. 3) with considerable degeneration of the LGNd, but two other animals (Nos. 1 and 7) with lesions which invaded only a very small area of the auditory cortex and showed no signs of degeneration in the LGNd were also considerably impaired. (See Table I). No correlation between the degree of impairments in the two task was found.

Comment

Results of Experiment I indicate that the behavioural outcome of lesions of the caudolateral cortex in the rat resemble the effects of inferotemporal cortical lesions in the monkeys: the caudolateral lesions impaired visual pattern discrimination, but not delayed alternation (e.g. Rosvold and Szwarcbart 1964, Dean 1981, Mishkin 1982, Yaginuma et al. 1982).

EXPERIMENT II

The behavioural impairment in the previous experiment was not strong and contribution to this impairment of damage to connections of the primary visual system was remotely possible. We have therefore designed another study in order to make smaller lesions (less likely to undercut the primary visual cortex), to examine thalamocortical connections of the primary visual cortex in operated animals after the behavioural tests and to increase difficulty of the visual discrimination task. We also introduced a sham-operated control group.

Methods

SUBJECTS

Fifteen male Wistar rats weighing about 200 g at the beginning of the experiment were used. They were treated as closely as possible like the animals from the previous experiment. In nine animals the caudolateral cortex was removed bilaterally and six rats received only sham operations (cutting and sewing the skin under anaesthesia).

APPARATUS AND PROCEDURES

The training and testing took place in the Grice box used in the previous experiment, with the same discriminanda and general procedure. During the postoperative retention test, the reluctance of the operated animals to run through the swinging doors required retraining similar to pre-discrimination shaping. When the animals started running again, they were given a new set of discriminanda: two different triangles each surrounded by identical circles. Both triangles were upright, the narrow one had the base 60 mm long and two sides 95 mm each; the broad triangle had a base 100 mm and the sides 75 mm each. Each triangle was surrounded by a circle, 153 mm in diameter. The distance from the middle of the triangle base to the circle vertically under was 30 mm for the tall triangle and 40 mm for the broad one. The rats were trained with the new set of discriminanda during five days. After the retention test the controls were sacrificed and the animals with cortical ablations were reoperated in Equithesin anaesthesia: The occipital cortex was covered with gelfoam soaked in one of two somatopetal fluorescent tracers. In six animals the tracer was 10% bisbenzimidazole (Sigma) applied bilaterally with patches 5 x 5 to 7 x 8 mm centred over the dorsal occipital dura. In two animals the tracer was Fluoro-Gold in 2% concentration. The ninth animal died by accident. After 24 h survival, these rats were perfused and their brains processed according to our standard protocol (Divac et al. 1987). The brains were stored in 15% sucrose solution in 10% formalin until sunk. They were then cut at 40 µm in a cryostat. A Nissl-stained series of sections was used for lesion reconstructions and study of degeneration of the lateral geniculate nucleus. The fluorescence series was studied to check labelling in the LGNd.

Results

HISTOLOGY

The reconstruction of lesions shows a smaller variation than in the previous experiment, both in

