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

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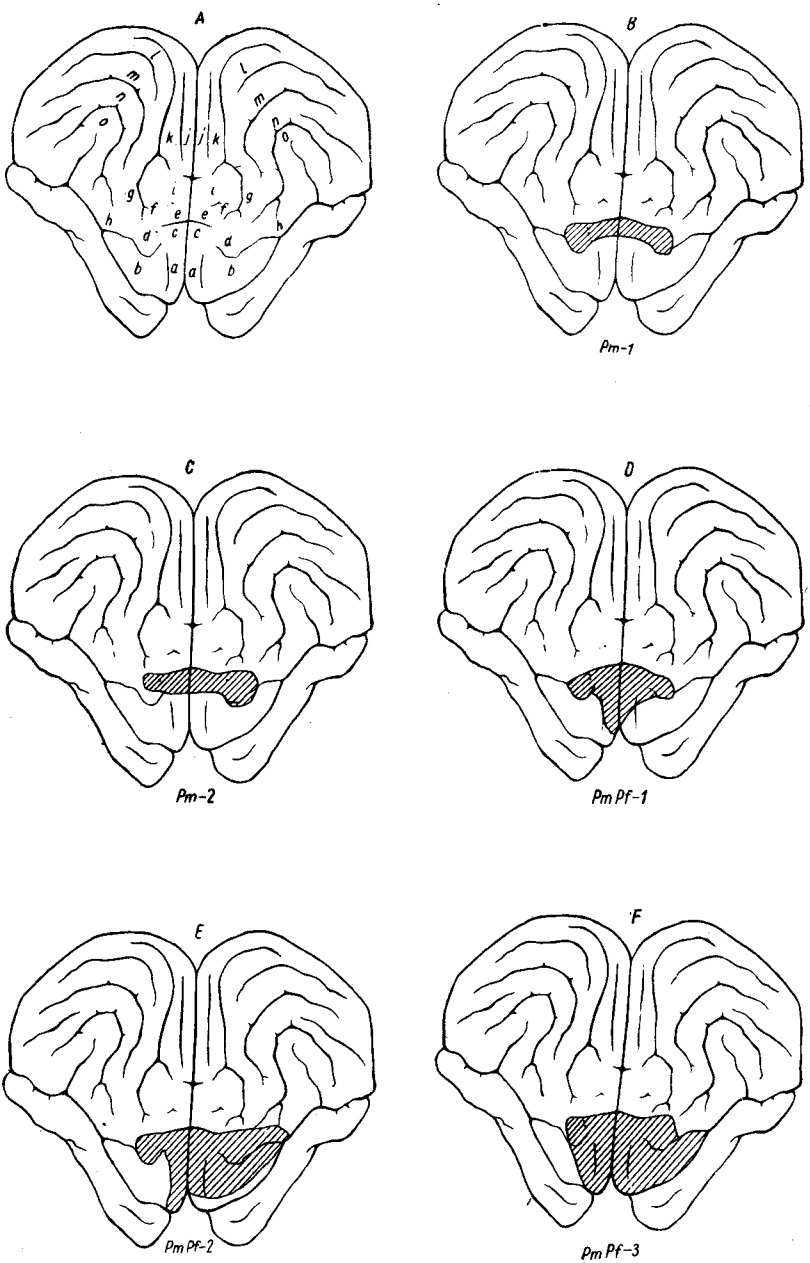
In most descriptions of the cerebral cortex of monkeys and apes it is stated that in front of the so called motor area sensu stricto (or area 4) another area is situated which differs from the first one both anatomically and physiologically and is called premotor area or area 6. Its chief anatomical characteristic is that it is thinner than the motor area, that it possesses a smaller amount of pyramidal cells and has no giant pyramidal cells in layer V. Electrical stimulation of this area in anesthetized animals does not evoke discrete movements of extremities, but rather coordinated movements of the whole body.

