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THE EFFECTS OF LESIONS WITHIN THE SENSORI-MOTOR CORTEX UPON INSTRUMENTAL RESPONSE TO THE „SPECIFIC TACTILE STIMULUS"

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In previous papers of this series (Dobrzecka and Wyrwicka 1960, Dobrzecka and Konorski 1962), it was shown that the alimentary type II CR established to a tactile stimulus administered to the leg participating in the instrumental response (hereinafter called „specific tactile stimulus", STS) has a number of properties differing it from the type II CRs established to other stimuli. First, the instrumental response to the STS is established much more easily than to other stimuli, both auditory and tactile, administered to other parts of the body. Then, if a type II CR is first established to the STS and afterwards to an auditory stimulus, the formation of the CR to the latter stimulus is much handicapped and the reflex permanently remains weaker than in normal condition. Third, the resistance to extinction of the STS, both acute and chronic, is much stronger than that to other CSi. Finally, if the animal is given food *ad lib.* before the experimental session, the instrumental response to the STS disappears much later than that to the auditory stimuli.

It has been shown that all these peculiar properties of the STS may be explained by an assumption that the connections between the STS center and the center of the corresponding motor act are stronger than the connections between other CSi and the latter center (cf. Dobrzecka and Konorski 1962, Fig. 5). This increased strength of the connections was attributed to the organisation of the sensori-motor cortex in which the sensory area representing the given limb lies in close vicinity to the corresponding motor area and these two areas are presumably interconnected. The dependence of the placing reflex on the integrity of this region is one of the manifestations of these interconnections.

Therefore, the problem arose what might be the effect of lesions produced in the sensori-motor cortex on the instrumental response to the STS executed by the contralateral limb. The most logical way of studying this problem was to produce such lesions which would simply separate the sensory and motor areas of the cortex by small incision through the grey matter of the cortex and underlying white matter. Besides this most crucial operation it was thought useful to remove separately the sensory and the motor cortex representing the limb participating in the instrumental response.

Much evidence has recently been provided that, in the dog, the motor and sensory areas are separated one from another, the boundary between them lying along the small dimple called „central sulcus", situated roughly half-way between the cruciate and ansate sulci and its prolongation both medially and laterally (Fig. 1a).

This evidence is brought forth by the study of Pinto Hamuy et al. (1956) in which the sensory cortex in dog has been mapped. Then, in acute experiments of Tarnecki and Konorski (unpublished) it has been shown that moving the stimulating electrode longitudinally from the rostral to the caudal points of the sensori-motor cortex, there is a sudden raise of threshold at the central sulcus line, although the movement evoked remains roughly the same. Even more clear distinction between the sensory and motor area is provided by the ablation studies. Stępień and Stępień (1959), Stępień et al. (1960), Dobrzecka and Konorski (in preparation) have shown that the symptoms produced by lesions in both these areas strikingly differ from each other. While the ablation of the motor cortex produces a hypermotility of the affected limb, ablation of the sensory cortex, on the contrary, produces its hypomotility. The atactic symptoms are rather characteristic for the sensory lesions, while paretic symptoms are characteristic for the motor lesions. Furthermore, the placing reaction is more affected by the sensory than by the motor ablations. Accordingly, the sensory and the motor area in dog may be considered separate structures, the more so that their ablations produce different patterns of subcortical degenerations, which will be shown in the present paper.

MATERIAL AND METHOD

Experimental procedure. Experiments were performed in a sound-proof CR chamber on 8 mongrel dogs 1.5 to 3 years old, weighing 10 to 18 kg. During testing, each animal was situated in a Pavlovian stand facing a foodtray containing 10 bowls which could be remotely, put into position.

In the preliminary training the animals were taught to lift the right foreleg (in one dog also the left foreleg) and place it on the foodtray to one of the following three stimuli: buzzer (B), metronome (M) and rhythmic tactile stimulus, administered to the wrist of the trained leg (STS). The method used for obtaining the instrumental response was that of passive movements being reinforced by the presentation of food. The number of presentations of each CS in the preliminary training was roughly the same. The animals were then overtrained and performed the instrumental response in 100%. Eight or nine trials separated by 3/4 to 2 min. intervals were given in each session.

The test used in this study was exactly the same as that applied in our previous paper (Dobrzecka and Konorski 1962). It was the test of chronic extinction. The experimental procedure was that in an extinction series two non-reinforced trials were interspersed among 8 reinforced trials in partially random order. The stimuli subjected to extinction were B and STS. Either of them was given once daily for 5 sec without reinforcement in such a way that, alternately, either first B and then STS was presented, or *vice versa*. The extinction series was carried out to criterion of three successive no-responses to the presentation of the CS which appeared more resistant to extinction. Then the CRs to both CSi were restored.

