ACTA NEUROBIOL. EXP. 1971, 31: 237-250

THE EFFECTS OF LESIONS OF AUDITORY CORTEX ON DISCRIMINATION OF SOUND LOCALIZATION IN DOG

Genowefa SZWEJKOWSKA and Barbara SYCHOWA [1]

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

The studies by Neff on cats (Neff et al. 1950, 1956) have demostrated that bilateral ablations of the temporal cortex produce dramatic impairments of auditory cue localization. It was considered useful to test his results by a completely different method, namely by utilizing go-no-go differentiation to two auditory stimuli, sounding from different places in standard conditioned reflex experiments.

MATERIAL AND EXPERIMENTAL PROCEDURE

The experiments were performed on 19 mongrel dogs 1.5-4 years old, weighing 11-16 kg. The animals were trained on the stand in a soundproof CR chamber. The feeder with ten bowls was situated in front of the animal. The bowls were successively put into position by remote control. Cubes of bread mixed with minced meat and moisted with broth were used for reinforcement.

After the animals had been habituated to the chamber and experimental procedure, they were trained in instrumental responding. The auditory stimulus, the source of which was in front of the dog, was presented, whereupon the technician raised the dog's right foreleg and placed it on the feeder. Then immediately the bowl with the food was presented and the stimulus was discontinued. When the leg was not raised, the food was not given.

After a few days the dog learned to place his foreleg on the feeder

[1] Present address: Laboratory of Neuroanatomy, Department of Comparative and Systematic Zoology, Polish Academy of Sciences, Cracow, Poland.

actively, in response to the CS, and the movement was immediately reinforced by food. The intertrial movements, not being reinforced, were extinguished.

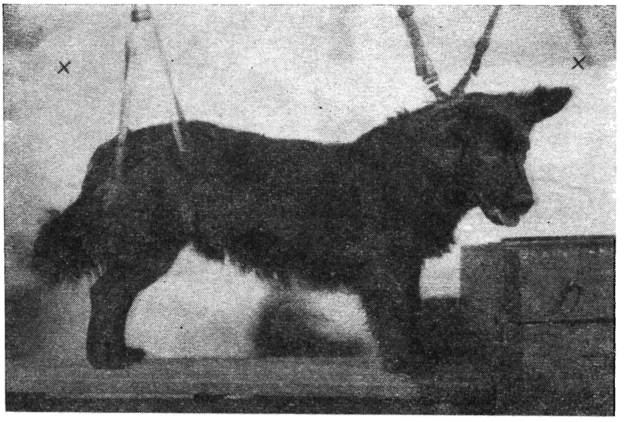

Fig. 1. The dog on the stand. × denotes the sources of the auditory stimuli.

When the dogs began to react regularly to the CS, differentiation training began. In some trials the auditory stimulus, the source of which was behind the dog (Fig. 1), was given and then the presentation of food did not follow. Five positive and five negative trials were given in each session in random order with 1–2 min intervals. The non-reinforced CS lasted always 5 sec.

Thirteen dogs were used in these experiments. In case of eight dogs two metronomes beating with the frequency of 120 per second were used as the CSs, the metronome sounding from the front being positive, and that from behind being negative. In the remaining five dogs the tones 900 cycle/sec emitted from two loudspeakers were used as the CSs, that in front being positive, that behind, negative.

The criterion of the differentiation training was 90% correct responses in a block of ten sessions (100 trials). After the dogs had reached this criterion, control experiments were performed in which the location of the devices producing the auditory stimuli were exchanged. This was done in order to see whether the animals were guided actually by directional cues, or by slight difference in the quality of both sounds (metronomes or tones). It turned out that this procedure produced, in the metronome group, a slight disorder in animals' responding, not exceeding however 10% of all responses. As far as the tone group is concerned, all the dogs were undisturbed, except one animal in which, for unknown reason, a considerable disinhibition of the negative CR occurred. This shows that the directional cues were in fact decisive in the animals' performance both for metronomes and tones, although the dogs did discriminate between the sounds of the metronomes produced by each of the two apparatuses used in these experiments.