The opinions concerning functional role of the premotor area are controversial. On the one hand it is considered as an integrative region controlling complex motor acts elicited by intermediary of the motor area. Chief protagonist of this view was Jacobsen (1936) who claimed that removal of the premotor area in monkeys produces a "motor apraxia". The same view is held by many neurologists. On the other hand other authors (Woolsey et al. 1950, Woolsey and Settlage 1950) consider this field simply as a part of motor area controlling movements of the head and axial musculature of the body.

Whatever view will prove to be correct, since ablations of the premotor area produce in monkeys symptoms very different from those produced by lesions of the motor cortex, it seemed necessary to study in dogs the symptoms of ablations of these two areas separately.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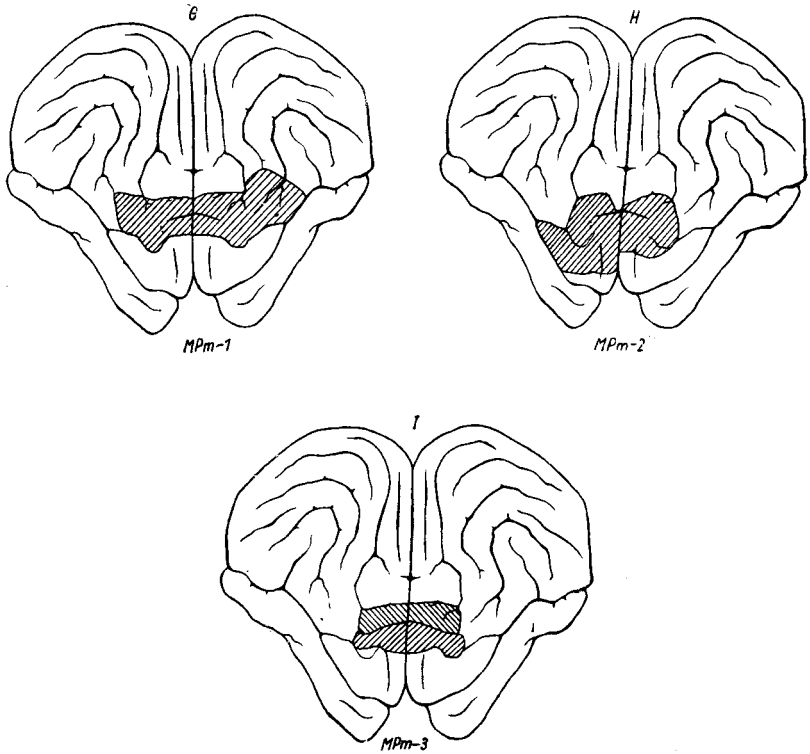

Fig. 1. The cerebral cortex of the dog flattened on the plain, and sites of lesions in experimental dogs

A — normal cerebral cortex. Denotations: a — *gyrus 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*. B — I, lesions of the cerebral cortex in various dogs as indicated in text.

Anatomical limits of the premotor area in dog are so far not well defined (for literature see Adrianov and Mering 1959), and therefore they must be chosen rather arbitrarily. We consider the premotor area in dog as a region limited caudally by the cruciate sulcus and its prolongation, rostrally by the presylvian sulcus, and laterally by the prolongation of the coronal sulcus. Thus, according to our definition, this area consists of precruciate gyrus and sigmoid anterior gyrus (Fig. 1A). As those boundaries are not certain, we performed in some dogs more extensive lesions including either parts of prefrontal areas (proreal gyrus and partially orbital

gyrus), or motor areas (postcruciate and posterior sigmoid gyri). As the symptoms observed after the ablations of both motor and prefrontal areas were already investigated in this laboratory (Brutkowski et al. 1956, Stępień et al. 1960) it was possible to assess which symptoms should be attributed to the region situated between them.

MATERIAL AND METHODS

Experiments were performed on 8 dogs, weighing 12—20 kg., aged 2—4 years. In two dogs Pm-1 and Pm-2 only premotor areas (boundaries as described above) were removed, in three other dogs PmPf-1, PmPf-2 and PmPf-3, parts of the prefrontal areas were also ablated, whereas in three remaining dogs, MPm-1, MPm-2 and Mpm-3 the lesions included motor areas (in MPm-2 also part of the prefrontal area).