The sound of M was always a positive CS, i.e. it was associated with food reinforcement during the entire period of testing. However, during extinction sessions the animals occasionally decreased the performance to the M presentations. In these cases the food was offered „gratis" after 5 sec of CS operation to avoid disturbing the normal course of experiments.

The course of experiments was not quite identical in all our dogs. Since, according to our previous data (Dobrzecka and Konorski 1962), in normal dogs the resistance to extinction of the CR to the STS is always much stronger than that to the auditory stimulus, the preoperative control was thought to be superfluous. And so, most animals were trained before operation in instrumental CRs to B, M and STS, and the extinction series was carried out only after operation. In some of the dogs extinction series were performed twice, separated by a long time intervals, either before and after operation, or only after operation, to see the remote effects of the surgery. In one dog the training began only after operation.

Surgery. All the operations were performed with aseptic precautions in nembutal anaesthesia. The sensori-motor area was unilaterally exposed, the sulci and gyri identified and the planned operation performed. Then the dura matter was sewed, as well as muscles, subcutaneous tissue and skin. In all the dogs the postoperative period was uneventful and after a few days the animals were suitable for CR experimentation.

As mentioned before, three types of surgery were made: (1) the separation of the sensory and motor area, (2) the partial removal of the sensory area, and (3) the partial removal of the motor area. All the operations were performed contralaterally to the foreleg trained within the foreleg area only.

(1) After the identification of the central sulcus an incision was made by a sharp knife along its course. The incision was about 5mm deep and 7mm and reached the coronal sulcus (Fig. 1b).

(2) The sensory area for the foreleg (Fig. 1c) between the ansate sulcus, coronal sulcus and central sulcus was removed by suction. The white matter was spared.

(3) The lesion in the motor area was made around the cruciate sulcus (Fig. 1d) up to the middle of its length on the dorsal surface of the cortex.

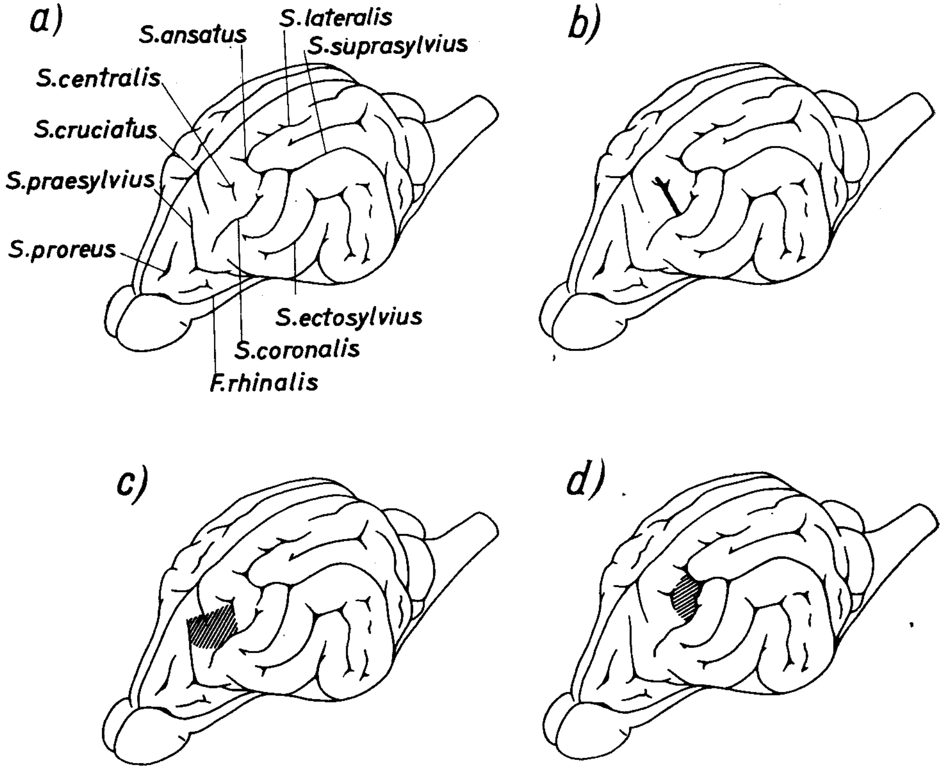

Fig. 1. The left hemisphere of the dog's brain with indication of the sustained lesions
a, normal cortex; b, incision between sensory and motor cortex; c, removal of the motor area; d, removal of the sensory area

Anatomy. After the postoperative series of experiments had been terminated and at least half a year had elapsed from the operation, the dogs were sacrificed, their brains perfused with 10 per cent formalin, embedded in paraffin and sectioned. Each fourth section was stained alternately by the Klüver and Nissl methods. The degenerations in the thalamus and brain white matter were carefully studied.

