Acta Biologiae Experimentalis, Vol. XX, 1960

THE EFFECTS OF BILATERAL LESIONS IN THE MOTOR CORTEX ON TYPE II CONDITIONED REFLEXES IN DOGS

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(Received 2 November 1959)

The present series of papers deals with the influence of various lesions in sensorimotor cortex upon motor, type II, conditioned reflexes. In the previous paper (Stępień and Stępień 1959) it was established that after bilateral ablations of sensory areas I and II the motor conditioned reflexes are abolished for a number of weeks and then they are gradually restored. The general behaviour of animals in the conditioned reflex chamber is, however, unimpaired: to conditioned stimuli the dog displays a pertinent alimentary reaction, and when the trained motor reflex is restored his state hardly differs from that before operation.

The present paper is concerned with the effects of bilateral ablations of the so called motor cortex on instrumental conditioned reflexes. According to the abundant evidence obtained by the method of electrical stimulation of the cerebral cortex since Fritch and Hitzig (1870), it is generally accepted that in dog this area forms a transversal strip of the cortex situated approximately between the cruciate sulcus and the central sulcus (and their lateral prolongations). The lateral boundary of this area is formed by the rostral prolongation of the suprasylvian sulcus. Thus, the motor area in dog comprises the following gyri: *postcruciatus*, the anterior part of *sigmoideus posterior* and anterior part of *coronalis* (Fig. 1A). The electrophysiological data are in good agreement with morphological description of the cortex of the dog. In fact, according to recent data (Morin 1951, Adria-

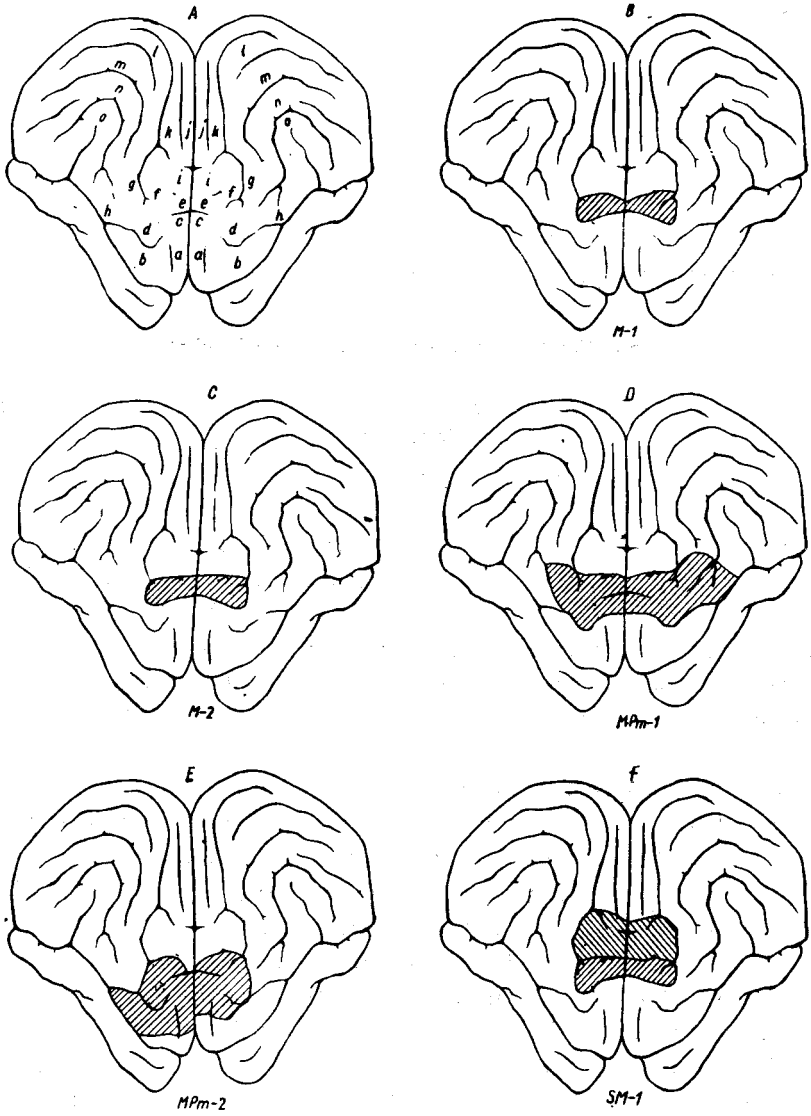

Fig. 1. The cerebral cortex of the dog flattened on the plain, and sites of lesions in experimental dogs. Note that we have subdivided the precruciate and postcruciate regions into two parts: the medial parts of these regions are called gyrus precruciatus and postcruciatus, the lateral parts gyrus sigmoideus anterior and posterior