In all the dogs instrumental alimentary conditioned reflexes to various acoustic stimuli were established before operation. The trained motor reaction consisted in lifting the right foreleg and putting it on the foodtray. This movement performed in response to conditioned stimuli was reinforced by presentation of food. Other details of the method and surgical procedure were described in a previous paper (Stępień and Stępień 1959). After operation the experiments started as soon as the animals were sufficiently recovered. When after operation the conditioned motor reflexes were found to be present, then the experimental sessions took their normal course. When they were absent the conditioned stimulus was sometimes reinforced and sometimes not, and after a few trials the experiment was discontinued. The next experiment was performed only after a week or so. This procedure was adopted to avoid any re-training of the animal after operation (for details see Stępień and Stępień 1959).

RESULTS

I. Ablations of the premotor area only

In two dogs Pm-1 and Pm-2 only small lesions including precruciate and anterior sigmoid gyri were performed.

Dog Pm-1 (Fig. 1B). From the first days after operation the dog was able to walk quite well without ataxia or sliding. Placing reaction was positive. Brought into a room he walked around during long periods of time. This walking had a stereotype character, and there was no tendency to explore the environment, as is typical for normal dogs. When called he displayed only a slight orienting reaction, but did not stop walking. Sometimes unexpectedly he stopped

in the middle of the room, and after a while he set out to walk again. While walking his head was bent down to the level of the back and the dog exhibited a tendency to pass beneath and not above the obstacles. These symptoms disappeared gradually within two weeks.

On the 5th day after operation, when brought into the conditioned-reflex chamber, he behaved more or less quietly, but performed some oscillating movements in front of the foodtray; such movements were never observed before. To conditioned stimuli the dog exhibited a strong orienting reaction towards the source of the sound, not seen before operation; then he turned towards the foodtray and performed alternately the movements towards the stimulus and towards the bowl several times without any tendency to lift the foreleg and put it on the foodtray. Once, however, during the first experiment he performed this movement in the interval between conditioned stimuli; it was performed quite skillfully and without any "technical" difficulties. During following experiments a similar picture was observed: to the conditioned stimuli the dog exhibited alternately orienting and alimentary reaction but the trained movement did not appear. Then in the 9th experiment (38th day after operation) on the third trial he executed the trained movement without any perceivable difficulty and with a very short latent period. In following experiments the trained movement appeared in every trial, although the orienting reaction towards the stimulus preceded it nearly always. Sometimes the movement appeared also during intervals between conditioned stimuli. This state remained almost without change throughout the period of observation. On 65th day after operation the dog was sacrificed.

Dog Pm-2 (Fig. 1C). Like dog Pm-1 this dog was also unimpaired in his motor performances from the first days after operation but he displayed a strong hyperactivity even more pronounced than that of the previous dog. He persistently walked about the room and, when on leash, made oscillating movements of the body. When walking, his head was bent and he tended to slip underneath tables and chairs. These symptoms gradually disappeared within a few weeks. Placing reaction was normal.

In the first experiment, in response to the conditioned stimulus, the animal displayed a very strong alimentary reaction but the trained movement did not appear. However, already in the next

experiment (9th day after operation) the animal started to perform the trained movement, although in some trials its latency was prolonged, due to the strong direct alimentary reaction which obviously inhibited the instrumental response. At the same time the animal started to perform the trained movement in intervals between trials and did so every few seconds. Both putting the leg on the foodtray and taking it off were quite skillful. Sometimes the intertrial movements were only abortive. They were most often not accompanied by alimentary reaction which was always observed with the movements executed to the conditioned stimuli. In the course of the experiment the intertrial movements decreased in number but the general restlessness of the dog and oscillating movements of the head persisted up to the end.

