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THE EFFECTS OF THE REMOVAL OF THE SOMATOSENSORY AREAS I AND II ON LEFT LEG-RIGHT LEG DIFFERENTIATION TO TACTILE STIMULI IN DOGS

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Abstract. **Dogs were trained** to lift the right forelegs to a rhythmic tactile stimulus applied to right side of the trunk, and to the lift the left forelegs to a tactile stimulus applied to the left side of the trunk. After training was completed various ablations of sensory I area and sensory II area were made. It was found that the task was impaired after unilateral or bilateral SII lesions, but was virtually preserved after SI lesions.

INTRODUCTION

In our previous experiments concerning instrumental responses to tactile stimuli in dogs it was shown that if two apparatuses for tactile stimulation are attached to the wrists of left and right forelegs respectively, and the dog is trained to lift the stimulated leg for food reinforcement, then the differentiation training is very easy and the animal's responses are almost errorless (C. Dobrzecka, in preparation, Konorski 1970).

The problem arose as to whether the same easiness of the formation left leg-right leg differentiation is encountered when tactile stimuli are applied, not to the legs involved in instrumental conditioning, but to the symmetrical parts of the body. The answer to this question was negative: the left leg-right leg differentiation to symmetrical tactile stimuli administered to the trunk is difficult and requires several hundreds of trials. The reasons of this difficulty will be discussed in the next paper (C. Dobrzecka, in preparation) where it will be shown that after sectioning of the corpus callosum this differentiation becomes quite easy.

The present paper is concerned with the problem of the role played by various parts of the somatosensory cortex in discrimination of tactile stimuli applied to the symmetrical parts of the body.

MATERIAL AND METHODS

The experiments were performed on 14 male dogs in a Pavlovian sound-proof CR chamber. The dog was placed on the stand and the feeder with moving bowls was situated in front of him. Food reinforcement was given by putting the bowl under an aperture of the feeder by remote control. The device serving to produce tactile conditioned stimuli (T-CSs) was composed of a small round plate with blunt needles fixed to a rubber harmonica and placed inside a small cylinder (Fig. 1). The cylinder was attached to the side of the trunk behind the chest. The needles did not touch the body, unless the harmonica was extended by the experimenter pressing a rubber bulb connected to the harmonica by a rubber tube. T-CS was rythmic, the rate being about 1 per second.

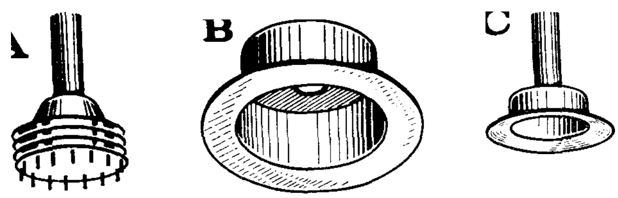

Fig. 1. Apparatus for tactile stimulation. *A,* harmonica with the plate furnished with blunt needles; B, the cylinder; C, the whole apparatus.

The experimenter observed the animal by the one-way window from the pre-chamber; he presented both T-CSs by pressing the corresponding rubber bulbs and putting the bowls into position by electrical control.

After preliminary training, in which the dog was habituated to the experimental conditions, he was trained, by the method of passive movements, to place the right foreleg on the feeder in response to the right T-CS (RT-CS) and to place the left foreleg on the feeder in response to the left T-CS (LT-CS). Immediately after the movement was executed food was presented.

The passive movements were attained by a technician standing in front of the animal and pulling a string with the end fixed to the wrist of the appropriate foreleg. After a few days of such training the animals learned to perform the required movements actively. When this stage was reached, the dog was left alone in the chamber. If he performed the wrong movement, that is, he raised the left foreleg in response to the RT-CS or raised the right foreleg in response to the LT-CS food was not presented. Food was also not given when in the same trial the animal performed first the wrong response and then the correct one, or when after a five second operation of the T-CS no movement followed.

Each experimental session consisted usually of nine trials separated by about 1 min intertrial intervals. No correction method was used and in each session four LT-CSs and five RT-CSs, or vice-versa, were given in random order. Experiments were performed daily, except on Sundays.