After the preoperative training had been completed, the animals were subjected to surgery. In Nembutal narcosis and in aseptic conditions the temporal areas of the cortex were removed on the right and on the left side in two stages. The interval between the two operations was 3–4 weeks. The gray matter was removed by subpial suction and care was taken to spare the white matter and claustrum. About 10 days after the surgery the experiments were resumed.

In the metronome group four dogs sustained ablations including the whole ectosylvian gyri (anterior, medial and posterior) and sylvian gyri (anterior and posterior); two dogs sustained only ectosylvian ablations and two dogs sustained only sylvian ablations. All five dogs in the tone group sustained the combined ectosylvian and sylvian ablations (Fig. 2).

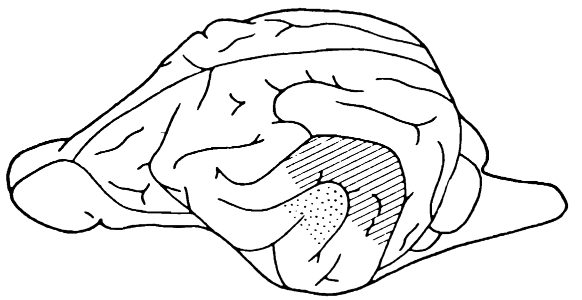

Fig. 2. Extent of lesions. Hatched area, ectosylvian lesion; dotted area, sylvian lesion.

Six other dogs were used as controls and were trained in non-directional cues. In three dogs the same two metrononomes were used, but they were placed side by side in front of the animals. One of the metronomes was positive, the other one negative. In the remaining three dogs two tones were given from a loudspeaker situated in front of the animals; tone 900 cycle/sec was positive, tone 400 cycle/sec was negative. All six dogs were subjected to combined ectosylvian-sylvian ablations.

To sum up the following six groups of animals were used in our experiments: M-D-ES group, M-D-E group, M-D-S group, T-D-ES group, M-noD-ES group and T-noD-S group. M-D, means metronome directional cues, T-D, tone directional cues; M-noD, metronome non-directional cues; T-noD, tone non-directional cues. ES, means combined ectosylvian-sylvian lesion; E, ectosylvian lesion; S, sylvian lesion.

RESULTS

Directional cues. After unilateral temporal lesions the general behavior of the dogs as well as their CR activity, was completely normal, except in a few cases in which the inhibitory responses to the negative CSs were disinhibited. After the second operation, however, the behavioral disturbances in some dogs were manifest: the animals were disquiet and failed to accept food. These symptoms were transient and disappeared after a few days. Only in one dog (M-D-ES 1), a clear visual deficit was observed after operation, and the CRs to the positive CSs were absent for a number of days.

TABLE I

Training in discrimination of directional cues before and after operation

Dog	Number of trials		Number of errors			
			Before operation		After operation	
	Before operation	After operation	Positive trials	Negative trials	Positive trials	Negative trials
M-D-ES 1	400	800	16	28	45	95
M-D-ES 2	300	700	6	35	3	152
M-D-ES 3	300	800	12	6	0	107
M-D-ES 4	400	500	15	40	0	81
M-D-E 1	300	800	21	16	3	202
M-D-E 2	300	600	9	12	2	80
M-D-S 1	300	100	11	59	0	7
M-D-S 2	200	100	5	8	0	2
T-D-ES 1	600	1500[a]	12	58	45	219
T-D-ES 2	500	1300	8	58	3	215
T-D-ES 3	900	1500[a]	15	180	31	465
T-D-ES 4	700	1500[a]	26	111	127	334
T-D-ES 5	700	1500[a]	17	104	7	234

[a] The dog failed to reach criterion.

The effects of bilateral lesions on the CR performance are presented in Table I and in Fig. 3 and 4. It can be immediately noticed that after joint ablations of ectosylvian and sylvian gyri there is a dramatic impairment of the differentiation of the directional CSs. This impairment was clearly visible on simple observation of the experimental dogs. Before operation both CSs, the positive and negative one, produced clear directional responses, consisting in the dog's looking intensely towards the source of the stimulus. After operation this response was gone: the animal reacted to the CS by increased alertness and an instrumental response, but failed to turn to its source; this was particularly manifest in respect to the negative (that is, posterior) stimulus.