Such state continued day after day during the whole period of observation (3 months), although the intertrial movements became less frequent and appeared chiefly in the beginning of each experiment.

II. Ablations of the premotor and prefrontal areas

Dog PmPf-1 (Fig. 1D) In this dog in addition to the removal of precruciate and anterior sigmoid gyri, the proreal gyrus was also ablated. The motor efficiency of this dog was, as in previous animals, perfect from the first days after operation. He displayed a strong locomotor hyperactivity with tendency to repeat again and again the same itinerary round the room. His head was bent below the line of the back and he tended to pass underneath the obstacles. Placing reaction was normal.

When brought to the experimental chamber (5th day after operation) he incessantly walked around the stand and frequently climbed the foodtray with his forelegs or even with all four legs. To the conditioned stimuli his first reactions were quite different than those before operation. He stretched out his head towards the source of the stimulus (situated behind the foodtray), climbed on the foodtray with his forelegs and paid no attention to the food presented in the bowl. If he noticed it accidentally, he started immediately to eat it.

In the third experiment (8th day after operation) besides the orienting reaction towards the source of the stimulus, the proper

alimentary reaction towards the bowl appeared also and after several seconds the right foreleg was put on the foodtray. In the next stage this movement appeared immediately after the application of the stimulus. The movement was performed either with the right foreleg or (rarely) with both.

In the intervals between trials the dog walked round the foodtray, licked the empty bowl, climbed repeatedly the foodtray and performed many times the trained movement. This abnormal behaviour remained unchanged throughout the observation period which lasted two months.

Dog PmPf-2 (Fig. 1E). The ablation in this dog included precruciate, anterior sigmoid and proreal gyri bilaterally; on the left side parts of orbital gyrus and of coronal gyrus as well as anterior compositive gyrus were ablated. The chief symptom which appeared immediately after operation was a very strong locomotor hyperactivity: on the fourth day after operation the dog walked incessantly around the room for 9 hours, till complete exhaustion. He also displayed a strong tendency to walk again and again along the same itinerary. His head was bent beneath the line of his back. He often slipped underneath the obstacles and entered the corners of the room staying there for a long time. He displayed no exploratory reactions towards the environment and reacted very poorly to extraneous stimuli. On the other hand his motor efficiency was perfect and placing reaction was normal. This state of affairs gradually improved, but the locomotor hyperactivity was permanent and lasted throughout the period of observation (one year).

In the first experiments (first week after operation) in the conditioned-reflex chamber the dog behaved as if the experimental situation were quite new to him. To conditioned stimuli he displayed only an orientation reaction and only accidentally found food presented to him. Throughout the experiment he incessantly walked round the foodtray (as far as the length of the leash allowed) and often climbed the foodtray from various sides.

Gradually the conditioned stimuli began to elicit alimentary reaction in addition to the orienting reaction. The alimentary reaction consisted in bending the head very low to the empty bowl and licking it, which was never seen before operation. The trained movement appeared for the first time in the 8th experiment (21 days

after operation), but only after the cessation of the stimulus. It was quite skillful and did not differ from that before operation. In the following experiments the trained movement appeared more and more often but nearly always with a long latent period: the stimulus evoked first the orientation reaction, then the direct reaction to the bowl and only after several seconds, when the food was not presented, did the animal put his leg on the foodtray. Only after several months the conditioned reactions improved to such a degree, that most of them were displayed immediately as before operation.

As soon as the trained movements began to appear to the conditioned stimulus, the animal started to perform them very often in the intertrial intervals. In consequence his whole behaviour in the conditioned-reflex chamber appeared to be most chaotical and unpredictable. The latent periods of conditioned reactions were variable, and it happened sometimes that to the conditioned stimulus the movement did not appear at all. On the contrary, during the intervals between trials the dog was in permanent motion, he performed the trained movement again and again, very often climbed the foodtray with his forelegs or with all four legs, and so on. The majority of intertrial movements had not an alimentary character. Such state of affairs changed but little up to the end of observation. Although conditioned reactions became more regular, the whole behaviour of the animal during intervals seemed to be quite "stupid".