Some dogs were trained in the same way to perform the movements of the forelegs not only to the T-CSs, but also to two auditory stimuli (A-CSs). In response to the tone 1500 cycle/sec emitted by the loudspeaker situated on the front wall of the chamber (FA-CS), the dog had to perform the movement with the right foreleg; in response to the tone 300 cycle sec entitled by the loudspeaker situated on the back wall of the chamber (HA-CS) be bad to perform the movement with the left foreleg.

When the differentiation training to the T-CSs, or T-CSs and A-CSs was completed and the animals committed no more than 5% of errors in 10 consecutive sessions, cortical ablations were made. They were either bilateral and involved either only sensory area I (SI), or sensory area II (SII), or both SI and SII. According to the character and sequence of lesions three groups of animals may be distinguished:

Group I (two dogs). Bilateral SI ablation followed after a few weeks by right SII ablation.

Group II (six dogs). SI and SII ablation on the right side followed (in five dogs) after a few weeks by SI and SII ablation on the left side.

Group III (six dogs). Bilateral SII ablation in one stage.

Surgery was performed under Nembutal narcosis in aseptic condition. After removal of the part of the bone incision in the dura mater was made and the cortex in the limits shown in Fig. 2 was removed by suction. The dura was closed, as well as subcutaneous tissue and skin. Operations were performed either in one stage or in two stages separated by a few weeks.

Experiments were resumed about 1 week after surgery and ran in exactly the same way as before operation. They lasted either till the second surgery, or till the animal reached criterion. Then the dog was sacrificed his brain was perfused by 10% formalin, and routine histological examination serving for reconstruction of lesion was made.

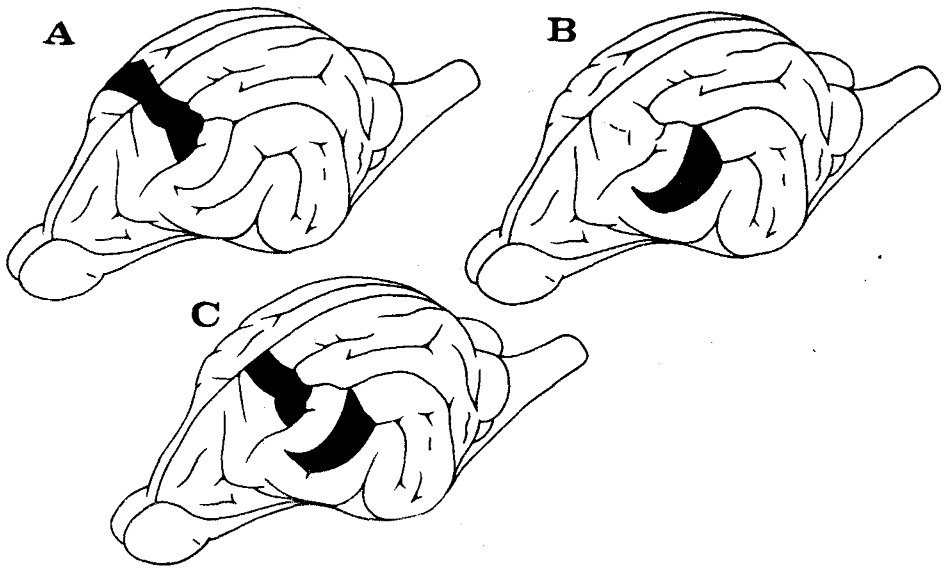

Fig. 2. The extent of operations performed in our dogs: A, SI operation, *B*, SII operation, C, SI + SII operation.

RESULTS

In contradistinction to the training in which the tactile stimuli are applied to the distal parts of the forelegs, the present training with the T-CSs applied to the symmetrical parts of the trunk appeared to be much more difficult. When the dogs learned to react to the T-CSs by placing one of the forelegs on the feeder, this did not mean that their responses were always correct. On the contrary, quite often the LT-CS was followed by lifting the right foreleg, or vice-versa. The training lasted on average several months and required more that 100 trials. A typical course of training concerning both tactile and auditory differentiation is presented in Fig. 3.

The effects of various cortical ablations are presented in Tables I and II. Table I represents wrong responses (or no-responses) to each CS in the first 20 trials given after surgery. In Dog 3 and 6 after the first operation only 10 trials for each CS are shown, because the second operation was performed earlier than in other dogs. Table II represents the percentage of wrong responses (including no-responses) to each CS after the final operation, till the animals reached criterion.

