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THE EFFECTS OF UNILATERAL AND BILATERAL ABLATIONS OF SENSORIMOTOR CORTEX ON THE INSTRUMENTAL (TYPE II) ALIMENTARY CONDITIONED REFLEXES IN DOGS

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One of the most important problems concerning the function of the so called sensorimotor area is connected with its functional organization. How much is this area functionally "equipotential", what is the significance of its particular parts, and what role it plays in the control of "voluntary" movements, these are the questions which have raised many discussions nearly from that time when this area was identified in Hitzig and Fritsch's experiments.

The problem may be subdivided into two different questions: 1° what is the organization and the functional role of the parts localized along the medio-lateral axis of the cortical surface, controlling movements of various parts of the body, and 2° what is the significance of particular tranversal "strips" situated alongside the caudo-rostral axis.

In the present series of papers we are concerned only with the second of these questions, and try to answer it on the basis of experimental material brought out by the conditioned reflex (CR) method. In our previous papers (Stępień and Stępień 1958, Stępień, Stępień and Konorski 1959, a and b) we did find that these strips are not equipotential, that each of them has its own functional role, and its lesion produces a number of characteristic symptoms. Therefore the classical subdivision of the sensorimotor region into three areas, conventionally called sensory area, motor area and premotor area, which subdivision has been sometimes put in doubt by some authors (e.g. Dusser de Barenne 1941) seems to be well substantiated.

The aim of this paper is to elucidate what are the effects of ablations of sensorimotor area as a whole upon motor CR's and whether or not these effects may be understood as a combination of effects produced by removal of each part of it separately.

MATERIAL AND METHODS

Experiments were performed on 13 mongrel male dogs aged 2—4 years, in a soundproof CR chamber. In the preliminary training instrumental CR's were established consisting in raising of the right foreleg and putting it on the foodtray situated in front of the dog in response to various auditory or audio-visual stimuli (CS). The CR's were elaborated by the method of passive movements. 8 trials with intervals of 1—2 minutes were applied in each experiment. Alimentary reinforcement consisted in automatic putting into position the bowl with minced meat mixed with bread and moisted by broth.

When the animals were well trained, i.e. when they performed the learned movement to every CS with minimal latency, and intertrial movements, present at the beginning of training, disappeared, (this took at least 3 months) the animals were subjected to surgery. In aseptical conditions the scalp from the region to be ablated was removed, the dura matter incised and cortical tissue destroyed by subpial suction. Then the dura matter was sutured and the muscles, galea and skin were closed in layers. Several days after operation the CR experiments were resumed and conducted from 2 to 10 months.

Since our aim was to test the animals' CR's in the postoperative period without recurring to any training, it was important to apply a very cautious experimental procedure. When the animal did not perform the trained movement in response to the CS, care had to be taken neither to extinguish the reflex by non-reinforcement, nor to transform it into classical CR by reinforcement. Therefore it was necessary to take the middle course, namely: 1° to apply only a few trials in an experimental session; 2° to perform experiments not every day but only twice a week; 3° to reinforce irregularly the CS in spite of the fact that the animal did not perform the trained movement. Only when this movement reappeared in at least 50% of trials, was it possible to resume normal experiments. In some animals in which the motor CR did not return spontaneously after several months the retraining by recourse of passive movements was undertaken.

The chosen movement of putting the foreleg on the foodtray proved to be, unfortunately, not quite appropriate for this study for the following reasons. First the animals after sensorimotor ablations were very strongly incapacitated in all their motor performances. They had often great difficulties in standing on the stand, they tumbled down very easily and often could not perform the required movement for purely "technical" reasons. Therefore it was sometimes difficult to judge which was the source of the lack of the motor CR: whether it was abolished as such, or only could not be displayed because of the postural difficulties. Secondly, the sensorimotor animals manifested very often a more or less strong hyperkinesia of the forelegs, and consequently it was sometimes difficult to decide whether the given movement was a true instrumental response in its abortive form, or whether it was merely the result of hyperkinesia.

The sensorimotor ablations were performed either bilaterally in one stage, or first on one side and then on the other, or else in several stages, each involving a particular transversal strip. The results of these last partial ablations were already described in previous papers of this series. Therefore, in this paper we shall deal only with: 1° sensorimotor unilateral ablations (contralateral to the trained movement), and 2° with bilateral sensorimotor ablations obtained after one or several operations.