A — normal cerebral cortex. Denotations: a — *gyrus proreus*, b — *g. orbitalis*, c — *g. precruciatus*, d — *g. sigmoideus anterior*, e — *g. postcruciatus*, f — *sigmoideus posterior*, g — *g. coronalis*, h — *g. compositus anterior*, i — *g. postcentralis*. B — F, lesions of the cerebral cortex in various dogs as indicated in text.

nov and Mering 1959) this area comprises the greatest percentage of giant pyramidal cells. The number of these cells falls down dramatically both rostrally and caudally to the motor area.

Studies concerning the motor area carried out either by electrophysiological methods, or by methods of ablations in chronic animals, show unequivocally that it is chiefly, or perhaps even exclusively, concerned with the control of movements of extremities and mouth. On the other hand, it is now believed that the so called premotor area controls the axial musculature and movements of the head (Woolsey et. al. 1950, Woolsey and Settlage 1950). Whatever the real functional significance of the premotor area, the symptoms produced by its ablation and those obtained after ablation of the motor area sensu stricto are quite different. This difference has been observed by a number of authors on monkeys and, as will be seen from the present series of papers, it also exists in dogs. For this reason it was decided to analyse the effects of lesions in these two areas separately. However, as the boundaries of these areas and their mutual overlapping are not precisely known, in some dogs ablations encroached into adjacent areas. Knowing the symptoms of removals of these other areas the results of the lesions of motor area itself could be understood.

MATERIAL AND METHODS

The lesions in motor areas were performed on five mongrel male dogs, two to four years old, weighing from 14 to 20 kg. In two of them M-1 and M-2, the lesions were limited to motor areas, in two other dogs, MPm-1 and MPm-2, they included both motor and premotor areas, and in one dog (MS-1) motor and sensory areas were removed. The method of experimentation was exactly the same as that applied in our previous paper (Stępień and Stępień 1959). We used acoustic conditioned stimuli (buzzers, bells, whistles etc.), and the motor conditioned reaction of the dog consisted in lifting of the right foreleg and putting it on the footray.

Surgical procedure was also described in detail in the previous paper. Postoperational experiments were started usually about one week after operation.

In those cases in which conditioned reflexes proved to be abolished or strongly impaired after operation the experiments were performed only once a week, or so, and consisted only of a few trials, some of which were reinforced by food and some were not (for details of this procedure see Stępień and Stępień 1959). Our aim was to observe the "spontaneous" restoration of motor conditioned reflexes, and therefore re-training was carefully avoided.

RESULTS

Dog M-1. Ablation of the motor area only (Fig. 1B)

In this dog the lesion comprised *gyrus postcruciatus* and anterior part of *gyrus sigmoideus posterior*. The anterior part of *gyrus coronalis* was spared in order not to impair the movements engaged in eating.

Several days after operation the dog manifested a very strong impairment in his motor performances, and besides that his general behaviour was rather chaotic, which symptom is characteristic for premotor ablations (see the next paper). This chaotic behaviour lasted only for a few days and was undoubtedly due to the transient oedema of the adjacent regions of the cortex. On the other hand the symptoms of motor disability were longlasting and although they somewhat improved in the course of time, they were clearly seen till the end of observation (i. e. during 7 months). These disorders consisted chiefly in the sliding of all four legs apart with the body falling limply to the floor. This occurred chiefly either when the dog ran on a smooth floor, or during the act of eating. He was not able to stand for a long time, as his hind legs bent slowly and he was compelled to sit down. Sometimes he crossed his forelegs or put the dorsal aspect of the foot to the ground. These last symptoms were only temporary and they practically disappeared after some weeks.

Nearly immediately after operation another prominent symptom appeared, namely hyperkinesis of extremities, seen chiefly in the forelegs. It was best seen when the animal was lifted in the air or when he stood on the stand in the conditioned reflex chamber. This hyperkinesis consisted in constant alternate lifting of both forelegs ("pedalling movements"). When the animal was lifted these movements were so strong that it was practically impossible to test his placing reaction. However, except a few days after operation, the dog did not exhibit any general disorder of his motor behaviour: in spite of hyperkinesis of the legs, no locomotor hyperactivity was observed, he kept his head in normal position (not bent down as is the case in premotor animals) and reacted adequately to all external stimuli.