RESULTS

1. Separation of the sensory and motor cortex. Experiments were performed on 4 dogs. In two of them (Nos. 2 and 4) the control extinction series was performed before operation and the test extinction series after the operation. The interval between two series was 5 and 8 months respectively. In dog No. 1 the CR training began only after the operation. In dog No. 4, in addition to the incision along the central sulcus, an incision along the cruciate sulcus was made unintendedly.

The general symptoms of the lesion were very insignificant. The animals ran and walked quite normally, jumped without any difficulty on the stand and behaved normally. In dog No. 3 slight ataxia of the right foreleg was seen. The placing reaction of the right foreleg was abolished in all the dogs for about one month.

In dogs Nos. 2 and 3, the instrumental CR was fully preserved. In dog No. 4, the CR disappeared after operation to all the CSi. However, it recovered without training after a few months of break in experimentation.

The training of the instrumental CR in dog No. 1 began after operation. It took more time than in normal animals, but once established it was skillful and prompt.

The results of extinction series of the CRs to STS and B are summarized in Table I, and the typical course of extinction both before and after the operation is shown in Fig. 2. It is seen that the exceedingly strong

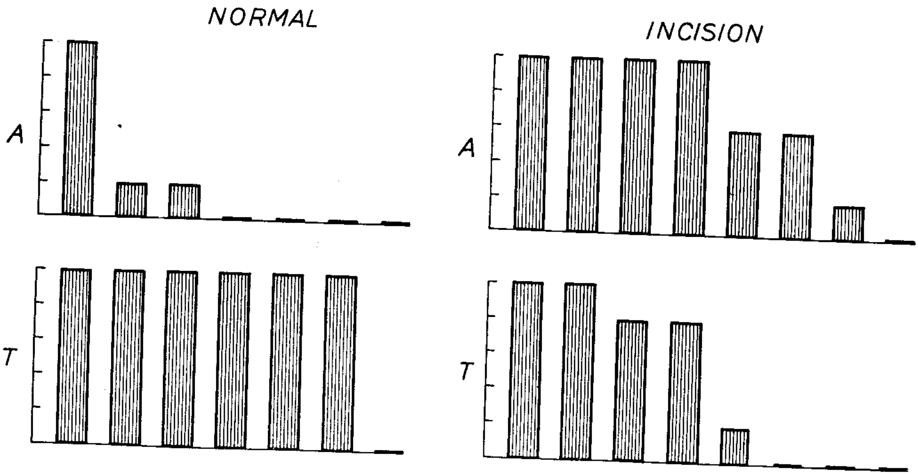

Fig. 2. The course of extinction series before (left) and after (right) separation of sensory and motor cortex in dog No. 2

A, auditory stimulus (Buzzer); T, specific tactile stimulus. Each column denotes the number of positive responses in 5 trial bock. Note the weak resistance to extinction to the auditory CS and strong one to the STS before operation and the partially reverse situation after operation

resistance to extinction of the CR to the STS observed under normal conditions disappeared completely after operation, and it became even slightly weaker than that to the auditory stimulus. This was not only owing to the decrease of the resistance to extinction of the response to the STS, but even more so owing to the increase of the resistance to the auditory CS. Another finding clearly shown in Table I is that indicating a radical change of the CR to M which has never been extinguished. As indicated in our previous paper, the instrumental CR to auditory CSi are suppressed by the mere presence of the CR to the STS. This was seen, among

Table I

The rate of extinction of auditory and tactile CR after incision between sensory and motor cortex

Dog No.	The total number of extinction trials of each CS	The numbers of trials till complete extinction		Extinction rate of STS in % of that of buzzer	The total number of positive trials in extinction series	The number of responses to positive CS	The percentage of positive response
		Buzzer	STS				
Before operation							
1							
2	32	7	30	429	224	51	23
3							
4	36	6	28	467	252	189	75
$\bar{x}$	34	6.5	29	448	238	120	49
After operation							
1	13(12)	12(5)	8(7)	67(140)	98(91)	98(91)	100(100)
2	35	27	19	70	245	245	100
3	34	26	29	112	238	238	100
4	19	13	11	85	103	95	92
$\bar{x}$	25	19	17	83	171	169	98

Numbers in parenthesis denote the results of the second extinction series.