Beneath we present in detail the effects of all operations.

Group I (Dogs 1 and 2). After bilateral removal of SI areas neither the tactile differentiation nor the auditory differentiation was impaired.

Table I

Number of wrong responses to each CS in first 20 trials after surgery

	Dogs	First operation	Numbers of wrong responses				Second operation	Numbers of wrong responses			
			RT-CS	LT-CS	FA-CS	HA-CS		RT-CS	LT-CS	FA-CS	HA-CS
Group I	1	SI bilateral	0	0	0	0	SII right side	0	19	0	0
	2	SI bilateral	1	2	—	—	SII right side	0	20	—	—
Group II	3	SI SII right side	0	(2) 8	0	0	SI SII right side	(5) 15	0	(1) 6	0
	4	SI SII right side	0	(1) 16	0	1	SI SII left side	(7) 7	4	0	0
	5	SI SII right side	0	12	—	—	SI SII left side	2	16	—	—
	6	SI SII right side	0	(2) 8	—	—	SI SII left side	19	1	—	—
	7	SI SII right side	0	(3) 7	—	—	SI SII left side	(4) 2	(4) 16	—	—
	8	SI SII right side	0	17	0	0					
Group III	9	SII bilateral	(3) 3	(7) 12	3	11					
	10	SII bilateral	(2) 3	(7) 9	8	6					
	11	SII bilateral	(4) 6	(3) 14	—	—					
	12	SII bilateral	7	(2) 8	—	—					
	13	SII bilateral	(2) 5	(1) 16	—	—					
	14	SII bilateral	(3) 11	(4) 13	—	—					

Numbers in parenthesis denote lack of responses. Numbers in quadrangles denote errors in first 10 trials.

TABLE II

The effects of cortical lesions on left leg–right leg differentiation

	Dogs	Operation	Percentage of wrong responses				Period of observation after last operation (in months)	Anatomy[a]			
			RT-CS	LT-CS	FA-CS	HA-CS		right side		left side	
								SI	SII	SI	SII
Group I	1	SI bilateral SII right side	0	70.00	0	0	2	t	t	t	—
	2	SI bilateral SII right side	0	69.44	—	—	2.5	t	t, EWM	t, EC	—
Group II	3	SI SII right side left side	100.00	0	3.33	0	more than 12	t	t, EWM	p	t
	4	SI SII right side left side	10.71	65.00	0	0	4	t	t	t	t
	5	SI SII right side left side	21.54	35.90	—	—	1	t	t	t	t
	6	SI SII right side left side	89.47	7.89	—	—	2	t	t	t	t, EWM
	7	SI SII right side left side	3.48	84.35	—	—	2	t	t, EWM	t, EWM	t, EWM
	8	SI SII right side	6.66	65.00	0	0	4	t	t, EWM	—	—
Group III	9	SII bilateral	14.00	70.00	8.00	46.00	1.5	not examined			
	10	SII bilateral	11.78	61.11	35.18	31.48	3	—	t, EWM	—	x, EWM
	11	SII bilateral	20.00	57.78	—	—	3.5	—	t	—	t
	12	SII bilateral	6.09	18.70	—	—	3	not examined			
	13	SII bilateral	16.47	30.59	—	—	2.5	—	t	—	t
	14	SII bilateral	36.67	61.67	—	—	1	—	t	—	t

[a] Denotations of lesions: t, total; p, partial; EC, encroaching coronal gyrus; EWM, encroaching white matter; x, ablation of coronal gyrus instead of anterior ectosylvian gyrus.