When brought to the experimental chamber (nine days after operation) the dog performed the trained movement from the very

beginning, although it was very awkward and atactic. Most often the movement appeared immediately after the application of the conditioned stimulus, but sometimes its latency was prolonged which was due to the "technical" difficulties of its performance. To the conditioned stimuli the dog displayed a more distinct orienting reaction than was seen before operation, a symptom which is also strongly developed after premotor lesions.

The awkwardness of trained motor conditioned reactions gradually disappeared, but some traces of it remained till the end of observation. The hyperkinesis of the forelegs was seen during the intervals between trials: every few seconds the animal lifted either his left or his right leg to about 10—20 cm. above the floor of the stand. These movements had nothing to do with the trained motor conditioned response and they were not accompanied by any alimentary reaction such as displayed to the conditioned stimuli.

Another defect observed in the conditioned reflex chamber in the first period after operation was that the dog, after putting his foreleg on the foodtray to a conditioned stimulus, was not able to take it off. Therefore after having eaten his portion of food, he stood for a long time with his leg on the foodtray, and only when he turned away did the leg passively fall to the floor.

But the most prominent symptom which appeared immediately after operation and remained during the whole period of observation was that the dog confused his forelegs and put on the foodtray either his right foreleg, trained before operation, or his left foreleg, or both. It should be noted that before operation the animal n e v e r performed the trained movement with his left foreleg. Now, after performing this movement, the dog displayed a normal alimentary reaction to the foodtray, as if not noticing that he used the "wrong leg".

It was soon observed that whether the animal lifted to the conditioned stimulus his right of left leg depended chiefly on the position of his body in relation to the foodtray. If, before the application of the stimulus, he was turned with his left side towards the foodtray, then to the sound of the conditioned stimulus he made a turn to the left and in this case his right leg was lifted and put on the foodtray. Vice-versa, if he stood with his right side directed to the foodtray, then in response to the stimulus he turned right and lifted his left foreleg (Fig. 2). We made some attempts to compel the animal to lift only the right foreleg by not reinforcing the

movements of the left foreleg. However this measure was not successful and the movements of the left foreleg appeared as often as the dog stood with his right side turned to the foodtray before application of the stimulus.

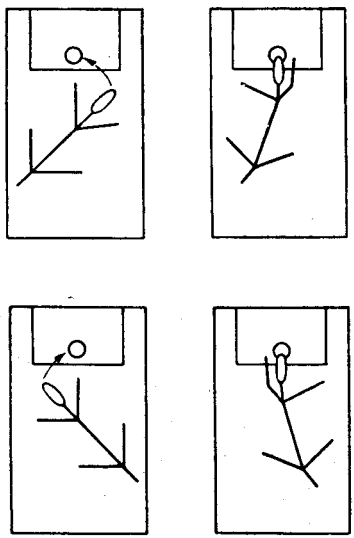

Fig. 2. Schematic representation of the mechanism of confusing legs in the performance of trained movement in motor dogs

Explanation in text.

Dog M-2. Ablation of the motor area (Fig. 1C)

The boundaries of the lesion were similar to those in dog M-1.

The general behaviour of the dog after operation, as well as his motor conditioned reactions, were very similar to those seen in dog M-1, except some details. Immediately after operation he did not display the premotor symptoms seen in dog M-1, but on the other hand his motor conditioned reflexes were almost absent in the first experiments: the dog displayed very clear and distinct alimentary reaction to the conditioned stimuli, but his forelegs remained on the floor. Only in the 7th experiment (one month after operation) conditioned motor reactions became regular. The movements were at first awkward and then they became nearly normal.

The hyperkinesis in this dog consisted in frequent lifting of either right or left foreleg, and holding them in the air for several seconds. These movements were quite different from the instrumental conditioned reactions. Owing to this hyperkinesis it was not possible to test the presence of the placing reaction.

The symptom of confusing the legs in the performance of motor conditioned reactions was as clearly seen in this dog as in the first one and it also persisted during the whole period of observation. He was also not able at the beginning to take off his leg actively from the foodtray.

After two months a premotor ablation was performed, the results of which will be described in the next paper.

Dog MPm-1. Ablation of the motor and premotor area (Fig. 1D)

The lesion in this dog included: gyri *postcruciatus* and *precruciatus* (bilaterally), anterior parts of *sigmoideus posterior*, and the whole of *sigmoideus anterior* (bilaterally), anterior parts of *gyrus coronalis* (bilaterally), and *compositus anterior* on the left side.