RESULTS

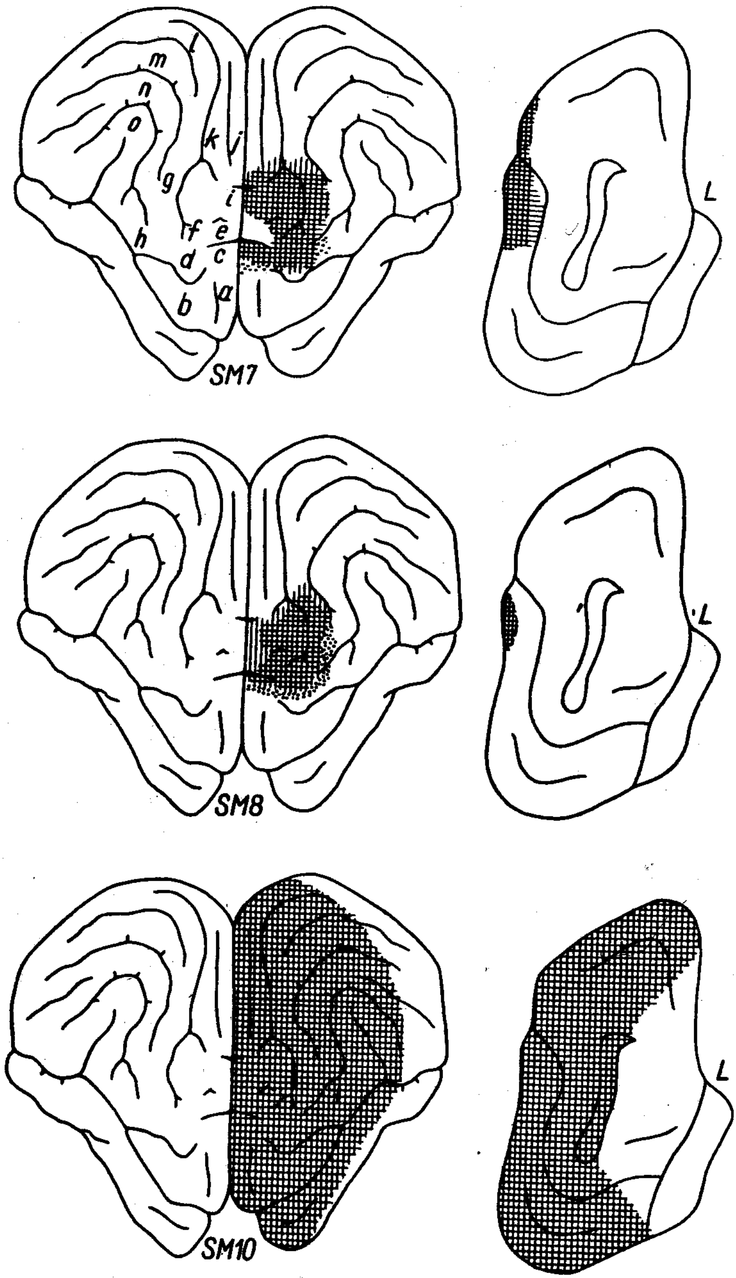
Unilateral sensorimotor ablations

The left sensorimotor ablations were performed in one stage in 2 dogs: SM 7 and SM 8. In dog SM 11 the whole left hemisphere was removed in one stage. In dog SM 12 first sensory and then motor-premotor areas as well as adjacent areas were removed, in dogs SM 10 and SM 13 first motor and then sensory area was removed, and in dog SM 10 additionally the whole left hemisphere was ablated in the third stage (Table I and Fig. 1).

In the first days after operation the dogs developed the ordinary and well known symptoms of ataxia, awkwardness of movements on the right side, etc. These symptoms were temporary and vanished usually within several weeks. Four dogs (SM 7, SM 11, SM 12 and SM 10 after third operation) displayed a strong tendency to turn left, which was particularly pronounced when the animal tried to run forward. These symptoms also became gradually almost imperceptible. Nearly all our dogs displayed a more or less strong hyperkinesia of the right foreleg, consisting either in many irregular movements of various amplitude, or in holding the leg permanently above the ground with small oscillations. This symptom was very persistent and only after a prolonged period subsided, but it reappeared whenever the animal was more excited. The general behaviour of the animals (even those with complete hemispherectomy) was fully adequate.

When first brought to the experimental situation and put on the stand the animals behaved normally, except for the effects mentioned above. The motor CR was present from the very beginning although the skillfulness of the movement was more or less impaired: either the animals were able to perform only the abortive movement, without putting the leg on the foodtray, or a full movement after several abortive attempts, or else a full, although awkward, movement from the very beginning. *Never* did the animals attempt to perform the movement with the unimpaired leg, however difficult it was for them to lift the right foreleg and put it on the foodtray.

The animals' motor performance improved rapidly, and some of them after several weeks became almost fully compensated.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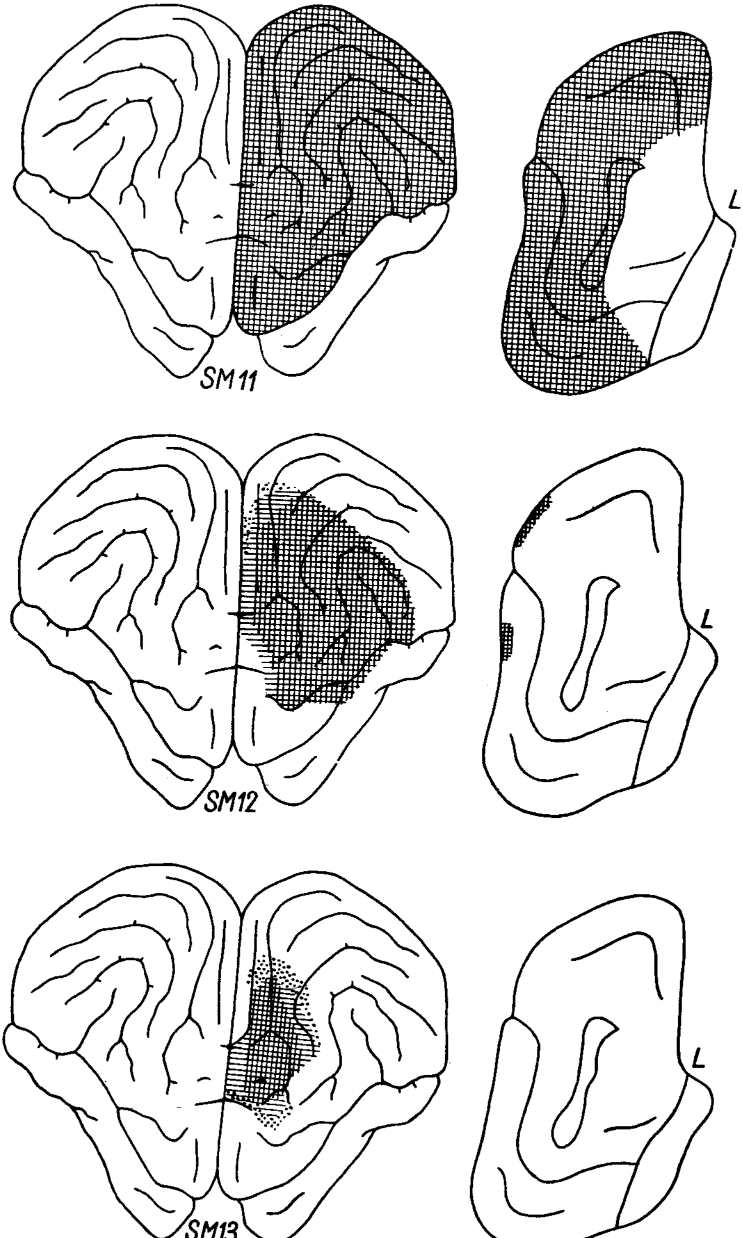


Fig. 1. Unilateral lesions of sensorimotor cortex. Flat projection of dog's cerebral cortex. Left — dorsal aspect. Right-medial aspect. Crosshatched — ablation of cortex with adjacent white matter. Hatched — ablation of cortex alone. Dotted — only superficial layers of the cortex removed.

Denotations: a — *g.proreus*, b — *g.orbitalis*, c — *g.precruciatus*, d — *g.sigmoideus anterior*, e — *g.postcruciatus*, f — *g.sigmoideus posterior*, g — *g.coronalis*, h — *g.compositus anterior*, i — *g.postcentralis*.