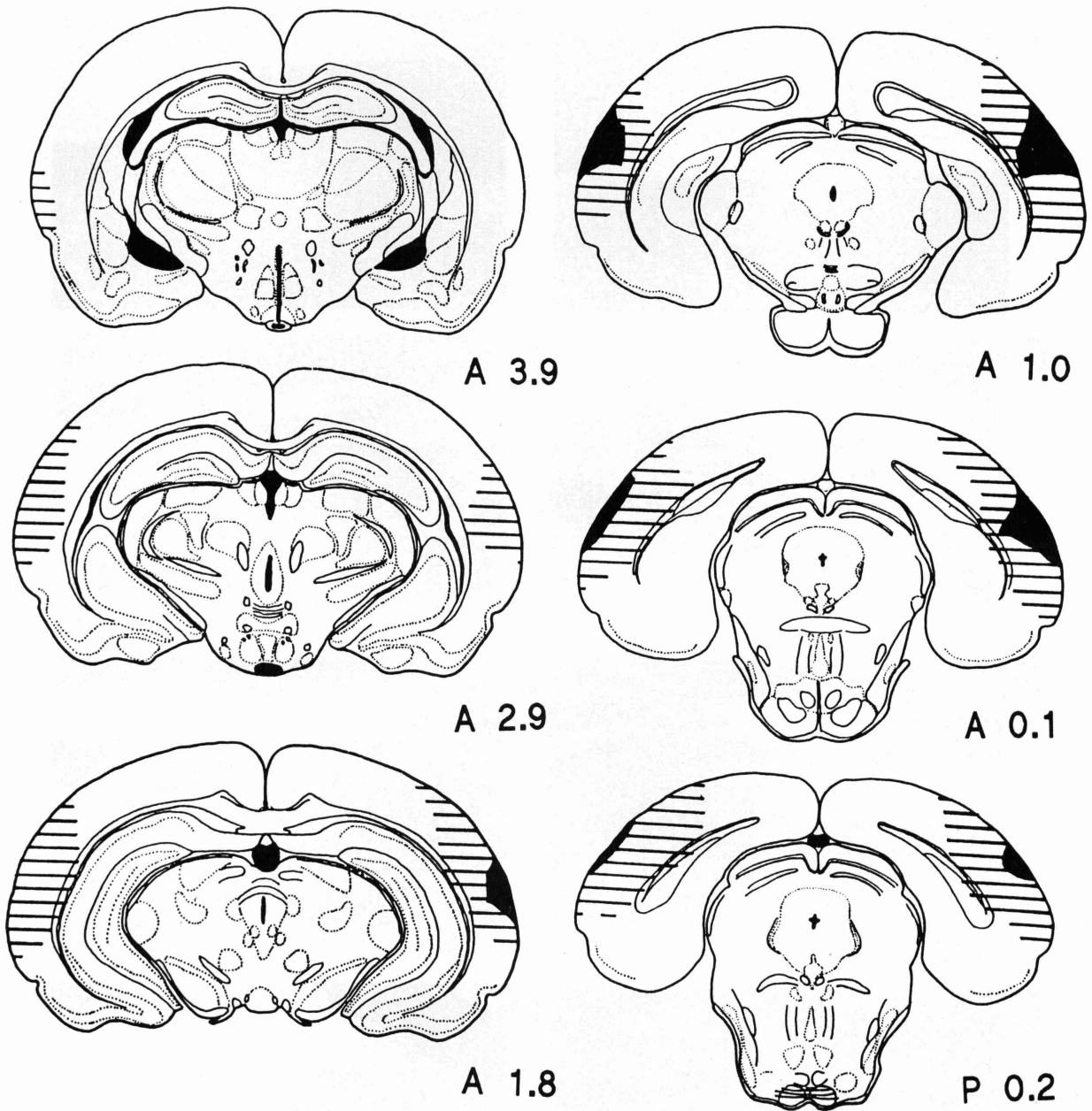


Fig. 3. Reconstruction of the caudolateral lesions in Experiment II. Black: the tissue removed in all animals. Horizontal stripes: the tissue removed in at least one animal.

different animals and between the two sides of each animal. The lesions included approximately two thirds of the Te2 area, 20-50% of OC2L, 10-30% of Te1 and a very small part of Te3. The primary visual cortex was not damaged in any animal (Fig. 3). No retrograde degeneration or gliosis was noticed anywhere in the dorsal lateral geniculate nucleus. Figure 4

illustrates the Nissl staining of the lateral geniculate bilaterally in one animal with caudolateral ablation.

Examination of fluorescence in the LGNd showed bilaterally numerous neurones labelled with bisbenzimidazole in six animals with caudolateral lesions (Fig. 4). Labelling with FG was present but weak due to the inadequate survival time.