This dog displayed, besides the symptoms seen in the two previous dogs, also additional symptoms, due to premotor lesion which will be described in the next paper. To the first group of symptoms belonged awkwardness of movements, sliding of the legs apart, their abnormal positions and hyperkinesis. To the second group belonged chaotical and inadequate behaviour, locomotor hyperactivity with the head bent down and a strong tendency to stereotyped movements. Because of the abnormal general behaviour, the conditioned reflexes were for a long time extremely chaotical: although the animal was able to perform the trained movement from the very beginning, his conditioned reactions were most irregular; often the dog performed the movement in the intervals between trials, but did not perform it to the conditioned stimulus itself (conditioned "disreflexia"). All this confusion in conditioned responses gradually decreased, but the motor hyperactivity and stereotypy of movements remained till the end of observation (the dog was sacrificed 7 months after operation).

From the very beginning of the post-operational period, as soon as motor conditioned reflexes reappeared, the dog started to perform the trained movement either with his right or his left foreleg or

with both of them. This confusion was observed both in responses to the conditioned stimuli and in the intervals. It persisted during the whole time of observation.

Dog MPm-2. Ablation of motor, premotor and partially prefrontal areas (Fig. 1E)

The lesion in this dog included bilaterally: the lateral part of *gyrus postcruciatus, gyrus precruciatus,* the anterior part of *sigmoideus posterior, sigmoideus anterior,* the posterior parts of the *proreus* and medial parts of *orbitalis*; on the right the lateral part of *gyrus orbitalis* was also removed.

As in this dog the lesion of the motor area was not extensive, the motor disability was rather slight. There was no awkwardness of movements, but the dog manifested hyperkinesis of the forelegs. The motor conditioned reactions were changed in such a way that, instead of putting the right foreleg on the foodtray, the animal always jumped onto it with both forelegs. Besides he manifested hyperactivity and a tendency to stereotyped movements.

Dog SM-1. Ablation of the sensory and motor cortex (Fig. 1F)

The dog was subjected first to the limited bilateral sensory ablation in which *gyrus postcentralis,* the posterior part of *gyrus sigmoideus posterior* and posterior part of *gyrus coronalis* were removed, and then, five weeks later, to the bilateral motor ablation in which *gyrus postcruciatus* and the anterior part of *gyrus sigmoideus posterior* were destroyed. After the first operation the dog was atactic, and his motor conditioned reflexes were abolished for 2—3 weeks. Thereafter they became normal. After the second operation the conditioned reflexes were again abolished for 3—4 weeks and then, when they were restored, the animal started to perform the trained movement either with his right or left foreleg, which was never seen after the first operation. This state persisted during the period of observation which lasted three months. The dog also had difficulties with taking his leg off the foodtray and did it passively when turning aside.

In general the deficit of motor performances seems in this dog to be stronger than in other dogs. This was due to the more extensive lesion in the sensori-motor cortex.

Table I

The chief symptoms observed in dogs after operation

Dogs	M-1	M-2	MPm-1	MPm-2	SM-1
Extent of lesion	motor	motor	motor premotor	motor premotor prefrontal	sensory motor
Postoperational period in months	7	2	7	1.5	3
Disorders in movements of legs					
awkwardness	strong* slight	strong slight	strong slight	absent	strong
sliding apart	strong slight	strong absent	strong medium	slight absent	strong
abnormal positions	slight absent	strong absent	strong absent	absent	strong
hyperkinesis	strong medium	medium	strong	strong	present
hyperactivity stereotypy	absent	absent	strong	strong	absent
Conditioned activity					
conditioned responses to CS	regular	irregular regular	irregular	irregular	absent regular
confusion of forelegs	present	present	present	present	present
intertrial movements	present absent	present absent	frequent	present	absent

* The first characteristic denotes the early stage after operation, the second characteristic denotes later stages.

The chief symptoms of our dogs after operation are summarised in Table I.

DISCUSSION

The general impairment of motor activity seen in our dogs after bilateral ablations of the motor cortex (except in dog MPm-2 in

which the lesion was small) is so well known that there is hardly any necessity to discuss it in detail. The only point worth mentioning is the difference between the motor defects seen in the "motor dogs", and in the "sensory dogs" described in our previous paper (Stępień and Stępień 1959). Whereas the chief defect of the latter dogs results from the impairment of the sense of position of the legs and consists in such symptoms as putting the dorsal aspect of the foot to the floor, crossing the forelegs etc., these symptoms are not so clearly seen in our "motor dogs". Instead their chief deficit consists in sliding of extremities and falling down when the dog is eating or running on a smooth floor. These symptoms may be considered as depending rather on the impairment of the motor performance itself than on lack of the sensory input.