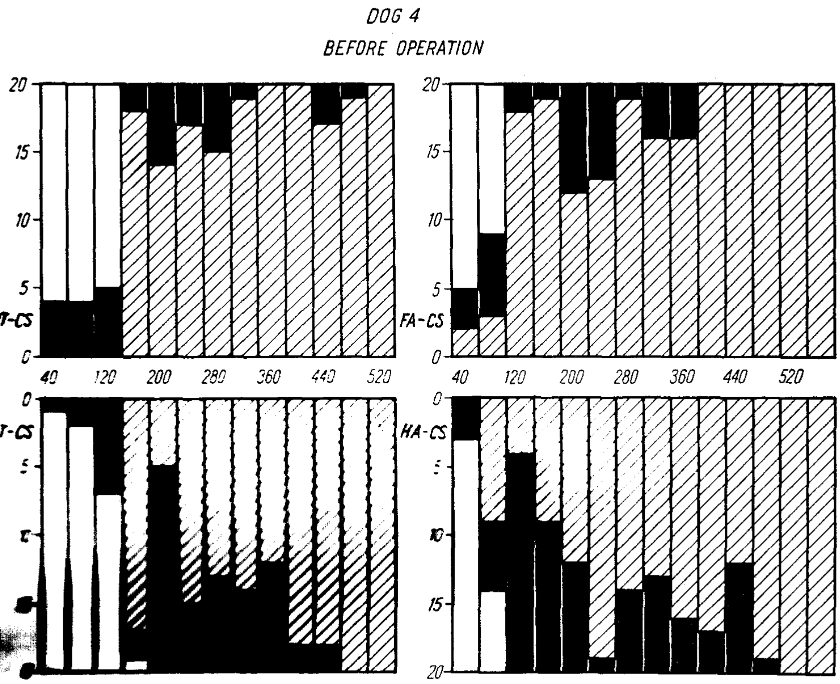

Fig. 3. Typical example of preliminary training of differentiation to T-CSs (left) and C-CSs (right). Each block denotes 20 trials. The responses to the CSs requiring movements of the right foreleg RT-CS and FA-CS are presented in the upper graphs, those requiring the movements of the left foreleg (LT-CS and HA-CS), on the lower graphs. Hatched parts of the blocks denote correct movements, black parts denote wrong movements; white parts, no active movements. It may be seen that tactile differentiation and auditory differentiation requires roughly the same number of trials.

Three erros committed by Dog 2 in 40 trials may be considered insignificant. However, when a few weeks after this operation the SII area was removed on the right side, the picture was changed: when the LT-CS (i.e. the tactile stimulus contralateral to the lesion) was presented, the animals consistently performed the trained movement with the right and not with the left foreleg (Fig. 4). Evidence showing that the afferent side of the CR arc and not the motor response of the left foreleg was impaired, is provided by the fact that the auditory differentiation in Dog 1 was completely normal. The animals had no "technical" difficulties in raising the leg and placing it on the feeder, although usual atactic symptoms in both legs were noticed after the first operation.

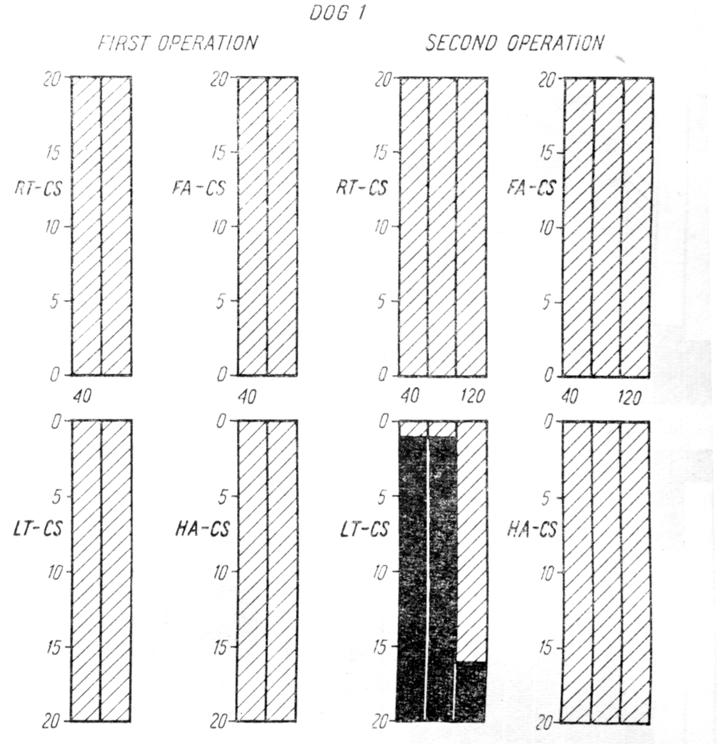

Fig. 4. Postoperative retraining after first operation (bilateral SI lesion) and second operation (right side SII lesion) in Dog 1. Denotations as in Fig. 3. Note that after bilateral SI lesion no impairment of either differentiation was observed. After unilateral SII lesion, auditory differentiation was not affected, whereas tactile differentiation was strongly impaired: in response to LT-CS the animal raised the right leg in as many as 50 trials.