Table I

Synopsis of case histories of experimental dogs

Dogs	Preoperative period in months	Extent of first lesion	Postoperative period in months	Extent of second lesion	Postoperative period in months	Extent of third lesion	Postoperative period in months	Extent of fourth lesion	Postoperative period in months	End
SM 1	7	Prefrontal (part), premotor (part), motor (part), sensory (part) bilateral	6							sacrificed
SM 2	14	Prefrontal (part), premotor, sensory I — bl.	5							sacrificed
SM 3	12	Prefrontal (part), premotor, motor, sensory I — bl.	6							sacrificed
SM 4	3	Sensory I — bl.	1	Motor — bl.	2	Premotor — bl.	2			sacrificed
SM 5	7	Motor — bl.	2	Premotor (part) — bl.	2	Sensory I — bl.	5	*Gyrus entolateralis* — bl.	6	sacrificed
SM 6	12	Parietal cortex — bl.	1.5	Prefrontal (part) — bl.	8	Premotor, motor, sensory I — bl.	9			sacrificed
SM 7	9	Premotor (part), motor (part), sensory I — left	4	Premotor, motor, sensory I — right	10					sacrificed
SM 8	3	Premotor (part), motor, sensory I (part), — left	0.75	Premotor (part) motor, sensory I — right	6					sacrificed
SM 9	3	Premotor, motor, sensory I and II — — right	0.75	Premotor, motor, sensory I and II — — left	2					sacrificed
SM 10	6	Motor (part) — left	1.5	Sensory I — left	5	Remaining cortex of the left hemisphere	1	Premotor (part), motor (part), sensory (part) — — right	2	died
SM 11	5	Hemidecortication — — left	2	Prefrontal, premotor, motor, sensory I and II, — right	6					sacrificed
SM 12	3	Sensory I (part), sensory II, parietal, temporal (part)	0.25	Lateral part of premotor, motor and neighbouring areas — left	2					sacrificed
SM 13	7	Motor — left	0.75	Sensory I, parietal cortex — left	6					sacrificed

Bilateral sensorimotor lesions

Bilateral lesions in one or more stages were performed in 11 dogs. Postmortem examination of the brains was performed by Dr J. Kreiner. Its results are represented in Fig. 2; the order of the operations is given in Table I. As seen from the Table in 3 dogs (SM 1, SM 2 and SM 3) bilateral ablation was made in one stage, in 3 dogs (SM 4, SM 5 and SM 6) in three stages, in 5 dogs (SM 7, SM 8, SM 9, SM 10 and SM 11) first the operation on one side (in one or more stages) and then on the other side was performed. Fig. 2 shows that the extents of lesions were not quite identical, nevertheless the whole of our material seemed to be rather uniform; this proves that in all our dogs the essential part of the region studied was removed and that the larger extent of the lesion did not contribute considerably to the symptom described in this paper.

During at least 3 days after operation the dogs lay on their bedding and were usually not able to get up. Then they began to try to walk, but at first their attempts were unsuccessful and the dogs fell down. After a week or so walking was already possible. However, when the floor was smooth they easily fell down, sprawling and not able to get up. While walking they usually thrust their forelegs forward. Standing was generally more disabled than walking. The legs assumed abnormal positions and after some time the animals got tired and fell down. Some of them displayed a more or less pronounced hyperkinesia of the forelegs. This prevented to test their placing reaction. If hyperkinesia was not present, placing reaction appeared to be absent. When food was put on the table, climbing on it with the forelegs was impossible. The dogs were also not able to jump on the stand as they did before operation (except dog SM 1). They did not manage to draw food with the paw, if it had been located outside the cage, instead they tried unsuccessfully to grasp it by mouth.

Some of the dogs (SM 5, SM 8, SM 9, SM 10, SM 11) had great difficulties with the act of eating. They couldn't easily seize the food with their teeth or hold it in their mouth, and the movement of chewing and licking were clumsy.

The severity of all these defects was generally in accord with the extent and location of the lesion. For instance dog SM 1, in whom the medial parts of the right sensorimotor area were spared was much more skillful (especially on the left side of the body) than the other dogs. Eating movements were particularly impaired in those dogs in which coronal and anterior compositus gyri were bilaterally removed.

According to the extent of lesion some of the dogs were motorically incapacitated for the whole time of observation, while others improved gradually, although full compensation of the motor activity never occurred.

The general behaviour of the animals seemed to be more changed in those dogs in which the lesions involved also middle regions of the cortex (SM 5, SM 6, SM 7, SM 9, SM 11). The most severe symptoms were: disorientation in the familiar surrounding, lack of investigatory behaviour towards the environment, rushing forward with no heed of obstacles, and so on. In this respect particularly illuminating were experiments with dog SM 5, in which after the fourth operation involving medial parts of both hemispheres the enumerated symptoms, previously absent became manifest.

The instrumental CR activity was disturbed in all our dogs in a much higher degree than after any other lesions described in earlier papers of this series.

The experiments were resumed after operation as soon as the dog was able to stand and to walk. In response to the CS the animals at first displayed strong orientation reaction towards the source of the stimulus. This reaction sooner or later (sometimes already in the first trials) gave way to the alimentary reaction either abnormal (licking the empty bowl), or normal — with head directed towards the foodtray. When the bowl with food was put into position two of the dogs (SM 6 and SM 11) did not notice it at once and behaved as if the whole situation were quite new to them; others began to eat immediately. After severtal experimental sessions the general reaction to the CS'i became more regular, and in most cases it was an orienting-alimentary reaction, i.e. the animal first turned his head for a shorter or a longer time to the source of the stimulus and only then turned towards the foodtray.

In the first trials the instrumental response in all our dogs was absent. However, in most of the dogs it reappeared spontaneously, either already in the first experiment (SM 9), or in one of the next experiments (SM 3, SM 7, SM 8) or after a longer time (SM 11). In dog SM 1 the trained movement did not return spontaneously during four months in spite of his relatively good general skillfulness; this lack of spontaneous recovery might have been caused by inappropriate experimental procedure after operation (too many reinforced trials, cf. method and discussion). In dog SM 2 the trained movement was also permanently lost after operation, but instead the animal performed very many abortive movements (without putting the leg onto the foodtray) so that it was impossible to decide whether these movements