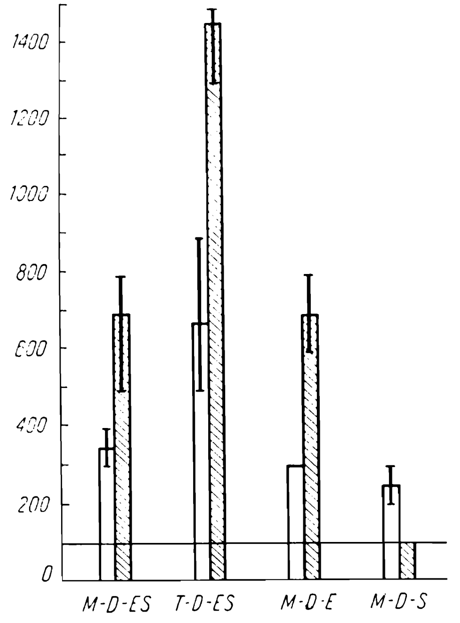

Fig. 3. The effect of temporal lesions in dogs trained in directional auditory discrimination. Each column denotes mean number of errors. White columns, before operation, hatched columns, after operation. The vertical lines show the range of number of trials. M-DE-S, M-D-E, M-D-S, metronome discrimination before and after ectosylvian-sylvian, ectosylvian and sylvian lesions respectively. T-DE-S, tone discrimination before and after ectosylvian-sylvian lesions. The line on the 100 trials level means training criterion.

It can be seen both in Table I and in Fig. 3 and 4 that the original training was much easier in case of the metronome differentiation than in the tone differentiation. The postoperative retraining took also a different course in both groups of animals. Whereas in the metronome group subjected to the joint ectosylvian-sylvian ablations, the animals reached criterion after twice as much trials as in original training, in the tone group only one animal (T-D-ES 2) reached criterion, while the rest failed to do so even after 1500 trials. As seen in Fig. 4, their performance did not improve after this lengthy retraining.

In order to see which part of the temporal cortex is essential for this test, the following partial lesions were made in four animals: in two of them the whole ectosylvian cortex was removed, in the two others the sylvian cortex was ablated. It can be seen that whereas the ectosylvian lesion produced a deficit quite identical to that obtained after joint lesion, the sylvian lesion failed to produce any deficit: both sylvian animals reached criterion in the first 100 trials.

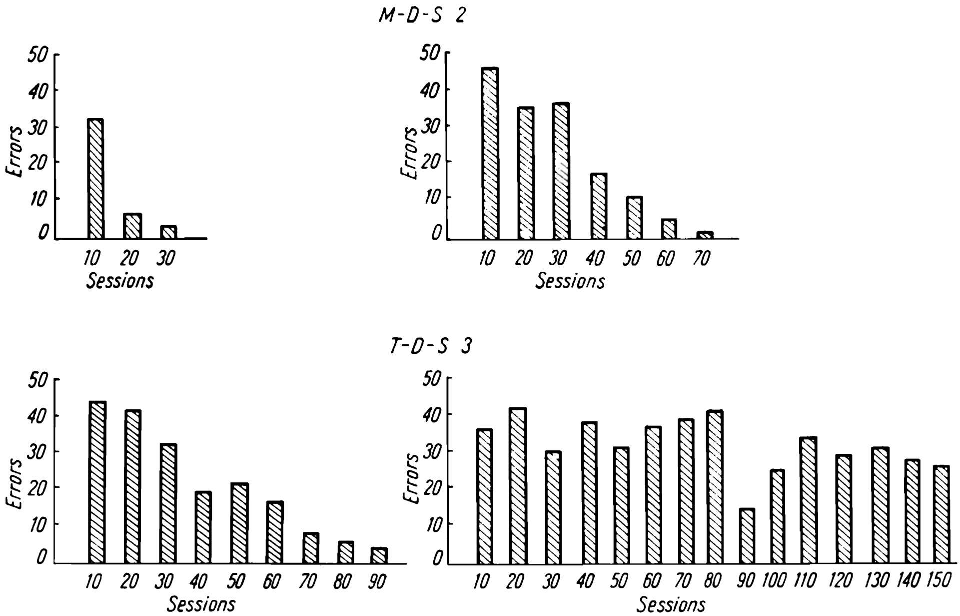

Fig. 4. Training before and after operation in one dog of the metronome group (M-D-ES 2) and in one dog in the tone group (T-D-ES 3).