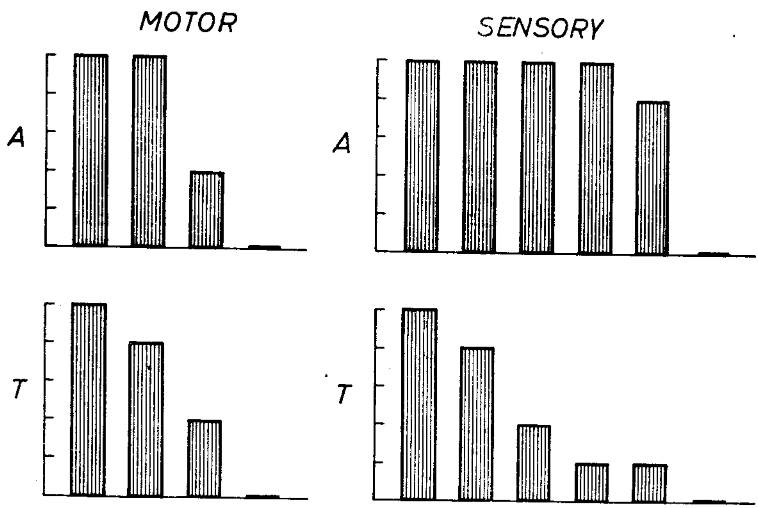

Fig. 3. The course of extinction series after the motor ablation in dog No. 5 (left) and after the sensory ablation in dog No. 8 (right)

Denotations as in Fig. 2. Note the weak resistance to extinction to both stimuli after motor ablation, and only to STS after sensory ablation other things in the instability of the CR to the reinforced CS, during the chronic extinction series. After the separation of the sensory and motor cortex this instability was abolished and the instrumental CR to M was elicited in 100 per cent.

The *post mortem* examination of the brains revealed that in dogs Nos. 1 and 2 the incision resulted in the degeneration of white matter beneath the lesion and the reduction of fibers in fasciculus subcallosus in the anterior dorsal part of the lateral ventricle (Figs. 4 and 5). In dog No. 2 the reduction of fibers in cingulum was also seen. No changes were found in the internal capsule, peduncle and thalamus.

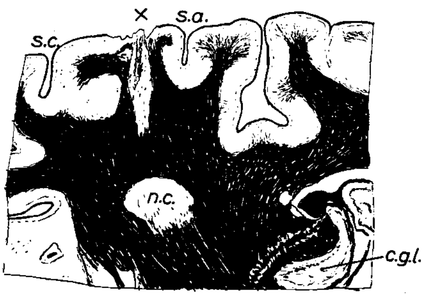

Fig. 4. Sagittal section of the brain of dog No. 1 to show cortical incision (x) s.c., cruciate sulcus; s.a., ansate sulcus; n.c., caudate nucleus; c.g.l., lateral geniculate body. Note the fiber degeneration underneath the place of lesion

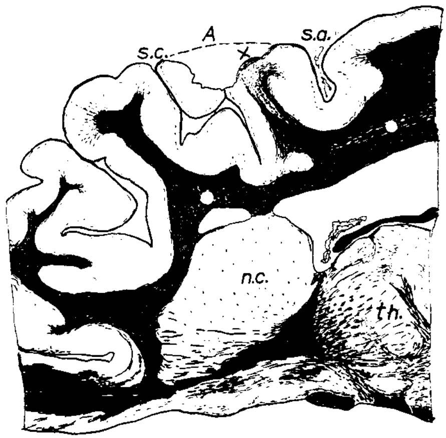

Fig. 5. Sagittal section of the brain of dog No. 2 to show cortical incision (x) s.c., s.a., n.c., as in Fig. 4; th, thalamus; A, artefact ablation of the scar. Note reduction of fibers in white matter indicated by white circles

In dog No. 3, the incision was made in front of the central sulcus (because it was situated more caudally as usually) and it was larger than that in the first two dogs (Fig. 6). There was found some degeneration of projective fibers in the internal capsule (Fig. 6b), which, however, could not be traced to the lower parts of the brain. Also, degeneration of U-fibers running to the frontal cortex was seen. Slight reduction of fibers in the fasciculus subcallosus. No changes in the thalamus and the peduncle.

In dog No. 4, two deep incisions were made, one in the central sulcus and the other in the precruciate cortex. Degeneration in the centrum semiovale, cingulum and internal capsule. Fasciculus subcallosus degenerated in the antero-dorsal part. Some degenerated fibers could be found in the peduncle, but in the thalamus no changes were observed.