After about 2 months of retraining, correct responses to the LT-CS were restored.

Group II. In six dogs, through 8, first the unilateral operations were performed in which SI and SII areas were removed on the right side, and thereafter in five dogs SI and SII areas were removed in the left hemisphere. The results of these operations were almost identical. In all these dogs, after unilateral operation on the right side, the responses to the RT-CSs were quite normal, whereas in response to the LT-CS the animals performed the movements with the right forelegs only. In a few trials, at the beginning of retraining, LT-CS failed to evoke any response (Dogs 3, 4, 6, and 7).

In three of these dogs (Dogs 3, 4, and 8) besides the tactile differentiation the auditory differentiation was also established. After the operation this differentiation turned out to be completely unimpaired.

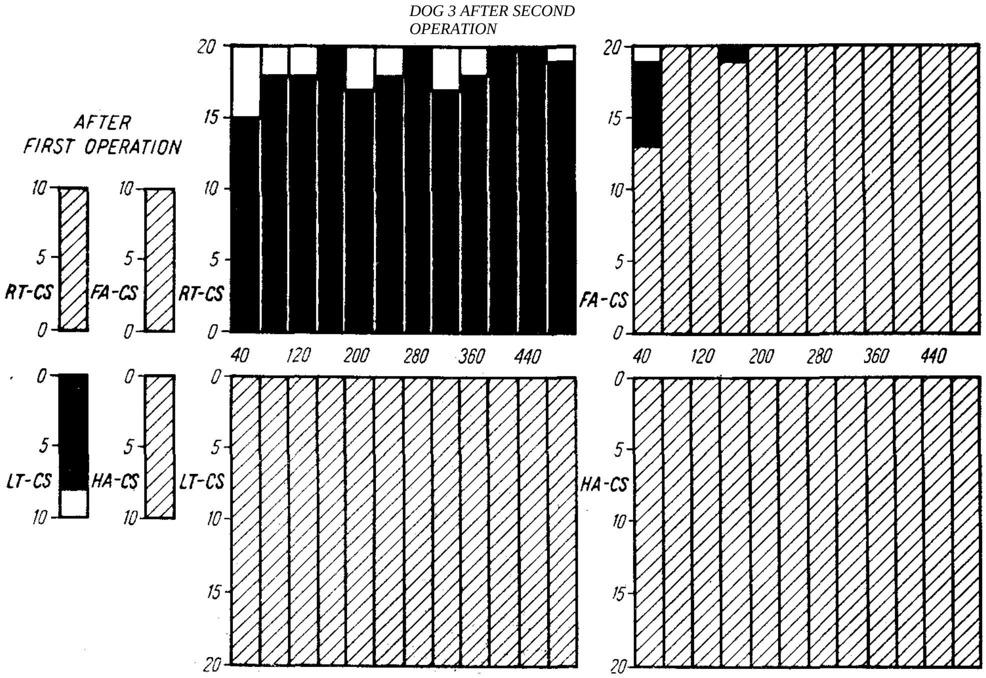

Fig. 5. Postoperative retraining after removal of right SI and SII areas (two left graphs) and after additional removal of the left SI and SII areas (two right graphs) in Dog 3. Denotations as in Fig. 3. All explanations in text.

The examples of these experiments are presented in Fig. 5 and 6.

When in these dogs (except Dog 8) the SI and SII areas were removed on the left side, the results were mixed (see Tables I and II): Dog 3 started to react correctly to the LT-CS, i. e. to a stimulus to which he reacted wrongly after the first operation, but instead he reacted wrongly to the RT-CS and his situation was not improved even after 1 year of retraining (Fig. 5). The same applied to Dog 6, but here the retraining was completed after 2 months. In Dogs 4, 5 and 7, after the second operation, the responses to the LT-CS continued to be strongly impaired whereas the responses to *the* RT-CS were less impaired (Fig. 6). In Dogs 3 and 4, in which the auditory differentiation was also trained, it was either not impaired after the second operation (Dog 4), or only slightly impaired (Dog 3) (Fig. 5 and 6).