Non-directional cues. As it has been mentioned in the description of the method, control experiments, consisting in the exchange of the devices producing the positive CS and the negative CS gave a somewhat unexpected result. The metronome transferred from the anterior position to the posterior position produced disinhibition in 9–10% of trials, thus showing that the dogs paid attention not only to the location of the stimuli, but also to their *quality.* This was not true with regard to tones which produced responses based entirely on the location of the sounds, the dog which displayed disinhibition in 30% of trials being an exception.

Therefore, the supposition arose that the successful, though difficult, retraining of the metronome differentiation after the operation may be due to the fact, that the animal can switch its strategy and base it now on the qualitative differences of the two stimuli, which before the operation played only a minor role. To test this supposition, in three animals both metronomes were located in front of the animals close to each other.

In these condition differentiation of two CSs was trained, and then the usual ablation of the temporal region was made.

TABLE II

Training in control experiments in which two metronomes were situated in front of the dog before and after operation

Dog	Number of trials		Number of errors			
	Before operation	After operation	Before operation		After operation	
			M +	M —	M +	M —
M-noD-ES 1	500	100	8	103	0	3
M-noD-ES 2	400	100	21	50	3	9
M-noD-ES 3	900	400	4	153	11	29

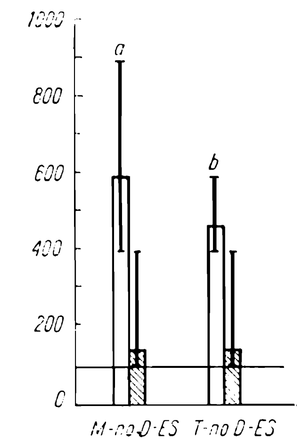

Fig. 5. Training before and after operation in control experiments. Each column denotes the mean number of trials before (white) and after (hatched) operation. *a*, two metronomes were situated in front of the dog; *b*, two tones came from the front of the dog. The vertical lines show the range of number of trials.

These experiments, presented in Table II and Fig. 5*a* confirmed this supposition. First, the original M-noD differentiation, although lasting longer than the previous M–D differentiation, was successful, thus showing that the two devices did in fact produce different sounds, which could be discriminated by the dogs. But secondly, it was found that after bilateral temporal lobotomy the animals' performance, although in two does not quite normal, very quickly reached the criterion manifesting good savings. In one dog the performance was quite correct. This result showed that after temporal lesion the sound–quality differentiation was in fact either not, or only slightly, affected and the deficit was easily compensated.

This finding was further corroborated by experiments performed on the other group of animals in which two tones from one loudspeaker situated in front of the dog were utilized: tone 900 cycle/sec was positive,

TABLE III

Taining in control experiments in which two tones sounded from the front of the dog before and after operation

Dog	Number of trials		Number of errors			
	Before operation	After operation	Before operation		After operation	
			T_{900} +	T_{400} −	T_{900} +	T_{400} −
T-noD-ES 1	600	100	17	60	0	8
T-noD-ES 2	400	100	19	32	0	7
T-noD-ES 3	400	400	7	64	12	27

tone 400 cycle/sec was negative. The results of these experiments are presented in Table III and Fig. 5*b*. It can be seen that this differentiation required roughly the same number of trials as that with M-D differentiation, but the temporal lesions had a quite different effect. In two dogs there were good savings and in one dog the performance was not affected at all.

Histological analysis

After the postoperational training had been completed the dogs were sacrificed, their brains were perfused with formaline and fixed. Every fifth paraffinal section (thickness 20μ) was stained by means of the Nissl method. Then the histological verification of lesions was made and the retrograde degeneration of the geniculate bodies was examined.