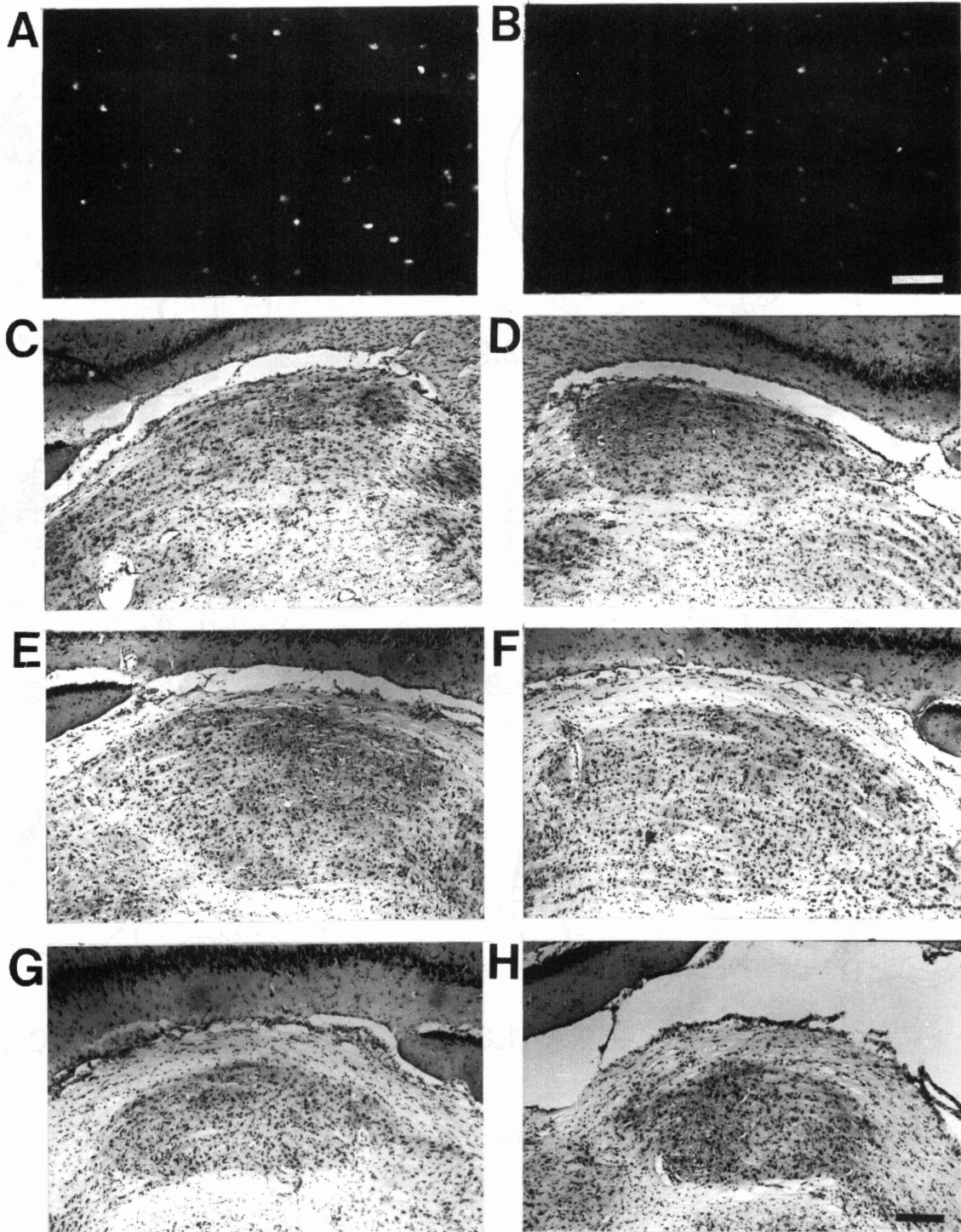


Fig. 4. Dorsal lateral geniculate nucleus (LGNd) in a representative animal from the group with ablation of the caudolateral isocortex in Experiment II. Since all ablated animals failed, illustration from one animal is justified. Left column of photos: the LGNd on the left side of the brain; right column: the LGNd on the right side of the brain. First row: bisbenzimidazole labelling of neuronal nuclei after deposit into the primary visual cortex. These photographs were taken of the middle level of LGNd near the levels E and F, respectively. Notice the difference in magnification of dark- and bright-field photographs. Second row: the rostral end of LGNd. Third row: A-P middle of LGNd. Fourth row: the caudal end of LG. The bar for the dark field pictures: 50 μ m; for the bright field pictures: 150 μ m.