2. Lesions in the motor area. Experiments with unilateral ablation of the motor cortex were performed in 3 dogs, Nos. 2, 5 and 6.

In dog No. 2, which had been in the experiments described in the previous section, a new instrumental CR was established, consisting in lifting the left foreleg and placing it on the foodtray in response to two auditory

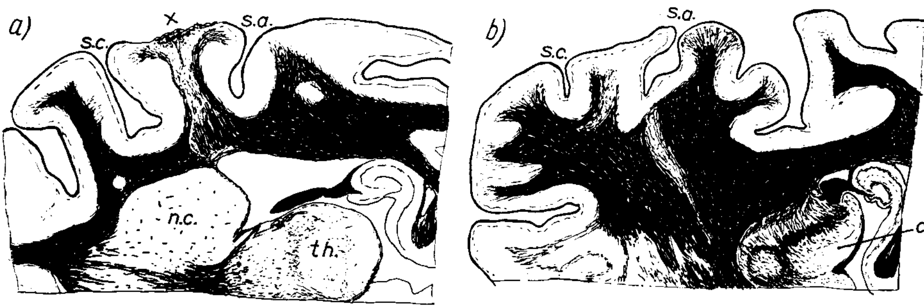

Fig. 6. Two sagittal sections of the brain in dog No. 3 to show cortical incision (x) and fiber degenerations

Connotations as in Figs. 1 and 2. Note degenerated bundles of fibers and slight reduction of fibers indicated by white circle.

CSi, the sounds of a whistle (W) and bubbling of water (Bu), as well as to the STS applied to the wrist of the left foreleg. Then the preoperative extinction series of Bu and STS was performed. Thereafter, the right motor area corresponding to the left foreleg was removed and after the recovery of CRs another extinction series to STS and Bu was carried out, W being the background positive CS.

In dogs Nos. 5 and 6, after the normal training of instrumental CRs to B, M and STS, the motor cortex for the right foreleg was removed, and after the recovery from the operation the extinction series of CRs to B and STS was performed with M as the background positive CS.

The alterations of gross behavior following the removal of the motor cortex were very insignificant and evanescent. The only permanent symptom was the hypermotility of the affected leg especially manifested in dog No. 6. Due to this hypermotility the placing reaction could not be reliably examined.

The instrumental response was present from the very beginning in dogs Nos. 5 and 6, while it was temporarily absent in dog No. 2. Occasionally, dog No. 2, instead of lifting the left foreleg, performed the trained response with the right foreleg. This interesting symptom will be described and discussed in detail in a separate paper. However, after a short retraining period the instrumental CR in this dog became normal.

The results of the extinction series are presented in Table II, and the typical course of experiments is shown in Fig. 3. It is clear that the resistance to extinction was after this operation nearly the same for STS as for the auditory stimulus. What is even more peculiar is that in this group of dogs the resistance to extinction of both CSi was weaker than that in the preceding group (in average 11 versus 20 trials). The CR to the reinforced CS was quite normal.

Table II

The rate of extinction of auditory and tactile CS after lesion in motor cortex

Dog No.	The total number of extinction trials of each CS	The number of trials till complete extinction		Extinction rate of STS in % of that of buzzer	The total number of positive trials in extinction series	The number of responses to positive CS	The percentage of positive response
		Buzzer	STS				
Before operation							
2	29	16	25	150	203	203	100
5							
6							
After operation							
2	17	8	7	87	119	119	100
5	17	12	11	92	119	119	100
6	19(12)	13(4)	11(4)	85(100)	133(84)	133(84)	100(100)
$\bar{x}$	18	12.5	11	88.5	124	124	100

Numbers in parenthesis denote the results of the second extinction series.

In dog No. 6, the second extinction series performed after one year manifested the same exceedingly weak resistance to extinction of both B and STS.

The post mortem examination of the brains revealed the similar picture in all three dogs (Fig. 7). The lesion involved the anterior and posterior sigmoid gyri around the lateral part of the cruciate sulcus. Extensive degeneration of U-fibers beneath the cruciate sulcus was seen. The degeneration of projective fibers from the place of the lesion could be traced in the peduncle. Degeneration was also found in cingulum and fasciculus subcallosus. No changes in the thalamus were found.

3. Lesions in the sensory area. Two dogs (Nos. 7 and 8) were used for these experiments. After establishing the instrumental CRs to M, B and STS, the ablation of the sensory cortex for the right foreleg was made and after the recovery two extinction series separated by a period of one year were carried out in each dog.