Large lesion of the acoustic area (ectosylvian and sylvian gyri). Four dogs with this type of lesion were studied: M-D-ES 1, M-D-ES 2, M-D-ES 3, M-D-ES 4. In all these animals the suprasylvian sulcus was practically the external boundary of the lesion except the ventral side which was different in particular cases. The largest lesion was made in the M–D–ES 3 dog. In the M–D–ES 4 only one the medial ectosylvian and sylvian gyrus were removed. Microscope examination of the surroundings of the lesions has shown that the underlying white matter was strongly involved in the lesion in the M-D-ES 1 dog, and slightly in M-D-ES 2 and M-D-ES 3. The lesion of M-D-ES 4 was superficial, the white matter in the subcortical region was practically undamaged (Fig. 6*A* and *B*).

In general a strong retrograde degeneration was found to occur in the medial geniculate bodies except their oral part in M-D-ES 2 and M-D-ES 3, where a number of normal cells were observed. The retrograde degeneration of M-D-ES 1 appeared to be the strongest one. All the changes mentioned above were correlated with an extensive degene-

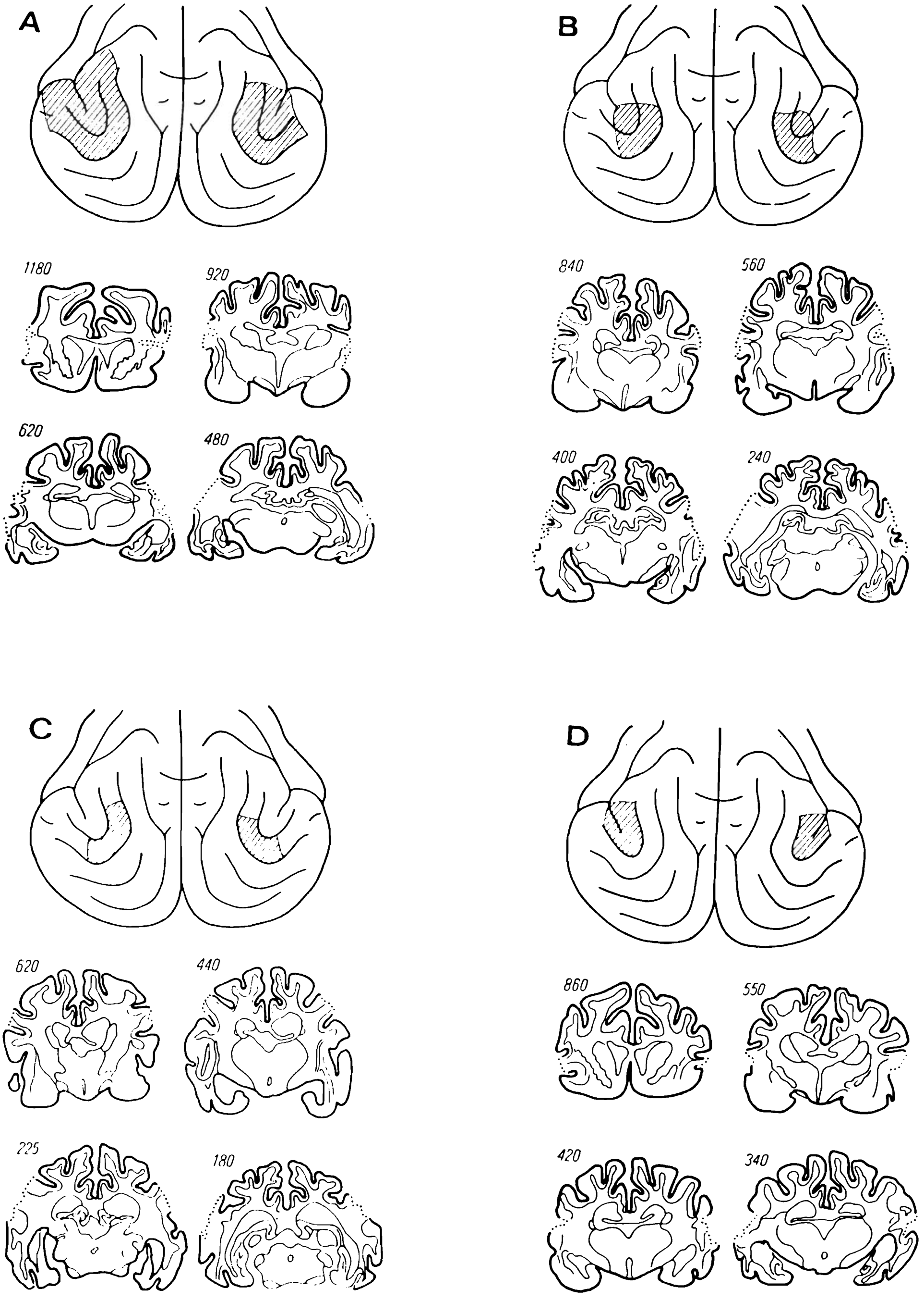

Fig. 6. Extent of lesion and serial frontal slides; *A,* dog M-D-ES 2; *B,* dog M-D-ES 4; *C,* dog M-D-E 1; *D,* dog M-D-S 1.

ration in different thalamic nuclei and the degree of those degeneration seems to be proportional to the size of damage of cortical connections in white matter (Sychowa 1963).