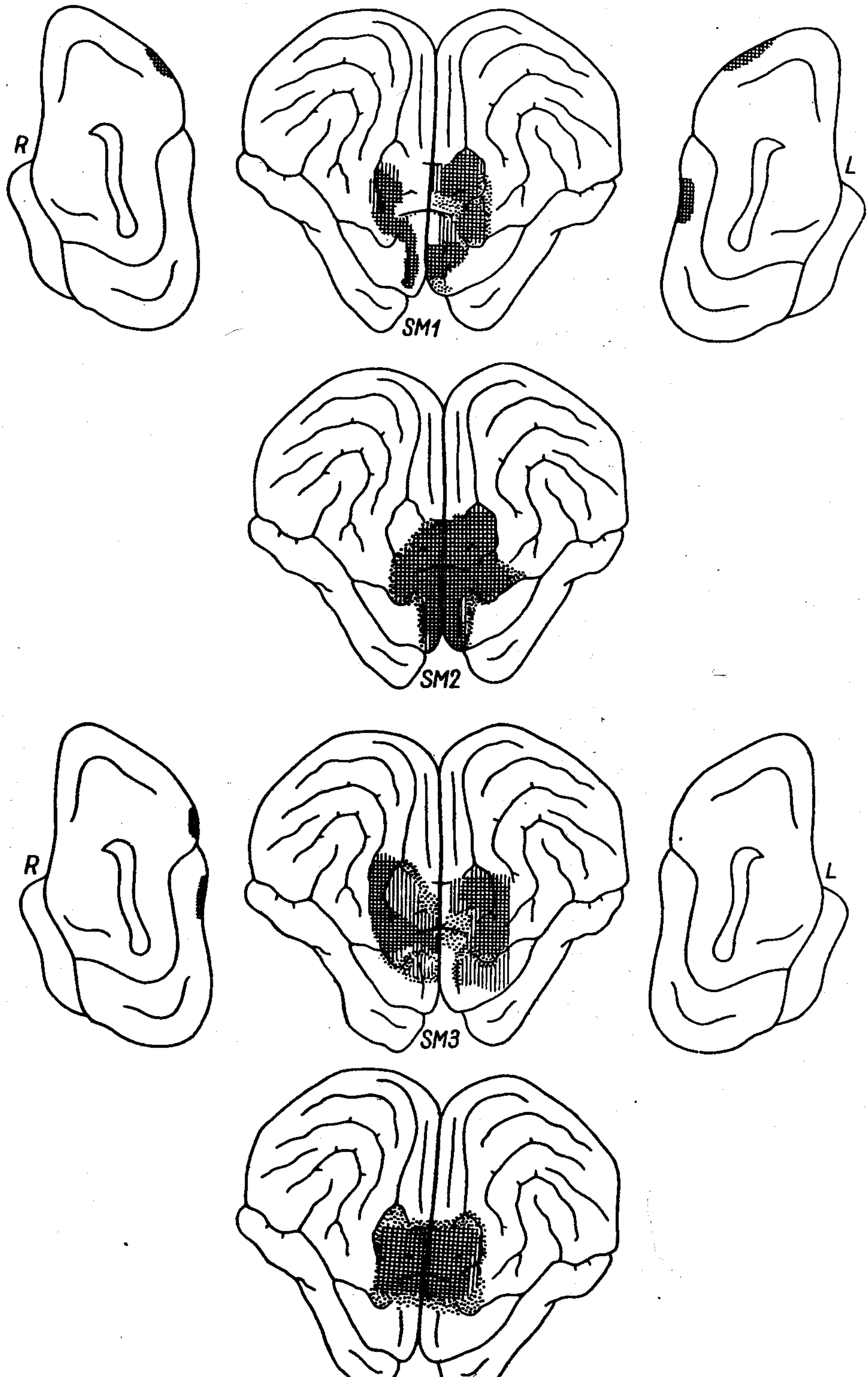
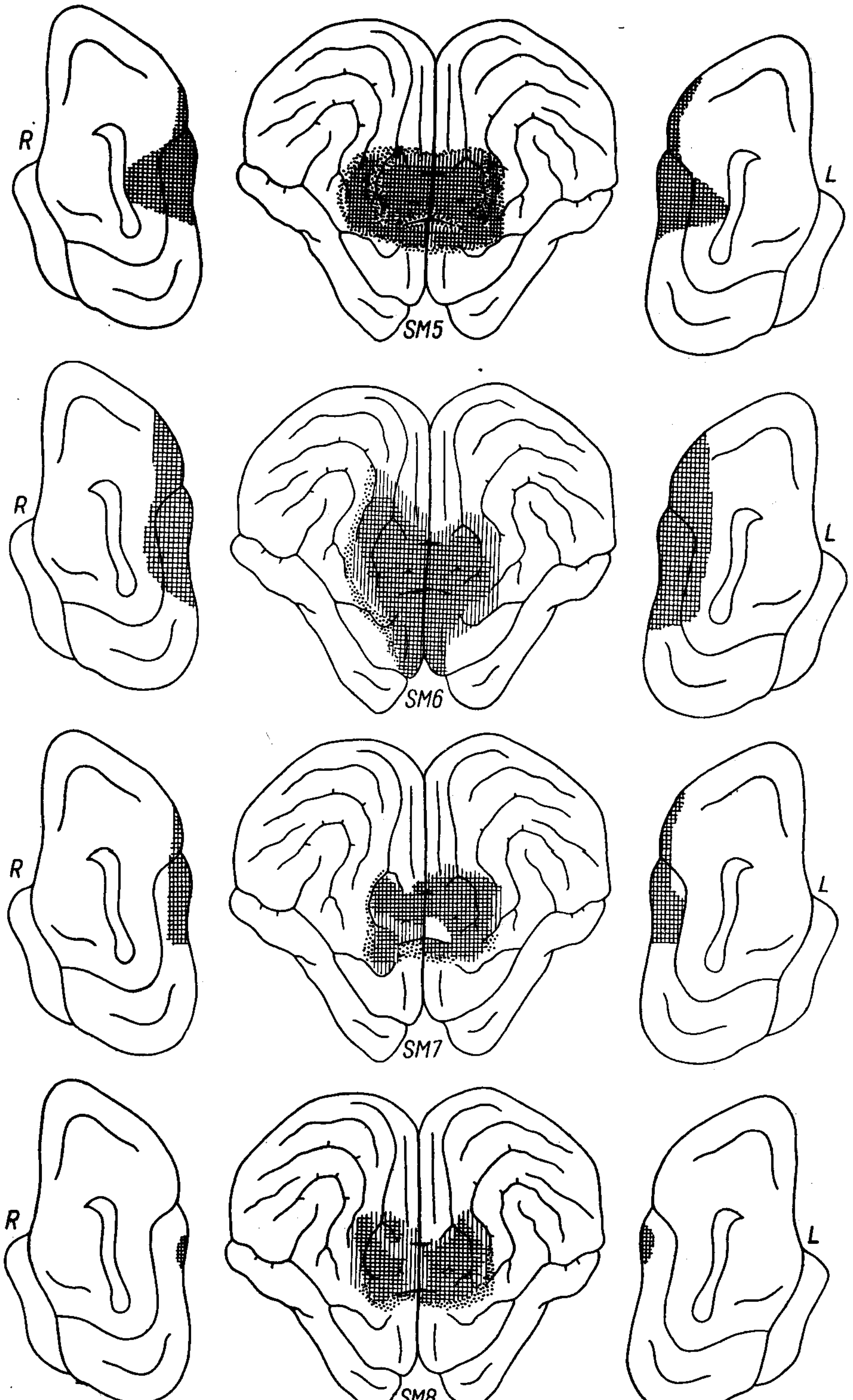


Fig. 2. Bilateral lesions of sensorimotor cortex. Flat projection of dog's cerebral cortex. Dorsal aspect in the middle. Medial aspects on both sides.