Dog 8 was not subjected to the second operation, in order to see how long the impairment of differentiation after the unilateral SI and SII lesion would last. The result was that the correct response was restored after 4 months, after roughly the same period which was necessary for

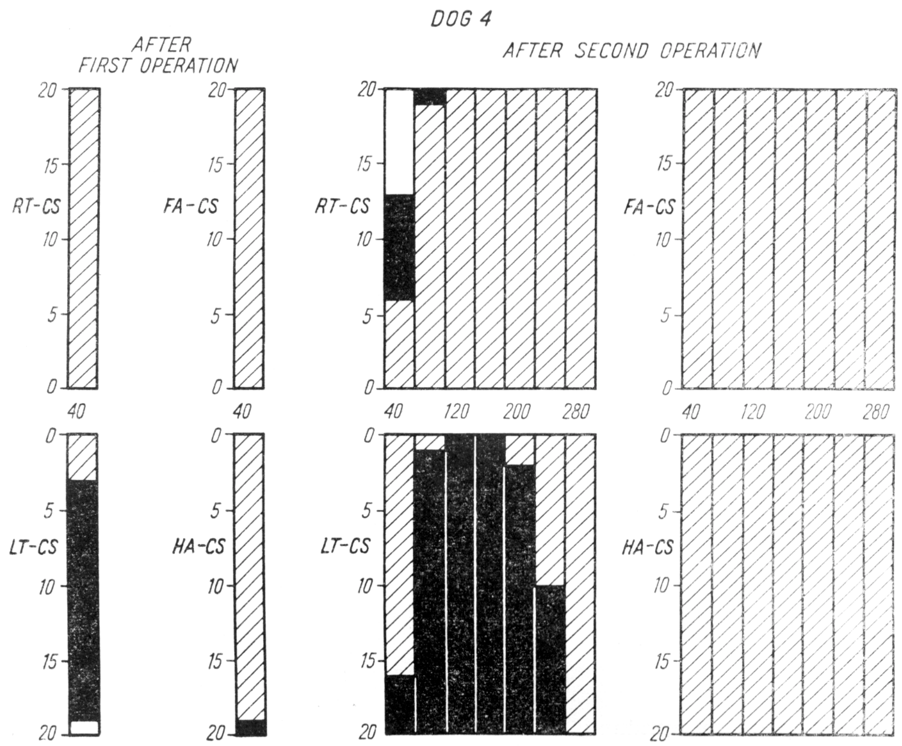

Fig. 6. Postoperative retraining after removal of right SI and SII areas (two left graphs) and after additional removal of the left SI and SII areas (two right graphs) in Dog 4. Denotations as in Fig. 3. All explanations in text.

restoring the tactile differentiation after bilateral SI and SII lesions (Fig. 7). This fact will be commented upon in the discussion.

The absence of responses immediately after surgery was observed in Dogs 3, 4 and 7.

Group III. In the remaining six dogs (9 through 14) only SII areas were removed bilaterally in one stage.

The results of the experiments in all these dogs were almost identical (see Table I). The operations produced severe impairment in tactile differentiation which lasted for several months. In contradistinction to unilateral lesions in the first operations in Group I and II, the animals performed wrong responses to both RT-CS and LT-CS. At the beginning of postoperative testing we notice also a number of no-responses to both tactile CSs (Table I). In general, however, the dogs had stronger tendency to respond with the right forelegs than with the left ones. This preference is probably due to the fact that the left border of