Lesion of the ectosylvian gyrus. Two dogs, M-D-E 1 and M-D-E 2 belonging to this group are described here. An elongated lesion covered the whole ectosylvian gyrus in M-D-E 1 but in M-D-E 2 only the medial ectosylvian gyrus was damaged. In both these cases microscope investigations have shown that only the cortical matter had been removed (Fig. 6C).

Retrograde degeneration was found to occur in the ventral–oral part of the medial geniculate body. There was a distinct difference between M-D-E 1 and M-D-E 2 as regards the degree of retrograde degeneration, which was stronger in M-D-E 1.

Lesion of the sylvian gyri. Two dogs of this type were examined, M-D-S 1 and M-D-S 2. The external extention of the ablation was limited by sulcus sylvii, and from the ventral side the lesion reached the

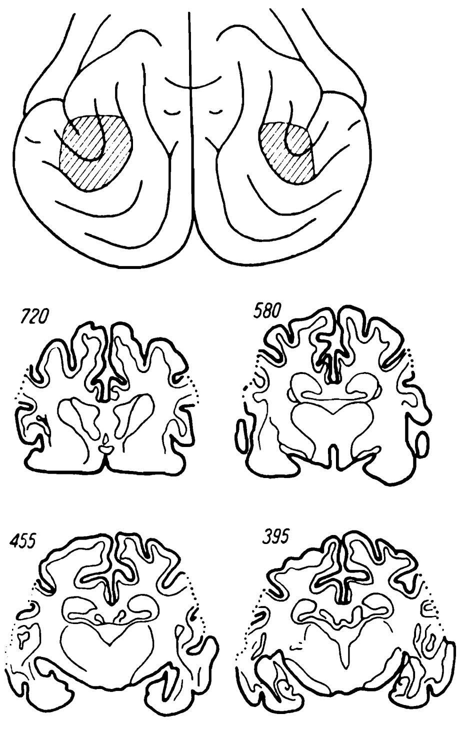

Fig. 7. Extent of lesion and serial frontal slides. Dog T-D-ES 3.

rhinal sulcus. Considerable damage of white matter was seen to occur in M-D-S 1 whereas in M-D-S 2 only cortical matter was involved.

Retrograde degeneration of the caudal part of the medial geniculate body could be easily seen. However, in M-D-S 1, where white matter was also damaged, the degeneration appeared to be stronger than in M-D-S 2 and orally elongated (Fig. 6*D*).