The neurological symptoms in both dogs consisted in a slight ataxia of the right foreleg and in total absence of placing for the period of at least several months.

The instrumental CR was present to all the CSi immediately after operation. In dog No. 7, however, the CR to the STS became weaker postoperatively than that to M and B: it was less energetic and had a latency of 3 to 4 sec. *versus* 1 sec. latency to other CSi.

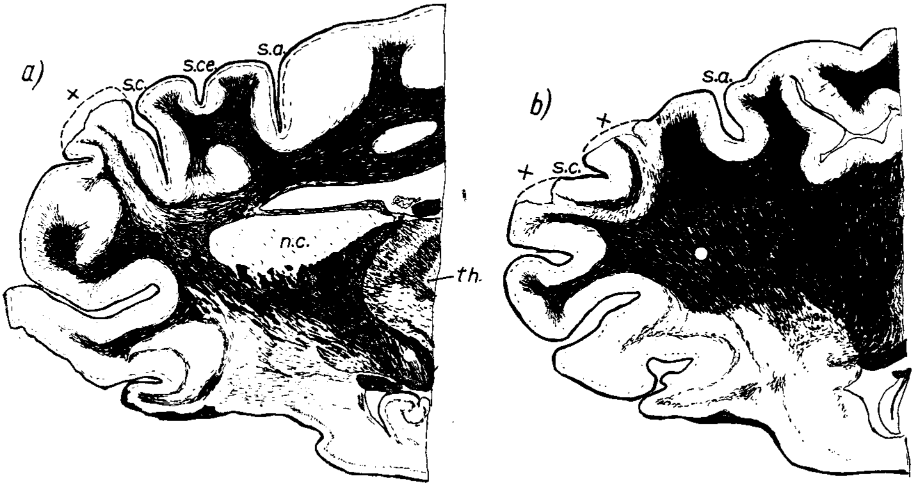

Fig. 7. Two sagittal sections of the brain in dog No. 2 (right hemisphere) to show cortical ablation (x) and fiber degenerations

Denotations as in preceding Figs; s.ce., sulcus centralis. Note gross degenerations of projective, longitudinal and U fibers traced in centrum semiovale and peduncle (white circles)

In the extinction series in both animals exactly the same results were observed (Table III and Fig. 3). The resistance to extinction of the CR to

Table III

The rate of extinction of auditory and tactile CS after lesion in sensory cortex

Dog No.	The total number of extinction trials of each CS	The number of trials till complete extinction		Extinction rate of STS in % of that of buzzer	The total number of positive trials in extinction series	The number of responses to positive CS	The percentage of positive response
		Buzzer	STS				
After operation							
7	19	16(25)	6(27)	37(108)	133(266)	133(266)	100(100)
8	28	24(18)	13(14)	54(77)	196(16)	196(161)	100(100)
$\bar{x}$	23(30)	20(21)	9(20)	45(94)	164(213)	164(213)	100(100)

Numbers in parenthesis denote the results of the second extinction series.

the STS became much weaker than that to the auditory CS. It is worth emphasising, however, that during the second extinction series conducted one year after operation, the difference between the effects of both stimuli disappeared.

The examination of the brain was made in dog No. 8 (Fig. 8). It is seen that from the place of cortical lesion situated in the lateral part of

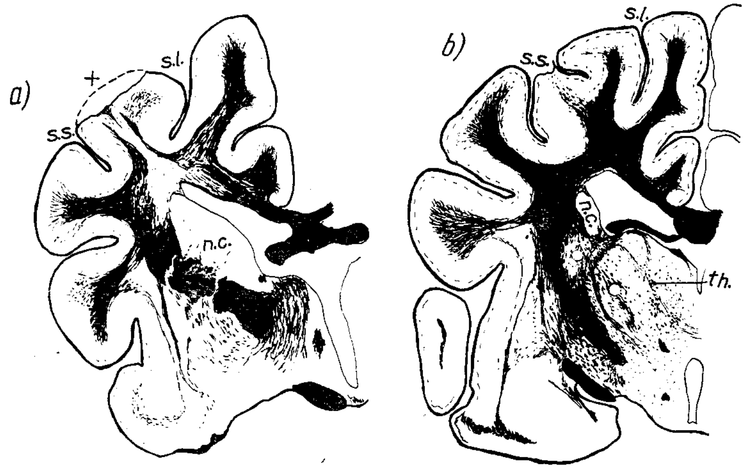

Fig. 8. Two frontal sections of the brain in dog No. 8 to show cortical ablation (x) and degeneration in projective fibers and thalamus (white circles)
s.s., sulcus suprasylvius; s.l., sulcus lateralis.

the postcentral gyrus the degenerated bundles of fibers run to the internal capsule, to the adjacent gyri, to corpus callosum and cingulum. The degeneration of projective fibers can be traced to the nucleus ventralis postero-lateralis of the thalamus.