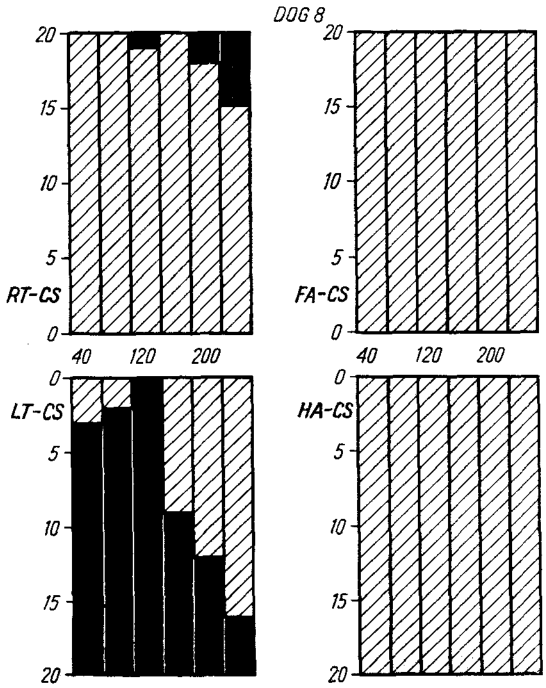

Fig. 7. Postoperative retraining after removal of right SI and SII areas in Dog 8. Denotations as in Fig. 3. Explanations in text.

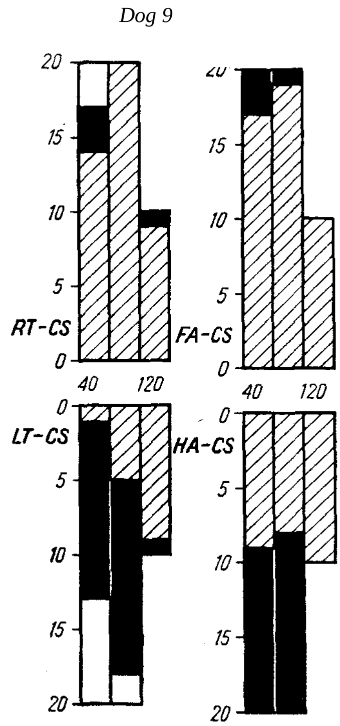

Fig. 8. Postoperative retraining atter bilateral SII lesions in Dog 9. Denotations as in Fig. 3. Explanations in text.

the stand touched on the wall of the chamber; therefore the technician helping the dog to raise both his forelegs in the preliminary training stood always at his right side.

In two dogs of this group, namely in Dogs 9 and 10, besides the tactile differentiation, the auditory differentiation was also established. It turned out that in contradistinction to the dogs of the preceding groups, the auditory differentiation was also impaired and became normal more or less in the same time as tactile differentiation (Fig. 8). This fact will be commented upon in the discussion.

The reconstructions of lesions summarized in Table II show that most lesions were almost exactly the same as planned. Only in one dog (Dog 10) was the coronal gyrus instead of the anterior ectosylvian gyrus removed on the left side with deep undercision of the latter gyrus. In some dogs the lesions encroached the white matter and in one dog (Dog 2) the coronal gyrus was encroached. We may observe that these additional lesions did not influence the disorders obtained after surgery.

DISCUSSION

If we look at the Tables I and II representing the summary of our results and at Fig. 4 through 8, showing the representative experiments, we may observe that ablations of SI areas failed to produce any significant impairment of the tactile differentiation to CSs applied to the symmetrical spots on the body (Group I). In contrast, ablations of SII areas produced in all our dogs severe impairment of this differentiation lasting for one to several .months and in one case more than 1 year. Moreover, if we compare bilateral ablations of SII areas (Group III) with ablations of SI and SII areas (Group II), it may be seen that the effects are roughly the same. This indicates that the SI area does not contribute visibly to this differentiation.

Concerning the character of the impairment of the left leg-right leg differentiation after SII lesions following observations seem to be relevant.

First, when after SII lessions the dogs committed errors, these were normally commission errors — the animal placed the wrong leg on the feeder. However, immediately after operation the commission errors also occurred — the animal occasionally made no response to the CS.

Secondly, after unilateral (right) SII lesions (which were made in dogs of Group II in the first operations and in dogs of Group I in the second operations) the animals performed always the movement with the ipsilateral (right) leg, both to the right and to the left tactile stimulus. After bilateral SII lesions (Group II after second operations, and Group III) the dogs used to commit errors in response to both RT-CS and LT-CS.

These results seem to indicate that ablation of SII area does not abolish the tactile sensation, but only impairs or abolishes its localization. After unilateral SII lesion the localization of the ipsilateral tactile stimuli is normal and therefore the animal reacts properly of these stimuli. On the other hand, the localization of the contralateral tactile stimuli is deficient. It may be guessed that in this condition the animal transfers the tactile sensation to the opposite side, hence the movement of the corresponding leg is performed. After bilateral lesions the tactile sensation is indefinite on both sides and therefore the dog has no cue to determine which leg should be raised. Accordingly, he adopts a partial reinforcement strategy raising preferably one foreleg and tolerating that not all CSs are reinforced.