Indications as in Fig. 1.



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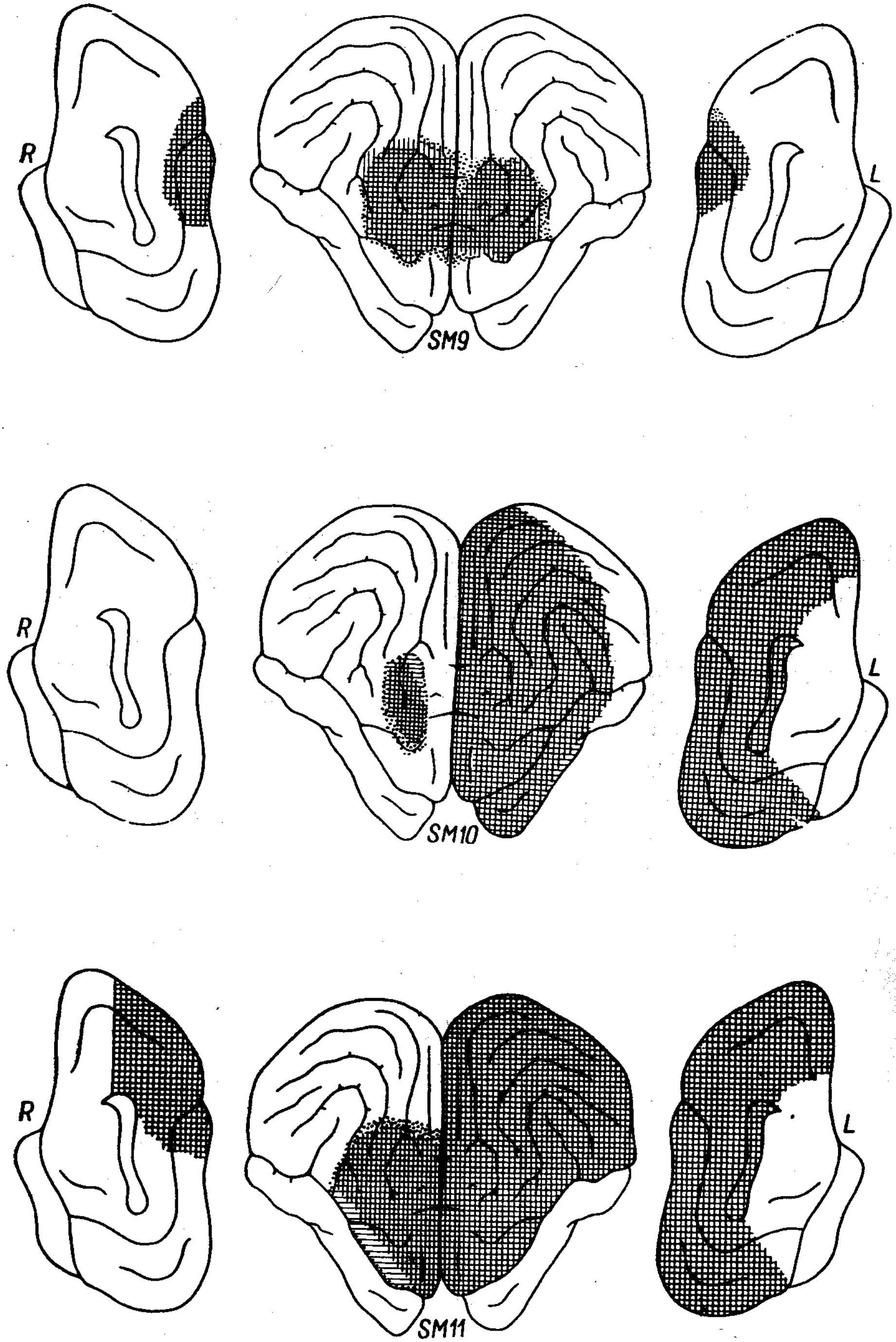

Fig. 2 — continued

were due to the preoperative training, or were simply a manifestation of hyperkinesia. The definite loss of the trained movement was also seen in dogs SM 5, after third operation, SM 6 and SM 10. Dogs SM 5 and SM 6 had very extensive lesions (cf. Fig. 2) and were very strongly impaired in their motor performances. The bad condition of SM 10 was due to epileptic seizures developed soon after last operation (see below).

In dogs SM 1, SM 5 and SM 6 after several months the retraining of the instrumental reflex was begun by recourse to passive movements. It appeared that the trained movement itself returned very quickly but its association with the CS was either lacking or very weak (see below).

Although the instrumental reaction was in all our dogs either preserved or easily retrained, the CR was severely deteriorated.

First, a great clumsiness of movements was in all animals (except SM 1 and SM 8) very pronounced. Often the proper movement was preceded by several abortive attempts to put the leg on the foodtray. The movement was unprecise, sometimes the dog put his leg into the bowl and was unable to change its position, so that the act of eating was much hindered. After eating the animals were usually not able to put the leg down actively on the floor, and could remain in such an awkward position for a long time till the leg was removed by the experimenter.

Another prominent symptom seen particularly in dogs SM 3, SM 4, SM 5, SM 6, SM 8, SM 9 and SM 11 was confusion of the legs. The animals put either left or right foreleg on the foodtray in a quite similar manner, as if not noticing any difference between these two movements. The preference of this or that leg depended on which leg was more free just before the performance of the movement. It is worth while to notice that in dog SM 6, which was retrained after operation by applying passive movements to the right foreleg, the movements of the left one started to appear as soon as the reflex was reestablished. In dog SM 3 an attempt was made to extinguish the movements of the left foreleg by not reinforcing them by food, but in spite of prolonged training of this sort, it proved to be unsuccessful (Fig. 3).