BEHAVIOUR

Postoperative performance on retention tests of the operated animals was confounded by their reaction to running into the blocked door. These errors were followed by exploratory behaviour with long running times and occasional reluctance to go through the correct door. Several animals failed to complete 20 runs on the first few postoperative days. Since this behaviour did not tell us much about discriminatory abilities of the ablated animals with cortical ablations, we retrained all rats to run through blank doors. When the latencies returned to maximally 20 s, the learning of the embedded discriminanda was introduced. The results are shown in Fig. 5. It is obvious that the sham-operated animals quickly learned the new discrimination, while all the rats with ablations of the caudolateral area remained at the chance level throughout the learning period. The range of total errors in five sessions (120 trials in all) was 43-58 for the lesioned group and 14-19 for the controls. On the last day of training the ablated rats made in 20 trials 7-12 errors while the range of the controls was 1-2. Mann-Whitney

U-tests (Siegel 1956) demonstrated group differences to be significant on all 5 sessions on at least the $P < 0.05$ level.

Comment

The behavioural results clearly separated the two groups: every operated rat, regardless of the size of its cortical lesion, failed to discriminate the embedded figures. Sham-operated animals rapidly learned this discrimination. Histology has shown bilateral preservation of viable connections from the LGNd to the striate cortex and lack of retrograde degeneration in the lateral geniculate in lesioned rats. We conclude that the impairment in visual pattern discrimination in the experimental group cannot be attributed to the damage of the primary visual system.

GENERAL DISCUSSION

The results of the two experiments show that the caudolateral cortex in the rat takes part in visual pattern discrimination. This supports Lashley's (1931)

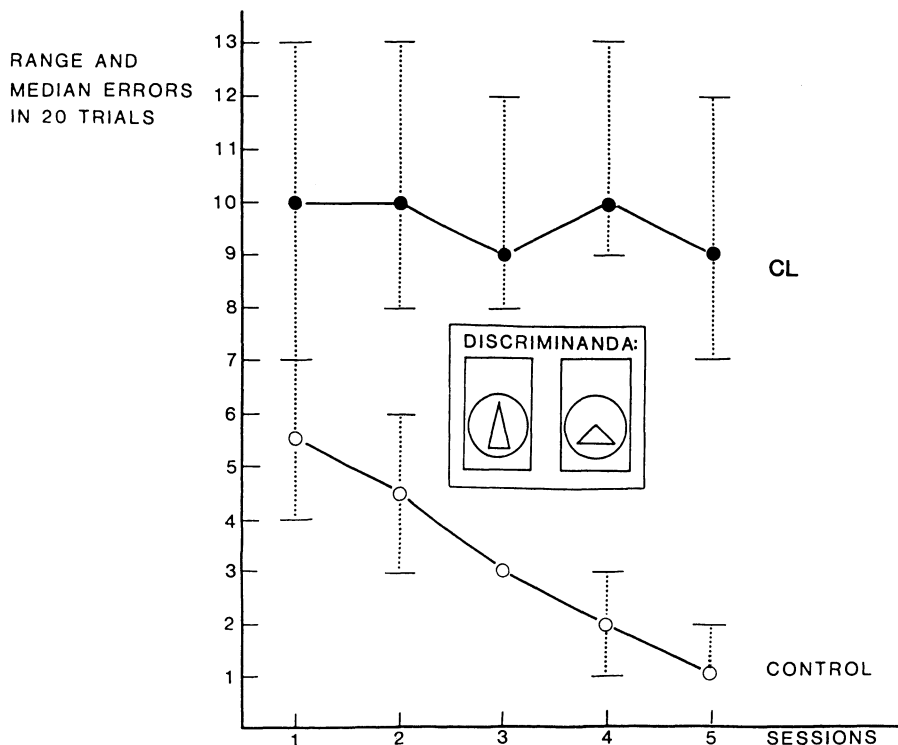


Fig. 5. The performance of the two groups of Experiment II in discrimination of embedded triangles. CL, the group with caudo-lateral lesions.