Dog PmPf-3 (Fig. 1F). The lesion in this dog was nearly the same as in the previous one, and all his symptoms were so similar that they will be only very briefly described. The dog displayed locomotor hyperactivity, connected with stereotype repeating of the same itinerary, with a tendency to enter into corners of the room and to pass underneath the obstacles. His motor efficiency and placing reaction were perfect. In the first experiments the motor conditioned reflex was absent, but the dog was very restless and often climbed the foodtray. To the conditioned stimuli he displayed first orienting and then alimentary reaction. The trained movement appeared about three weeks after operation, its latency was variable and he performed it very often in intervals. Such state lasted during the whole period of observation (8 months).

III. Ablations of the premotor and motor area

Dog MPm-1 (Fig. 1G). The lesion in this dog included bilaterally postcruciate and precruciate gyri, anterior parts of posterior sigmoid, the whole of anterior sigmoid and anterior part of coronal gyrus; on the left side anterior composite gyrus was removed.

The symptoms connected with the removal of the motor cortex were described in the previous paper (Stępień et al. 1960). They included disorders of motor acts, sliding apart of legs, hyperkinesis of the forelegs and confusion of legs in execution of the trained movement. In addition to these symptoms the dog displayed a locomotor hyperactivity with his head bent and entering the corners of the room. This state disappeared within two weeks.

During the first days after operation the animal's behaviour in the experimental chamber was so chaotical, restless and awkward that conducting experiments was impossible. Then, gradually his behaviour improved: the dog began to perform the trained movement to conditioned stimuli, but this movement appeared only occasionally and with variable latency. To the conditioned stimuli the dog displayed both the orienting reaction and the direct reaction to the bowl. These reactions interfered with the performance of the trained movement. The direct reaction to the bowl was soon converted into persistent gnawing of the border of the bowl, manifested even when the dog was satiated. During such gnawing the animal did not react at all to conditioned stimuli. In those periods in which gnawing of the bowl was not present, the dog performed the trained movement in the intervals again and again, he climbed the foodtray etc. After several months the motor reactions to the conditioned stimuli became more regular and the dog was able to perform them immediately after the application of the stimulus. However in intervals the "stupid" behaviour with gnawing the bowl and other forms of hyperactivity remained till the end of observation i. e. 7.5 months.

Dog PMm-2 (Fig. 1H). The lesion in this dog included bilaterally: the lateral part of postcruciate gyrus, precruciate gyrus, the anterior part of posterior sigmoid, anterior sigmoid, the posterior parts of proreal and medial parts of orbital gyrus; on the right side the lateral part of orbital gyrus was also removed.

The impairment of motor acts was in this dog only slight because of the limited extent of the lesion in the motor cortex

(cf. Stępień et al. 1960). On the other hand all the premotor symptoms were manifest.

Dog MPm-3 (Fig. 1I). This dog was first subjected to the ablation of the motor cortex and was described in the previous paper as dog M-2. (Stępień et al. 1960). Two months later the second operation was performed in which precruciate gyrus and anterior sigmoid were bilaterally removed. The second operation produced striking changes in the animal's behaviour. At first the trained movement appeared to the conditioned stimuli very irregularly and unpredictably. It was noticed that to the stimulus situated in front of the animal the motor reaction was prompt, while to the stimulus situated in the corner of the chamber the response did not appear. This was caused by the fact that in the first case the orienting reaction towards the stimulus was allied with, while in the second case it was antagonistic to the trained motor reaction. As soon as the motor reaction to the conditioned stimulus became more or less regular, the animal began to perform it in intervals. As the dog was not able to take his leg off the foodtray without help (the result of the first operation), he stood for long periods of time with his leg on the foodtray, but if the leg was taken off he immediately lifted it again. The motor reactions both to the conditioned stimuli and in intervals were performed either with right or with left foreleg, or with both. Such behaviour was due to the lesion in the motor area.