But perhaps the most pronounced symptom exhibited by our dogs was the utmost irregularity of the whole CR activity. The animals' performance was completely chaotic and unpredictable. First, it could be quite different on different days for no obvious reasons: in one session CR's seemed to be relatively good, and in the majority of trials the animal reacted correctly; in the next session, on the contrary, no

CR's appeared at all. Latent periods were greatly variable; while before operation the trained movements appeared always immediately after the onset of the CS, now the latencies lasted at least several seconds. Sometimes the animal did not perform the movement during the operation of the stimulus but did so after its cessation. The movements appeared also in a quite unpredictable way in intertrial intervals. In some cases the animals performed the movement in interwals rather than to the CS, but in most cases they either performed it both to CS'i and in intervals, or on the contrary neither to CS'i nor in

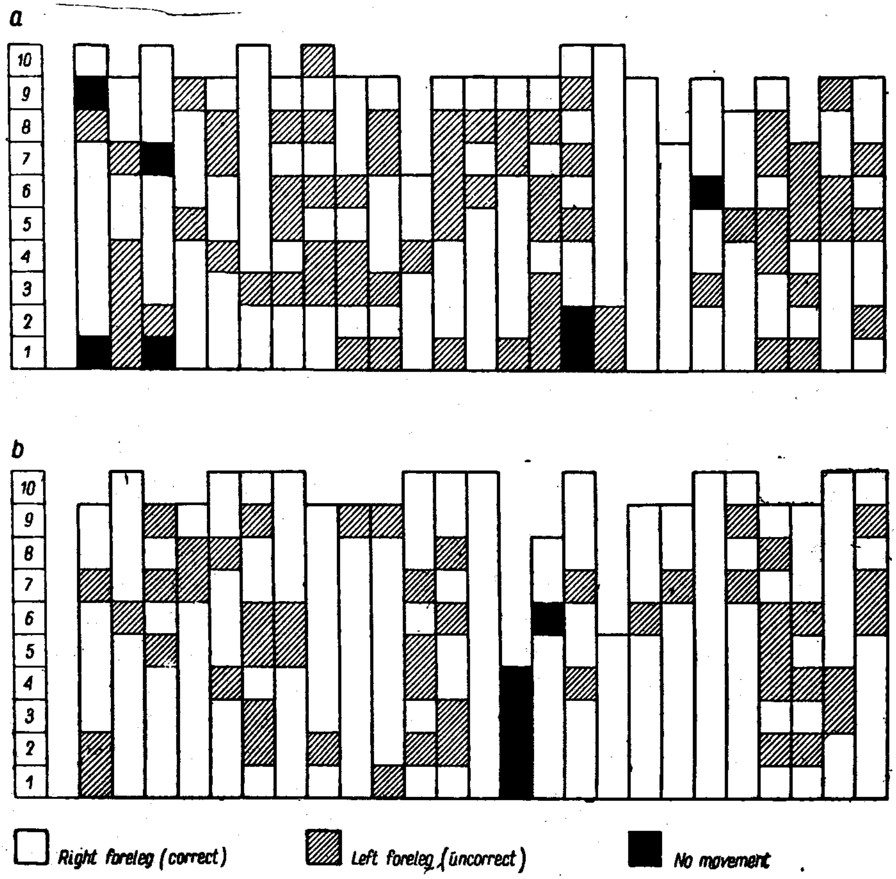

Fig. 3. Pattern of motor conditioned activity in dog SM 3 after operation, before and after training of extinction.

a — 25 experimental sessions preceding the series in which the extinction of movements of the left foreleg was trained. b — 25 successive experimental sessions during which extinction of movements of the left foreleg was trained. Ordinates: successive trials during an experimental session, 4 to 10 trials were made at each session. Abscissae: successive experimental sessions.

intervals. This depended on how much the animal was motorically excited in the given session. This state of affairs in some dogs did not improve at all (SM 5, SM 6, SM 11) while in others after several months the CR activity became more regular.

For illustration in Fig. 4 we present the course of experiments with dog SM 3 showing all types of irregularities described above. In Fig. 5

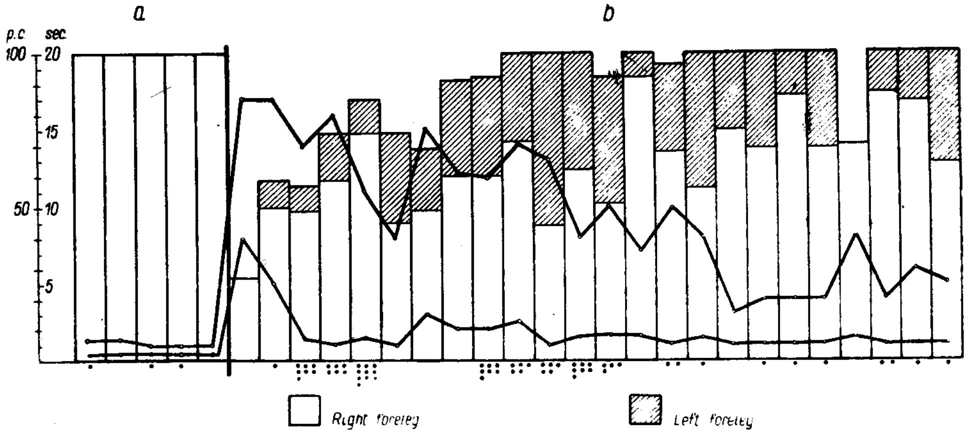

Fig. 4. Diagram showing the pre- and postoperative data of CR activity of dog SM 3. Averages of 3 successive experimental sessions are give Column — percentage of CRs (with either foreleg) Upper curve — longest latent period, lower curve — shortest latent period of CRs. Dots below show the numbers of intertrial movements.

Ordinates: percentage of performance of the trained movement in response to CS (with either right or left foreleg) and time in seconds. Abscissae: groups of 3 successive experimental sessions. a — preoperative period, b — postoperative period.

the comparison of the effects after unilateral and bilateral sensorimotor lesion is presented in dog SM 9. While after unilateral lesion the changes in animal's performances were insignificant, after the second operation his CR activity became strongly deteriorated.

In spite of this irregularity it was revealed that there are some factors which make the instrumental response more or less probable.

When the experimenter stood near the dog, even motionless, this often helped the animal to perform the movement. Other facilitating factors were: plaing with the dog, putting the hand on the foodtray („encouraging gestures"), slight touching the right foreleg, etc. On the contrary, when the dog stood alone and was not reinforced in some trials, this made the situation worse.