Gradually, after several months all the animals except one restored their capacity to react properly to both tactile stimuli. We do not know whether this compensation was due to the fact that the cortical lesions were too limited, or whether some other structures took over the discriminative function.

The role of SII area in tactile discrimination was emphasized by several other authors.

Allen (1947) established in dogs Pavlovian differentiation to two frequencies of rhythmic tactile stimuli applied to the same place of the body. After bilateral ablations of SI and SII areas this differentiation was irreversibly abolished. Bilateral SI lesions produced only minor impairment of this differentiation, but bilateral SII lesions abolished it completely, but retraining was possible.

Zubek (1952) established in cats differentiation of various degrees of roughness of the floor and found again that SII lesions produced abolition of differentiation, while SI lesions gave only a minor deficit.

Finally, in a recent study by Glassman (1970) on cats it has again been shown that unilateral ablation of the SII area produced an impairment of localization of tactile stimuli, while ablation of SI area failed to produce this defect.

In some dogs auditory left leg-right leg differentiation was trained side by side with tactile differentiation. The purpose of this additional training was to test, whether the impairment of tactile differentiation task after somatosensory lesions might depend, not only on the afferent, but also on the efferent (or proprioceptive) part of the instrumental reflex arc. This supposition appeared to be wrong because in Dog 1, 3, 4 and 8, in spite of a severe impairment of the differentiation task to tactile stimuli the differentiation task to auditory stimuli was unaffected.

Yet in dogs of Group III (which sustained the bilateral SII lesions in one stage) auditory differentiation was as strongly impaired as tactile differentiation (cf. Fig. 8).

In order to explain this result we should remember that the anterior ectosylvian gyrus, being a site of the SII area, is also the anterior extension of the auditory area (Tunturi's AIII area, 1945). According to recent experiments of Szwejkowska and Sychowa (1971) bilateral temporal lesions produce severe impairment of differentiation of directional auditory stimuli, whereas unilateral lesions are without effect. In our present experiments bilateral lesions of the anterior ectosylvian gyrus produced an analogous impairment when they were performed in one stage (as in Dogs 9 and 10), but failed to do so when performed in two separate stages separated by a few weeks (Dogs 1, 3 and 4). In Szwejkowska and Sychowa's experiments the strong impairment of the auditory differentiation task was obtained even when the operations were performed in two stages, but here the lesions were much more extensive.

It is interesting to note that whereas the cortical representation of the tactile stimuli in the SII area is lateralized, the representation of the auditory stimuli in the auditory area is not: in fact, unilateral ablation of anterior ectosylvian gyrus is sufficient to produce a severe impairment of discrimination of tactile stimuli, whereas analogous impairment of discrimination of auditory stimuli is produced only after bilateral removal of this gyrus.

SUMMARY

1. In 14 dogs differentiation of tactile stimuli applied to symmetrical spots of the body was trained. In response to the left tactile stimulus (LT-CS), the dog had to lift the left foreleg and place it on the feeder, in response to the right tactile stimulus (RT-CS) this same movement with the right foreleg was required.
2. This task appeared to be difficult and required long training in contrast to the analogous task when the tactile stimuli were applied to the wrists of the appropriate forelegs.
3. When the SI areas were bilaterally removed, the differentiation was completely preserved. When, however, SII areas were either unilaterally or bilaterally removed, the differentiation was abolished and was restored after retraining lasting for several months. In one dog the impairment lasted at least more than a year.
4. In six dogs besides the tactile differentiation the analogous auditory differentiation was also trained. This differentiation was unimpaired after ablations of the SI area as well as after ablations of right and left SII areas in two stages separated by a few weeks. If, however, SII areas were bilaterally removed in one stage the auditory differentiation was impaired. This was because the SII area partially overlaps the auditory area.
5. The conclusion may be reached that the SII area is concerned with analysis and/or localization of cutaneous stimuli, whereas the SI area is concerned mainly with proprioceptive (articular) sensation.

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