DISCUSSION

In our previous paper (Dobrzecka and Konorski 1962) it was supposed that the peculiar properties of the instrumental CR to the STS are due to the close intercortical relations existing between the sensory and the motor area of the cerebral cortex. This hypothesis brought us to the idea that the separation of these two areas by simple incision penetrating into the white matter might deprive the STS of its peculiar properties and convert this stimulus into a regular CS of an instrumental reflex.

This hypothesis has been fully confirmed by the present experiments.

It has been shown that separating the sensory and motor area of the cerebral cortex, producing quite insignificant and transient disorders of the motor responses of the affected leg, leads to a complete abolition of the peculiar characted of the STS. The resistance to extinction of STS becomes equal to, or slightly weaker than, that of the auditory stimuli, and what is even more interesting, the suppressing influence exerted by the STS upon the instrumental responses to other stimuli is totally removed. This is documented by the fact that the resistance to extinction of the auditory CSi, exceedingly weak before operation, increased after operation and that the instrumental CR to the reinforced background CS, being defective before operation, became quite normal postoperatively. Accordingly, it may be assumed that a small branch of the instrumental CR arc responsible for the particular strength of the CR to the STS was identified.

It is clear that the anatomical examination of the effects produced by the incisions has a great importance for the interpretation of our results, because it had to be verified whether the damage of projective fibers outgoing from, or ingoing to the cortex also took place. It seems that this examination gave a satisfactory result. In two dogs (Nos. 1 and 2) no impairment of the projective fibers in the internal capsule was found and the only slight degeneration was found in the longitudinal bundles running through the cingulum and tapetum (fasciculus subcallosus). In dog No 3, some slight degeneration of the projective fibers was found which, however, could not be traced in the thalamus or the peduncle. Only in dog No. 4 cannot the incision be considered as a pure one, because, in addition to the degeneration in the longitudinal bundles, the projective fibers were also affected which could be traced till the peduncle. This degeneration was undoubtedly due to the incision in the precruciate area. Since, however, the damage to the projective fibers was incomparably smaller than that produced by ablations of the motor cortex, this dog was left within the incision group.

Considering the results obtained in each dog we find that the resistance to extinction both of the auditory CS and the STS was considerable in dogs Nos. 2 and 3, and rather weak in dogs Nos. 1 and 4. The weak resistance to extinction in dog No. 1 may be due to the fact that the CRs were trained in this dog only after operation and, therefore, they could be not as strong as those trained before operation. This supposition is supported by the fact that the establishment of the CRs in this dog was undoubtedly more difficult than in normal dogs. On the other hand, the low resistance to extinction in dog No. 4 may be compared to that observed after the motor lesions.

The results of our experiments with incision of the cortex have raised a new problem, namely, that concerning the role of the sensory and motor areas themselves in instrumental CRs produced by the STS. This problem can also be explained on the basis of our results.

The lesions in the motor area produced „equalization" of the resistance to extinction of the auditory stimulus and the STS on a low level. Indeed, the resistance to extinction of the auditory stimulus was in average much weaker after the motor lesion than either after the sensory lesion or the incision (12.5 trials *versus* 20 trials and 19 trials respectively). This means that the attenuation of the instrumental CR after the motor lesion is due to the impairment of the „final common path" of the instrumental CR. In earlier papers of this laboratory (Stępień, Stępień, and Konorski 1960, 1961) it was shown that the instrumental CR of placing the foreleg on a platform was not destroyed by the removal of the motor area. From the present experiments it is seen that this area, although not crucial for the preservation of the CR, plays nonetheless some facilitatory or supporting role in its occurrence. This conclusion will be convincingly confirmed by further data which will be presented in the next paper of this series.

The question may be asked as to why the lesion in the motor cortex producing a clearcut degeneration in the descendant pathways traced in the peduncle causes no visible retrograde degeneration in the ventro-lateral nucleus of the thalamus. The answer to this question is that probably the same neurons of the VL nucleus send their axons both to the motor and premotor cortex, thus preventing the development of the retrograde degeneration after removal of the motor cortex alone. In this respect the Rose's idea of the supporting innervation seems to be relevant (Rose 1955).