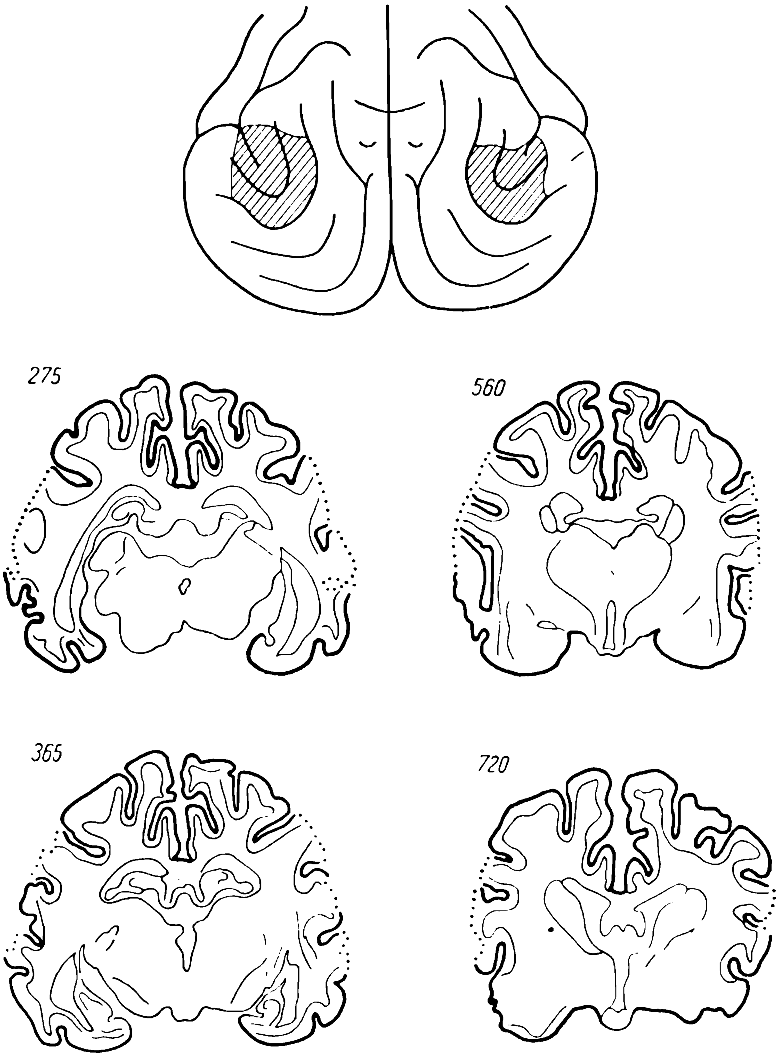

Fig. 8. Extent of lesion and serial frontal slides. Dog M-noD-ES 2.

Lesions in the tone group. Besides the metronome group, a large lesion of the acoustic area was in the tone group. Five dogs of this group were accomplished (T-D-ES 1, T-D-ES 2, T-D-ES 3, T-D-ES 4 and T-D-ES 5). The extention of the ablation was practically similar to the metronome group, however, in the tone group, only the cortical layer had been removed (Fig. 7). In all cases microscope investigation of the medial geniculate body shows retrograde degeneration in its ventral part.

Lesions in the control groups. In both control groups (first group: M–noD–ES 1, M–noD–ES 2, M–noD–ES 3, second group: T–noD–ES 1, T–noD–ES 2 and T–noD–ES 3) the extention of lesions and retrograde degeneration in the medial geniculate body were similar to those in the group with a large lesion in the acoustic area (Fig. 8). In these control dogs the conditioned reflexes were not impaired.

DISCUSSION

Present experiments entirely support the view, earlier advanced by Neff (1950, 1956) to the effect that lesions in the temporal region are detrimental for the discrimination of directions from which the sounds are produced. Even the discrimination of a difference of sound directions as great as the one that was used in the present experiments, when one sound was emitted from in front of the dog, and the other one from behind, does not remain after the bilateral temporal lesion and makes the dog completely and irreversibly helpless, as it is seen in experiments with T-D differentiation. The fact that omission errors in positive trials are much less frequent than commission in negative trials is easily explainable by the circumstance that the dog eventually adopts the strategy used in irregular reinforcement; in fact, this way of reacting ensures the animal to receive the maximal amount of reinforcement in each session.

The experiments with the metronomes are very significant, although their interest was totally due to a methodological error: the experimenter failed to notice that the sounds emitted by the two metronomes had a slightly different timbre, and therefore their recognition could be made not only on basis of their direction, but also on basis of their quality. Accordingly, when after the temporal lesions the directional cues were no longer relevant, the dogs switched to the qualitative ones and thus solved the problem. This switching was not possible in those cases in which the two identical tones were presented, hence the task appeared to be unsolvable. However, when the two tones did differ in their quality (900 cycle/sec versus 400 cycle/sec), the temporal lesion impaired their discrimination very slightly, or not at all.