It was also discovered that the location of the stimulus played a very important role for the elicitation of the movement. If, for instance, the metronome was located in front of the animal (behind the foodtray) so that the orienting reaction towards it was not antagonistic with putting the foreleg on the foodtray, the reflex was easier elicitable than when it was located in a corner of the chamber. Also, when the

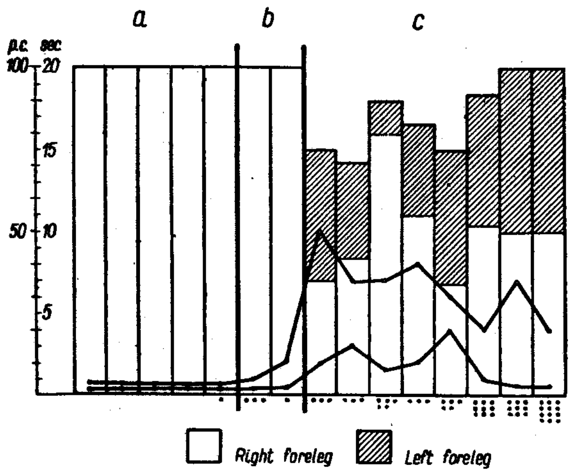

Fig. 5. Diagram showing pre- and postoperative data of CR activity of dog SM 9.

a — preoperative period, b — after unilateral ablation of sensorimotor cortex, c — after bilateral ablation of sensorimotor cortex. Other explanations as in Fig. 4.

apparatus provided not only auditory, but also visual sensations it acted even stronger. Therefore, it appeared that the noisily rotating toymill situated before the animal was the most „motogenic" stimulus. In some experiments it was proved that two CS'i acting together were also more „motogenic" than when acting separately.

The last point to be raised here is the effect of epileptic seizures which developed in some of our dogs sooner or later after operation. It was found that during the period in which seizures occurred the CR activity of the dog was strongly deteriorated, and all the symptoms observed in the first period after operation (full areflexia, strong irregularity of CR, etc.) reappeared. Also, after strong seizures the condition of the sensorimotor animals grew worse for several days and only slowly improved again. Therefore, the treatment with luminal which prevented the seizures had usually a beneficial effect on the sensorimotor animals.

Table II

Dogs	SM 1	SM 2	SM 3	SM 4	SM 5	SM 6	SM 7		SM 8		SM 9		SM 10		SM 11		SM 12	SM 13
				after third oper.			after first (left) oper.	after second (right) oper.	after first (left) oper.	after second (right) oper.	after first (right) oper.	after second (left) oper.	after third (left) oper.	after fourth (right) oper.	after first (left) oper.	after second (right) oper.		
Disorders of movements awkwardness	present absent	present absent	present absent	present	present absent	present absent	absent	present	absent	present absent	absent	present	absent	present	present absent	present	present absent	absent
sliding apart of legs	present absent	present absent	present absent	present	present absent	present absent	present in right legs	present	present absent	present	present in left legs absent	present	present in right legs	present	present in right legs	strong present	present in right legs absent	present in right legs
abnormal position of legs	present absent	present absent	present	present	present	present	present in right legs	present	present	present	present in left legs	present	present in right legs	present	present in right legs	present	present in right legs	present
hyperkinesia	slight	present	present	present	present	present	slight	present	slight	slight	absent	present	strong	strong	absent	absent	slight	strong present
hyperactivity	absent	absent	slight absent	present	absent	slight absent	absent	absent	absent	absent	absent	present absent	absent	slight absent	absent	present absent	present absent	absent
eating	not impaired	imaired normal	impaired	not impaired	impaired	impaired normal	not impaired	slightly impaired	not impaired	impaired	not impaired	much impaired	not impaired	impaired	slightly impaired, normal	much impaired	not impaired	not impaired
Conditioned activity general response to CS	alimentary: normal or abnormal	orienta-tion orient-ali-ment.	orientation: orient-ali-mentary	indefinite or orienta-tion, orient-ali-ment, ali-mentary	orient. or alimentary	orienta-tion or orient-ali-mentary	normal alimentary	orienta-tion orient-ali-mentary	alimentary	orienta-tion orient-ali-ment or alimentary	alimentary or orient-alimentary	orienta-tion or orient-ali-mentary	alimentary	indefinite	alimentary	orienta-tion, orient-ali-ment. or abnormal alimentary	alimentary	alimentary
instrumental response to CS	absent chaotic after retraining	absent? (hyperkine sia)	chaotic(?)	absent chaotic	absent chaotic after retraining	absent chaotic after retraining	present	absent chaotic ±regular	present	absent chaotic regular	present	chaotic	present	absent	present	absent chaotic absent	present	present
latency of CR	chaotic after retraining		chaotic	chaotic	chaotic after retraining	very pro-longed chaotic after retraining	prolonged short	chaotic	short	chaotic short	short	chaotic	short only sometimes slightly prolonged		short only sometimes slightly prolonged	chaotic	prolonged short	short
confusion of legs	absent		present	present	present after retraining	present after retraining	absent	absent	absent	present	absent	present	absent		absent	present	absent	absent
intertrial movements	absent	very few	numerous present or absent	present	very few	present	very few	present	absent	present	very few	present	absent circles	absent	absent circles	present or absent	present circles	present

DISCUSSION

The data presented in this paper show that extensive sensorimotor ablations produce heavy deterioration of all motor performances and a very severe and longlasting impairment of instrumental CR's: all movements of trunk, mouth and legs are defective, the proprioception is nearly abolished, and in addition the CR activity as a whole is strongly disturbed (Table II).

It may seem that this picture is the result of simply very extensive lesion in the sensorimotor area and cannot be subjected to any further analysis. However, if we compare the data obtained in this paper with the results described in the previous papers of this series, caused by partial ablations of sensorimotor cortex, we can easily discover that every symptom found in the present experiments may be also traced in particular partial lesions. And so, the syndrome consisting of irregular CR activity, the exaggerated orientation reaction to the stimuli, and the abnormal direct alimentary reaction is the effect of premotor lesions. Hyperkinesia and confusion of the legs in performing the trained movement are specific symptoms of motor lesions. The abnormal positions of the legs are chiefly due to the sensory lesions. Lastly, the general motor disability, also contributing to the impairment and irregularity of motor CR's, is the common result of both motor and sensory lesions. Therefore, the conclusion follows that the very complicated picture produced by sensorimotor ablations is nothing else than a combination of effects produced by definite partial ablations. In other words, the sensorimotor area must be considered not as an undifferentiated whole, but as a highly organized construction in which different parts play a different role.