Till the end of observation, lasting two months, this state did not change: to the conditioned stimuli the trained movement was executed with variable latent periods, since orienting reaction or the direct alimentary reaction appeared before it. On the other hand, in intervals the dog raised his leg immediately after it was taken off the foodtray.

The chief symptoms observed in all our dogs are presented in Table I.

DISCUSSION

The experimental data presented in this paper, together with the results described previously (Brutkowski et al. 1956, Stępień et al. 1960, Stępień and Stępień 1959) allow us to draw some conclusions as to which symptoms produced by

Table I

The chief symptoms observed in dogs after operation

Dogs	Pm-1	Pm-2	PmPf-1	PmPf-2	PmPf-3	MPm-1	MPm-2	MPm-3
Extent of lesion	premotor	premotor	premotor* prefrontal	premotor prefrontal	premotor prefrontal	motor premotor	motor premotor	motor premotor
Postoperational period in months	2	3	2	12	8	7	1.5	2
Disorders of movements awkwardness	absent	absent	absent	absent	absent	strong slight	absent	present
head bent	present absent	present absent	present absent	present absent	present absent	present absent	present absent	present absent
sliding apart of legs	absent	absent	absent	absent	absent	strong medium	slight absent	absent
abnormal position of legs	absent	absent	absent	absent	absent	strong absent	absent	absent
hyperkinesis	absent	absent	absent	absent	absent	strong	strong	present
hyperactivity and stereotypy	present absent	strong	strong	strong	strong	strong	strong	present
Conditioned activity conditioned responses to CS	absent regular	absent irregular regular	absent irregular regular	absent irregular	absent irregular	irregular	irregular	irregular
confusion of forelegs intertrial movements	absent	absent	absent	absent	absent	present	present	present
	rare	frequent	frequent	frequent	frequent	frequent	frequent	present

* The first characteristic denotes the early stage after operation, the second characteristic (or the third one) denotes later stages.

ablations of the so called premotor area may be considered as specific for this site of lesions.

The most spectacular difference between the lesions in the premotor area and those in sensori-motor area (in the stricter sense) is that whereas the latter lesions always produce prominent, and more or less persistent, defects in movements of the legs, the premotor animals, even immediately after operation, are as skillful as before. Neither abnormal positions of the legs, nor awkwardness of movements, nor sliding of legs apart are ever seen. Placing reaction, which is totally absent after sensory lesions and dubious after motor lesions (owing to the perpetual "pedalling" movements), is prompt and unmistakable in the premotor animals.

On the other hand, if we draw attention to the behavioural aspects of motor activity we see that the premotor dogs are much more changed in comparison with their preoperational state than the sensory or motor dogs. The s e n s o r y ablations make the animals awkward and atactic but their general pattern of behaviour is unchanged. After m o t o r ablations the animals are behaviouristically less normal, as confusion of legs and putting the left foreleg instead of the right one on the foodtray may be considered as a disorder of the whole motor act. But the strongest disorders of behaviour are seen after premotor lesions. These disorders may be divided into the following groups:

1) Perseveration or stereotypy of movements. All our premotor animals exhibited a symptom which is generally called hyperactivity, although it would be better to call it: "stereotypy or perseveration of motor acts". This symptom consists in that the animal when starting some sort of activity repeats it again and again for a long time. Its simplest form is the so called "locomotor hyperactivity" consisting in persistent walking around a room, most often along the same itinerary. The periods of walking are interspersed with periods of complete rest.

But it must be stressed that locomotor stereotypy is not the only sort of perseverative behaviour observed in the premotor dogs. In the experimental chamber they performed repeatedly hundreds of times the following movements: putting the right foreleg on the foodtray (the trained movement); jumping with both forelegs, or with all four legs on the foodtray and then back on the floor of the stand; oscillating movements of the head or the body; incessant gnawing of the border of the bowl.