conclusion about the mechanism of pattern vision in rats. Involvement of this area in mediation of delayed response-type behaviour is insignificant. The same general pattern of behavioural effects is seen after ablations of the inferotemporal cortex in rhesus monkeys (review in Dean 1981). Further similarity between effects of ablations of the inferotemporal cortex in monkeys and the caudolateral area in rats is seen in the severity of impairment in the discrimination of embedded patterns (c.f. Butter 1972 and the results of our Experiment II). Some other similarities between these two areas in monkeys and rats are cited in the Introduction. Similarity between the caudolateral area in the rat and the inferotemporal cortex in the monkey should, however, be considered preliminary for at least two reasons: (1) The impairment seen with simple patterns in the rat is milder than that found in the rhesus monkey. Similar species difference has been found in the consequence of prefrontal ablation on delayed alternation (Wikmark et al. 1973) as well as in the effects of motor cortex lesions (Fulton 1949). We are tempted therefore to attribute the presently observed comparatively mild impairment in retention of visual pattern discrimination to generally smaller consequences of cortical damage in rats than in primates. Alternatively, our lesions did not remove the entire area that mediates pattern vision. (2) Visual pattern discrimination in the two species may in principle be impaired for different reasons. Therefore, only further analysis of behaviour of rats with caudolateral cortical lesions will provide new insights about the nature of the presently noted dysfunction. Some causes of the impairment, however, are ruled out by the close-to-normal performance of the same group in delayed alternation.

Although the combined lesion of thalamic projections to the primary visual and "association" cortex produces a stronger impairment on pattern discrimination than each of them separately (c.f. Hughes 1977), for several reasons we doubt that damage to the primary visual system, indicated by retrograde degeneration of some cells in the lateral geniculate in Experiment I played a decisive role in the outcome. Firstly, rats 1 and 7, without apparent

degeneration of the lateral geniculate nucleus were also considerably impaired. Secondly, in each lesioned rat of Experiment II the discrimination impairment was profound although in none we saw degeneration of LGNd. Furthermore, in the latter group, the preserved thalamocortical connections of the primary visual area have been demonstrated by tracers of axonal transport. Thirdly, Lashley (1939) has shown that simple pattern discriminations similar to that used in Experiment I can be mediated if as few as 700 neurones remain preserved.

The caudolateral cortex in the rat differs anatomically from the macaque monkey inferotemporal cortex in at least two respects: first, the latter receives information from the striate cortex "after at least two stages of processing in prestriate cortex" (Desimone et al. 1980, see also Pandya and Seltzer 1982), whereas OC₂L and Te2 areas are directly connected with the primary visual cortex (Miller and Vogt 1984). In the area "37" of the rat (including Te2 and parts of OC₂L, Krieg 1946, Zilles 1985) about 20% of the neurones project both to the ipsilateral area 17 and the contralateral visuotopically organized visual cortex (Dreher et al. 1990). Sanderson et al. (1991) showed that the ventral portion of the area 36, i.e. Te2 area, projects to visual areas. This observation suggests that area Te2 is a "higher-order" visual area in the rat cortex. The second apparent difference between these areas in macaque monkeys and rats is that in the rat Te2 area receives thalamic innervation not only from the caudolateral nucleus (Mason and Gross 1981, Deacon et al. 1983) but also from the medial geniculate complex (Arnault and Roger 1990). The latter authors believe that Te2 area belongs to the auditory system and that the visual system involves OC₂L and the dorsal bank of the posterior end of the rhinal sulcus.

The intricacy of species comparisons of visual systems has been repeatedly emphasized by Diamond (e.g. Diamond 1979, Diamond et al. 1985). Yet, it is tempting to draw parallels. Thus, in a cortical area of rabbits which topographically closely corresponds to Te2 area of rats, Chow et al. (1977) identified neurones with large visual receptive fields. Neurones with similar properties have

been described in the inferotemporal area of the macaque monkey. Connections of this area in the rabbit brain were shown to resemble those of the inferotemporal area of macaque monkeys (Mathers et al. 1977). In cats, neurobehavioural results (Hara et al. 1974, Campbell 1978) following lesions of caudolateral temporal cortex resemble those reported here.

In conclusion, the occipito-temporal cortex in macaque monkeys and the caudolateral cortex, including areas OC₂L or Te2 or both in rats, show some hodological and functional similarities but also some differences. The visual system in other mammalian species may be similarly organised (see above). It is tempting to propose a correspondence of cortical systems consisting of areas 18, 19 and 20 in macaque monkeys and OC₂L and Te2 in rats.

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