The next symptom characteristic for "motor dogs" is hyperkinesis of forelegs. It consists in incessant lifting of the legs to various height, mostly in the form of "pedalling". This symptom was never seen in our "sensory dogs". The origin of it is not quite clear; it depends probably on removal together with the motor area itself, also of the suppressor area 4s, which may just control and inhibit this sort of movements.

It is very important to draw attention to the difference between the symptom of hyperkinesis, characteristic of dogs with motor lesions, and that of hyperactivity and stereotyped movements, observed after premotor lesions. Whereas the first symptom consists in incessant small movements of the legs, unrelated to the general behaviour of the animal, the second symptom concerns the animal's motor acts and consists in their repeated performance. As we shall see in the next paper locomotor hyperactivity is only one of the instances of this sort of disorder.

As far as motor conditioned reflexes are concerned their performance after motor lesions was more or less defective and was parallel with the general impairment of movements resulting from the operation. It seems that after pure motor lesions the animals are in general able to perform the trained movement from the very beginning (cf. dog M-1) in contrast to the state observed after sensory lesions when the movement is abolished for a certain time*.

* The disappearance of the motor conditioned reflexes in dog SM-1 was probably due to the fact that in this animal not only the motor area but also the sensory area was removed.

However the movement of taking the leg off the foodtray was generally much impaired and returned only after some time.

The chief symptom found after lesions of the motor cortex consisted in confusion of legs, in the performance of the trained movement. This symptom observed in all our dogs seems to be characteristic of these lesions, since it was not seen either after pure sensory lesions or premotor ones. How remarkable and extra-ordinary this symptom is, may be clearly understood if we take into account that not only in normal dogs such an exchange of movements does not occur, but it even does not happen in dogs with contralateral cortical lesions. In fact, following left sensori-motor ablations or even full left hemispherectomy, the animals, trained to perform the instrumental movement with their right foreleg, continue to do so, although this movement may be very defective, and do not display any tendency to substitute the movement of right by that of left foreleg (S t ę p i e ń and S t ę p i e ń, in preparation).

The problem arises how this symptom of confusing the legs may be explained. If we assume that performance of the trained movement by a given foreleg, and not by the symmetric one, is due to some sort of differentiation of two flows of afferent impulses generated by performance of movements with each leg, then we may say that this differentiation is lost after bilateral motor ablation. There is an anatomical evidence to support the view that the so called motor area represents a receptive field concerned with the analysis of m o v e m e n t s, as contrasted to the sensory area which is concerned with the analysis of p o s i t i o n s of limbs. As the representation of proprioception of movements is both contralateral and ipsilateral, after contralateral ablation of the motor area, the ipsilateral area is sufficient for differentiation of movements of both extremities. On the other hand bilateral removal of this area makes this differentiation impossible. The symptom of confusing legs seems to be permanent, as even after a long period of time after operation the tendency to perform the trained movement with the "wrong" foreleg remains. Although we were not specially concerned with the possibility of differentiation of both movements, we have evidence that this differentiation would not be easily obtained.

It was noticed that whether the animal performed the trained movement with his right or left foreleg depended on the turn the animal made just before its execution. If the turn in the direction of the foodtray was to the right, then the animal's body was sup-

ported by the right legs while the left foreleg was "free". Then it is with this leg that the animal performs the trained movement in such an occasion. It is well known that, according to the Sherrington's principles of postural reflexes, turning right produces the extension of the right foreleg and flexion of the left one. Therefore it may be concluded that this postural reflex of flexion is in our experimental condition allied to the instrumental reflex of putting the leg on the foodtray and consequently determines with which leg this movement is executed. The very interesting point is that this alliance, if existing in a normal animal, is totally suppressed by the training of the movement of a particular leg (e.g. the right one) and can be revealed only after the bilateral lesion of the motor cortex, when the proprioceptive feedback from the performance of the movement is abolished.

SUMMARY

The effects of bilateral ablations of the so called motor area of the cerebral cortex in dogs on their motor activity, and in particular on type II conditioned reflexes (consisting in lifting the foreleg and putting it on the foodtray), were investigated.

The following symptoms were observed:

1. The impairment of movement of extremities consisting chiefly in sliding of the legs apart and, in a lesser degree, in atactic symptoms.

2. Hyperkinesis manifested particularly in forelegs ("pedalling movements").

3. Confusion of the forelegs in the performance of motor conditioned responses.

The above symptoms are compared to those observed after either sensory lesions or premotor lesions and their origin is discussed.

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