It should be noted that, when the dog performed continuously the trained movements in the intervals between trials, these movements did not have a clear alimentary significance. It was noticed that the animal performed them in quite a different manner than he did to the conditioned stimulus itself, namely he did not display any explicit alimentary reaction, always present in response to the conditioned stimuli. (Unfortunately salivation was not examined in those dogs).

It was observed that not all of our dogs presented the symptom of stereotype movements in the same degree. In dog Pm-1 this symptom was seen only for a short time after operation. On the other hand in dog Pm-2 with nearly the same lesion it was very well marked. As, generally speaking, in all our premotor-prefrontal dogs the tendency to hyperactivity and perseveration of motor acts was very strong and persistent, it might be concluded that ablations of these two areas jointly are responsible for this symptom. But, taking into account that dogs Pm-2 and MPm-1 did manifest strong perseverative tendency in spite of the fact that their prefrontal areas were left intact, and, on the other hand, "pure" prefrontal animals do n o t display this symptom at all, we are rather inclined to believe that there is some intermediate zone, including some parts of our premotor area a n d of prefrontal area, ablations of which produce this sort of disorder. After all one should remember that the boundary between our premotor and prefrontal area is taken rather arbitrarily, so we do not know how much the region possessing the physiological role of the premotor area involves the prefrontal area. Perhaps a careful investigation of the anatomical subdivisions of the frontal region combined with the detailed analysis of lesions produced in our dogs could answer this question.

To summarize this point it should be once more pointed out that the increased tendency to perseveration is a general symptom and it concerns a l l possible kinds of motor acts and not only the walking. In the dogs in which we observe locomotor "hyperactivity" in an empty room, we may notice oscillating movements of the head in the stand and/or gnawing of the bowl and/or putting the leg on the foodtray, etc. In this connection it is worthwhile to mention that in Ł a w i c k a's experiments (1957) in which vocal conditioned reflexes were established in a dog, the animal displayed a quite

clear vocal hyperactivity (or rather perseveration) after premotor-prefrontal ablation: in the experimental situation in which vocal conditioned reflexes to the sporadic stimuli were trained (but n o t e l s e w h e r e), the dog barked almost incessantly throughout the experimental session and this symptom appeared to be permanent; it was quite analogous to the symptom of incessant putting the right foreleg on the foodtray established in this dog in another experimental situation and repeatedly executed in that situation.

2) The next symptom of premotor dogs is the tendency to walk with head bent beneath the level of the back, to pass underneath the obstacles instead of jumping over them, as do normal animals, to slip under furniture and to enter the corners of the room. Again this symptom seemed to be more prominent in premotor-prefrontal animals than in "pure" premotor animals.

3) The third symptom observed after premotor ablations consists in alteration of reactions to the conditioned stimuli. Before operation the animals put the leg on the foodtray as quickly as possible. After operation they display at first a very strong orientation reaction toward the source of the stimulus (as if it were quite new to them), then after a number of reinforcements of this stimulus by food, they manifest a not less intensive but abnormal alimentary reaction toward the bowl consisting in licking it, gnawing its borders, etc. These reactions strongly interfere with the execution of the trained movement, which at this stage either does not appear at all, or it appears with a very long latency, or appears in intertrial intervals but not to the stimulus. In consequence, the conditioned-reflex activity is highly chaotic and unpredictable in striking contrast with the quite normal character of the performance of the movements themselves. We have called such a state "c o n d i t i o n e d d i s r e f l e x i a". Owing to it even on superficial observation the behaviour of these animals makes the impression of being silly and absurd.

It remains to compare the symptoms ensuing from premotor ablations with those following prefrontal ablations, or with those obtained after combined lesions of these two areas. When the lesion includes only the frontal poles rostrally to presylvian sulcus, the condition of animals is quite different from that described in this paper. Most often these animals are quite quiet even immediately after operation and in the majority of cases they do not display any signs of hyperactivity or stereotypy, either locomotor or other.