The best illustration of this conclusion is provided in Fig. 6; it represents the experiments with dog SM 4 in which 3 bilateral ablations were performed successively: in the first only sensory areas were removed, in the second, motor areas, and in the third premotor areas were ablated. As seen in the Fig. 6 while after the first operation only the temporary disappearance of the CR was observed, after the second one we notice the symptom of confusing the legs, while after the third one the considerable irregularity of conditioned responses together with intertrial movements are added.

Such an approach allows us to understand also some seemingly significant differences in the symptoms found in the different dogs and not substantiated by anatomical findings. We have here in view the total abolition of instrumental reflexes in some animals and spontaneous recovery, even after a short time, in others. In previous papers we found that both after premotor lesions and after sensory lesions there is usually a temporary abolition of the instrumental reflex, but this reflex returns spontaneously after a lapse of time. The cause of this abolition is different in each of these cases. While after sensory ablation it is due to the disorganization of proprioception, which in normal conditions facilitated the performance of the movement, after

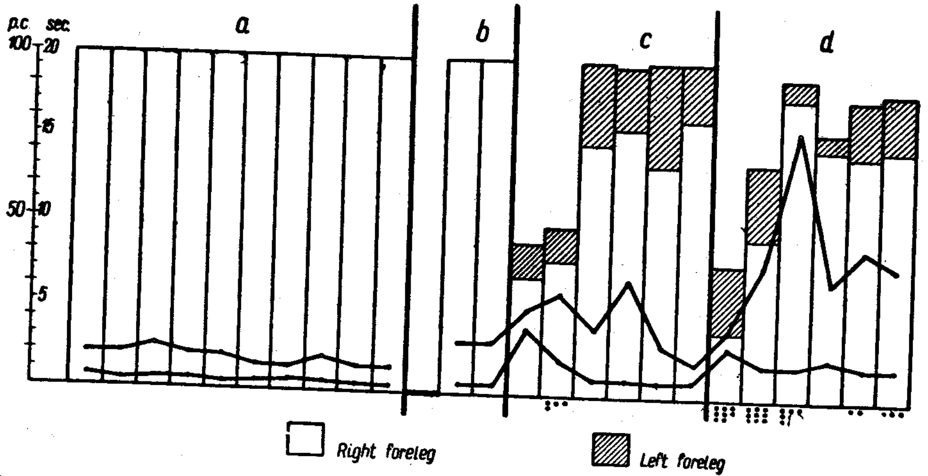

Fig. 6. Diagram showing pre- and postoperative data of CR activity of dog SM 4.
a — preoperative period, b — after bilateral ablation of sensory cortex, c — after bilateral ablation of motor cortex, d — after bilateral ablation of premotor cortex. Other explanations as in Fig. 4.

premotor ablation it is the effect of antagonism between the strongly disinhibited direct reactions to the stimulus (orientation and alimentary) and the instrumental act. After complete sensorimotor ablations these two mechanisms are jointly in operation, hence the probability of abolition of the trained movement is increased. In consequence the absence of this movement may be more prolonged. The longer is the period of the lack of movement — the more difficult is its recovery, since every testing experiment is inevitably connected with a counter training: the animal may learn to obtain food without performing the trained movement. Therefore, whether the trained movement is permanently or only temporarily abolished after sensorimotor lesions, may depend on some accidental factors, such as a greater or lesser agility of the animal, slight differences in postoperative training, etc. The proof of the correctness of this consideration is that the retraining of the instrumental reflex is very prompt but, when established, this reflex exhibits all the defective features and its irregularities characteristic for this type of lesion. It should be emphasized that while the three transversal strips of the sensorimotor region contribute in different way to the performance of the movement, this is not so with the left or right parts of these strips. It is of course a well known fact that the contralateral side of the sensory and motor cortex contributes more to the dexterity of movements than does the ipsilateral side; but in dog the defects produced by unilateral lesions are easily compensated by the corresponding ipsilateral areas. In consequence, the bilateral lesions, even not very extensive, are in the long run more harmful than even very extensive unilateral lesions. The strong impairment of the mouth movements brought about by bilateral, but not by unilateral lesions, may provide a good example.

Now we pass to the most important problem, namely that of the role played by the sensorimotor cortex in instrumental conditioned reflexes. First, one should stress that while after sensorimotor lesions the instrumental reflexes are always severely impaired, it is not so with classical reflexes. Although salivation was not measured in our experiments, nevertheless the observation of animals shows that the alimentary CR to the stimulus is either preserved after operation or very quickly restored. Therefore, it seems that lesions in this part of the cerebral cortex affect chiefly, if not exclusively, the instrumental part of the CR, leaving the classical part more or less intact. However, the exact role played by the sensorimotor area in the performance of instrumental reflexes is far from being clear. The fact that practically we were not able to abolish totally and irreversibly (with no possibility of retraining) the instrumental reflex shows that, although the area in question plays a substantial role in these reflexes, this role is not so simple. May be that this problem will become more elucidated when the effects of sensorimotor ablations upon other motor acts than those used in the present series are investigated.

SUMMARY

1. The effects of unilateral and bilateral ablations of the sensorimotor cortex (including premotor, motor and sensory areas) upon motor type II CR's and general animal's behaviour were investigated in dogs. The motor conditioned reflex consisted in putting the right foreleg on the foodtray to auditory and visuo-auditory stimuli.

2. After unilateral ablation of this region the motor performances on the contralateral side are temporarily impaired, but after a lapse of time they are largely compensated. The general behaviour of the animal is unchanged. Motor conditioned reflexes involving movement

of the contralateral side may be absent after ablation, but they are later spontaneously restored, although for some time they may be awkward and atactic.

3. Bilateral ablations of the sensorimotor cortex, performed either in one or in several stages result in strong impairment of motor performances, general animal's behaviour and instrumental conditioned reflexes.

4. When the operation has been radical the animal's limbs are strongly paretic and atactic. This defect is compensated very slowly and incompletely.

5. In dogs with extensive lesions (especially including medial parts of the hemispheres) the general behaviour is chaotic and inadequate. This state does not alter much with the lapse of time.

Instrumental conditioned reflexes undergo severe disturbances. Absent at the beginning they may or may not reappear spontaneously. They may however be retrained without special difficulty. Recovered either spontaneously or by training they manifest a considerable irregularity and imperfection: the latent periods are variable, the movements tend to appear in intervals and the animal often uses left foreleg instead of right. The conditioned response seems to be much better to stimuli situated in front of the animal and having visual component than to those operating from other places.

6. The analysis of these symptoms reveals that they are a combination of symptoms produced by separate lesions of premotor, motor and sensory areas.

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