The lesions in the sensory area of the cortex produce a different effect. Here, the resistance to extinction of the STS, or, more generally, of all the tactile stimuli, is much reduced, showing a great impairment of the CRs to those stimuli. On the other hand, the resistance to extinction of the auditory CS is high, thus showing that the defect concerns only the stimuli of the somatic analyzer. And so we may conclude that the ablation of this area, not destroying completely the reception of the tactile stimuli, produces its significant attenuation. Of course, the retrograde degeneration in the VPL thalamic nucleus is in perfect agreement with this finding.

The comparison of the effects of each of the three lesions (incision, motor ablation and sensory ablation) is shown in Fig. 9.

In conclusion we can state that while the lesion in the sensory area

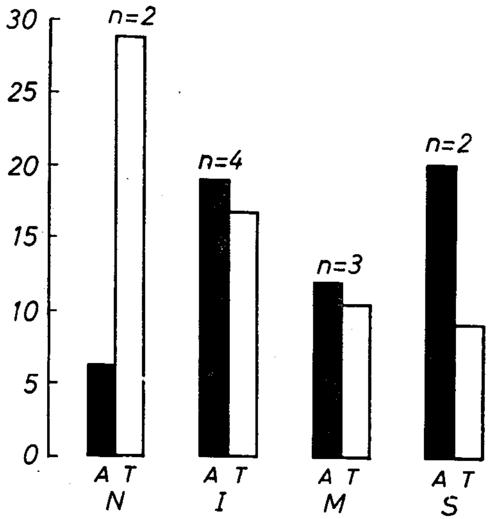

Fig. 9. Mean resistance to extinction to auditory (A) and specific tactile (T) stimuli in normal (N) dogs and in dogs with incision in the sensori-motor cortex (I), with motor (M) and sensory (S) ablation

Explanations in text

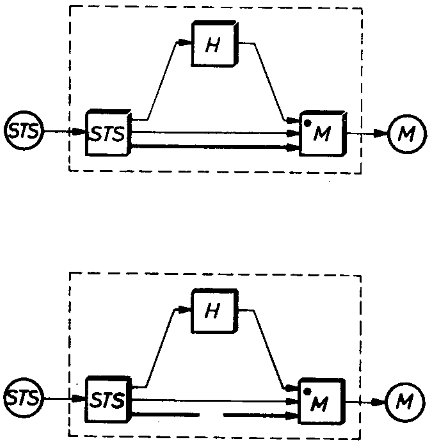

Fig. 10. Model of CR arc to STS

STS, receptor and center of specific tactile stimulus; H, hunger center, M, motor center and effector. The direct connection between STS and M has additional pathway which is cut by separation of the sensory and motor area impairs the input of somatic CSi, and the lesion in the motor area impairs the output of the instrumental CRs to all stimuli, the incision between the two areas does not produce any of these effects; instead it changes the particular structure of the instrumental CR arc to the STS by depriving it of one branch responsible for its particular properties. These relations are shown diagramatically in Fig. 10.

An additional finding of this paper is related to the problem of restitution of the defects produced by the above cortical lesions after a lapse of time. This important problem was only slightly touched in the present paper, however, the preliminary results show that such a restitution takes in fact place. In two dogs in which the second extinction series was carried out about one year after the sensory lesion, partial recovery of the defect could be seen. This was, however, not true in respect to the lesion of the motor area; here the second extinction series manifested even the poorer resistance to extinction than the first one. This whole problem certainly needs a more thorough examination.

SUMMARY

1) The resistance to extinction of the instrumental food CR to the specific tactile CS and an auditory CS in chronic extinction series was investigated after (1) separation of the sensory and motor cortex, (2) removal of the motor area, and (3) removal of the sensory area. All operations were contralateral to the leg used in instrumental conditioning.

2) After separation of the sensory and motor area by incision made between them, the exceedingly strong resistance to extinction of the specific tactile stimulus manifested in normal dogs is abolished, as well as the suppressing effect of that stimulus on the CR to the auditory stimuli. In consequence the resistance to extinction of the two CSi becomes nearly equal.

3) After removal of the motor cortex the resistance to extinction of both CSi becomes equal and is weaker than in the preceding case.

4) After removal of the sensory area the resistance to extinction of the CR to the specific tactile stimulus becomes much weaker than that to the auditory stimulus.

5) The anatomical verification of lesions shows that after separation of the two areas only some degeneration of the longitudinal but not projective fibers are found; after removal of the motor area the degeneration of the projective fibers occurs traced in peduncles; after removal of the sensory area degeneration of projective fibers traced till nucleus postero-lateralis thalami is observed.

6) The physiological mechanism of the results obtained after each operation is discussed.

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