Therefore, their general behaviour appears to be quite normal and it hardly differs from that before operation. Their positive conditioned reactions (classical or instrumental) are also normal or somewhat increased. On the other hand they display a marked disinhibition of inhibitory conditioned reflexes manifested in all sorts of conditioning: instrumental alimentary (Brutkowski et al. 1956, Ławicka 1957), classical alimentary (Brutkowski 1957), instrumental drinking (Żernicki 1960), classical defensive (Auleytner and Brutkowski 1960). As a rule, after a sufficiently long postoperative retraining inhibitory reflexes can be restored.

Since the prefrontal animals in the first period after operation do execute the instrumental conditioned reaction also in intervals between trials as the effect of disinhibition, it is worthwhile to compare this symptom to the analogous one seen after premotor, or premotor-prefrontal lesions. The prefrontal animals perform the trained movement in intervals only occasionally in a similar way as they did it in the first stage of the pre-operational training. These intertrial movements are accompanied with an alimentary reaction and after several days they disappear. On the other hand, as described in this paper, in premotor dogs these intertrial reactions, as well as other manifestations of motor stereotypy are very frequent and abundant. They remain either permanently, or for a very long time, and do not present a clear alimentary character.

In spite of the fact that the symptoms of premotor lesions are very clear-cut and distinct, their explanation encounters great difficulties and needs perhaps much more experimental work. The fact is that in contrast to the impairment of the discrete movements of the legs, characteristic for pure sensori-motor ablations, the premotor lesions produce the impairment of the general behaviour and of whole motor acts. This could be explained either by accepting the older hypothesis of destruction of some "higher" centres controlling the behaviour, or else by Woolsey's conception of the destruction of the head-body cortical representation. The symptoms of hyperactivity and motor stereotypy seem to be analogous to the symptoms of hyperkinesis observed after motor ablations (cf. Stępień et al. 1960). May be that in the vicinity of both motor area and premotor area two adjacent suppressing areas are situated whose functional role is to refrain

and check the motor performances either on the level of simple movements (area 4s?) or on the level of the whole motor acts.

The symptom of locomotor hyperactivity after lesions in the frontal region was often described in other animals such as rats (Richter and Hawkes 1939), cats (Langworthy and Richter 1939) and monkeys (Richter and Hines 1938, Kennard et al. 1941, Ruch and Shenkin 1943 and others). The precise localisation of lesions producing this symptom is not clear, however we have some evidence that they do involve our premotor area. For, according to our results (Ławicka and Konorski in preparation) cats with strictly prefrontal lesions (rostral to presylvian gyrus) do not exhibit any hyperactivity. All this experimental material seems to indicate that there exists in various species of animals an area situated somewhere in the frontal lobes rostrally to the motor cortex, whose function consists in inhibiting superfluous motor acts, or rather in cutting short those activities which are no more necessary. Hence the ablations of this area lead to motor perseveration and stereotype movements. The probable physiological mechanism of this impairment was discussed in detail by Konorski elsewhere (Konorski 1957).

SUMMARY

The present paper deals with the effects of ablations of the premotor cortex on the general behaviour and motor conditioned reflexes in dogs. The chief symptoms observed after these ablations were as follows:

1. The tendency to repeat again and again the same motor activity such as: walking in a room along the same itinerary, performance of the trained movement in the experimental situation, gnawing of the bowl, etc.

2. The tendency to slip beneath the obstacles and to stick in the corners of the room.

3. The disorders of the conditioned-reflex activity consisting in the loosening of the bond between the conditioned stimulus and the conditioned motor reaction. To the conditioned stimulus the animals display an exaggerated orienting reaction towards the source of the stimulus and an exaggerated and abnormal direct alimentary reaction. These reactions interfere with the performance

of the trained movement. On the other hand this movement is repeatedly performed in intertrial intervals.

These symptoms seem to be more pronounced if in addition to the premotor area parts of the prefrontal area are removed but they are not observed after removals of prefrontal area alone. On the other hand no impairments of discrete movements of extremities are seen after prefrontal ablations.

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