According to other authors, the effects of temporal lesions upon tone frequency discrimination are ambiguous. According to some of them (Butler et al. 1957, Goldberg et al. 1958, Thompson 1958, Goldberg and Neff 1961), after these lesions have occurred cats are able to discriminate tone frequencies, although in most cases the task has to be retrained. On the contrary, Meyer and Woolsey (1952) obtained opposite results, but since they used avoidance training, these results are not conclusive. The fact that in our experiments the impairment was quite insignificant, if present at all seems to solve the problem at least for dogs. It should be noted, however, that our tone differentiation was rather crude, and we do not know what effect would be obtained, if the difference of frequency were small. Anyhow, it is quite clear that after bilateral removal of the auditory area the defect of directional auditory discrimination is incomparably greater, than discrimination of sound qualities.

According to our data the ablations of ectosylvian gyri produce the same defects of directional discrimination as ablations of the ectosylvian and sylvian areas. On the other hand, the sylvian ablation seems to be almost ineffective. These results are in good agreement with the recent data of Strominger (1969).

SUMMARY AND CONCLUSIONS

1. The experiments were concerned with the problem of the effects of temporal lesions on the go–no-go differentiation of sounds emitted from different places (in front of the animal and behind it) in dogs.

2. It was found that when the quality of the auditory stimuli is identical, as was the case with the same tones emitted by two loudspeakers, the bilateral removal of the ectosylvian and sylvian gyri produce an irreversible loss of tone differentiation; this shows that the temporal region of the cortex is indispensable for discrimination of the location of sound stimuli.

3. When the auditory stimuli differ not only in their location, but also slightly in their timbre (as was the case with two metronomes), then after the ablation of the temporal cortex, the differentiation can be retrained, although it requires twice as many trials as before the operation.

4. The differentiation of two qualities of auditory stimuli sounding from the same place is slightly or not at all impaired after bilateral temporal lesions.

5. Partial removal of the temporal cortex including only the whole ectosylvian gyrus produces the same effect as the total lesion; on the other hand, the removal of the sylvian gyri does not produce any defect in the location of sounds. Unilateral lesions are also without effect.

6. The histological analysis of the lesions is in good agreement with the behavioral data.

The authors are indebted to Professor L. Stępień and Mrs. Maria Raurowicz who kindly performed the operations.

REFERENCES

BUTLER, R. A., DIAMOND, I. T. and NEFF, W. D. 1957. Role of auditory cortex in discrimination of changes in frequency. J. Neurophysiol. 20: 108–120.

GOLDBERG, J. M., DIAMOND, I. T. and NEFF, W. D. 1958. Frequency discrimination after ablation of cortical projection areas of the auditory system. Fed. Proc. 17: 55. (Abstr.).

GOLDBERG, J. M. and NEFF, W. D. 1961. Frequency discrimination after bilateral ablation of cortical auditory areas. J. Neurophysiol. 24: 119–128.

MEYER, D. R. and WOOLSEY, C. N. 1952. Effects of localized cortical destruction on auditory discriminative conditioning in cat. J. Neurophysiol. 15: 149–162.

NEFF, W. D., ARNOTT, G. P. and FISHER, J. D. 1950. Function of auditory cortex: localization of sound in space. Amer. J. Physiol. 163: 738. (Abstr.).

NEFF, W. D., FISHER, J. F., DIAMOND, I. T. and YELA, M. 1956. Role of auditory cortex in discrimination requiring localization of sound in space. J. Neurophysiol. 19: 500–512.

STROMINGER, N. L. 1969. Subdivisions of auditory cortex and their role in localization of sound in space. Exp. Neurol. 24: 348–362.

SYCHOWA, B. 1963. Degenerations of the medial geniculate body following ablations of various temporal regions in the dog. Acta Biol. Exp. 23: 75–99.

THOMPSON, R. F. 1958. Function of auditory cortex of cat in frequency discrimination. Fed. Proc. 17: 163 (Abstr.).

Received 19 October 1970