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MOTOR EFFECTS OF CORTICAL STIMULATION AFTER CHRONIC LESION OF MEDULLARY PYRAMID IN THE DOG

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Abstract. In dogs with unilateral pyramidal lesions the motor cortex on both hemispheres was stimulated under Nembutal anesthesia to study the effects of pyramidotomy upon cortically induced movements. Pyramidal lesions resulted in an almost complete abolition of foretoes flexions and marked reduction of wrist ventriflexions. Other movements were not noticeably affected, except for their increased thresholds. The increase in the thresholds of movements elicited from the affected hemispheres diminished as a function of the length of postoperative survival period, so that 6 mo after pyramidotomy the thresholds on the operated side approximated the values obtained on the normal hemispheres.

INTRODUCTION

Pyramidal lesions in the dog result in relatively little motor impairment. Already Starlinger (30, 31) in his pioneer experiments with transection of the medullary pyramids noted that bilaterally pyramidotomized dogs could hardly be distinquished from normal ones when playing together and that they could be taught such simple tricks like

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[1] The experiments were performed at the University of Wisconsin, with T.G. on leave of absence from the Nencki Institute.

"giving a paw". These results have been, in general, confirmed in further studies. Maffre (22) reported some deficits in the placing and hopping reactions after pyramidotomy in dogs, but the general motor behavior of operated animals was found not to be markedly impaired. In experiments using the conditioning technique (7, 9, 16-18) the instrumental responses consisting of relatively simple movements, like flexion of the fore- or hindlimb, were not abolished after uni- or bilateral pyramidal lesions and could be, in general, easily established in naive bilaterally operated animals (9). The postoperative impairment was limited essentially to a relatively small increase in the latency of instrumental movements and/or a decrease in their amplitude (9).

The aim of the present paper was to study the effects of pyramidal lesions on movements elicited by stimulation of the cortical motor areas in the dog (10, 35, 36). In similar experiments in monkeys (37) movements elicited from the hemisphere with the transected pyramid were characterized by a marked increase in the thresholds and a lack of finger movements and these effects were observed even after 1.5 year of postoperative survival. The motor deficits found in stimulation experiments were correlated with a general slowness of movements in pyramidotomized monkeys and their inability to use fingers independently observed behaviorally (3, 21, 37). Since in the dog behavioral studies suggested that the pyramidal tract contributes much less to motor control, it seemed interesting to find out whether movements elicited by cortical stimulation in this species would be also less affected after pyramidotomy than in the monkey. Some preliminary results have been reported (34).

MATERIAL AND METHODS

Seven adult mongrel dogs, weighting 8.0–12.5 kg were used. In all the animals the left pyramid was transected under aseptic conditions using the parapharyngeal approach. The animals' postoperative survival time ranged between 2 and 6 mo (Table I).

In all the animals, the neurological status was periodically examined after the surgery. The examination included observation of the gait, testing of placing and hopping reactions, muscle tone, etc.

The stimulation experiments were carried out under Nembutal (Sodium pentobarbital) anesthesia, administered intraperitoneally. The initial dose was 40 mg/kg of body weight and additional doses of 3.0 mg/kg were given, as needed, throughout the experiment, in order to prevent spontaneous movements. In 5 out of 7 dogs the average maintenance doses of anesthesia were relatively low, ranging between 2.4 and 3.5

mg/kg/h (Table I, first 5 dogs listed). The data obtained in these animals served as a basis for describing the effects of pyramidal lesion on cortically induced movements. In the remaining 2 dogs (No. 68-103 and 68–75) much larger maintenance doses of anesthetic had to be administered and the results obtained in these animals are described separately in the last section of the Results.

The surgical and stimulation procedures were similar to those described for normal dogs (10). The cortical surface was exposed bilaterally between the ansate, lateral and coronal junction caudally and the presylvian sulcus rostrally and from the midline to the coronal sulcus laterally. The animal's body was supported horizontally with limbs pendant to allow maximal freedom of movements. The head was fixed rigidly in a headholder. The hair on the entire body was clipped in order to facilitate observation of movements.

Monopolar stimulation was used throughout. A stainless steel wire 0.5 mm in diameter, insulated except for the tip, served as the stimulating electrode. The indifferent electrode was attached to a saline soaked cotton ring on the scalp. The brain was kept moist with warm Ringer solution and a chamber constructed of saline-saturated cotton was erected over the exposed region in order to prevent drying of the pial surface. 60-cycle sine wave current was delivered through a high impedance device, the amount of current (RMS values) being preset and read directly in milliampers. Each stimulus lasted 2.5 s and a minimal interval of 2 min was allowed to elapse between successive stimulations regardless of whether or not a detectable response occurred (38). Each point was stimulated several (usually 3–4) times in order to determine the threshold current producing a visible movement and to analyze movements recruited with suprathreshold (up to 150% of threshold values) stimulation. The maximal current strength did not exceed usually 3.0 mA and only in dogs with high doses of anesthetic was a current of 4.0 mA used.

The cortex of both hemispheres was explored in 2 mm steps, both in the medio-lateral and rostro-caudal direction. The stimulation of the two hemispheres was carried out alternately, i. e. after stimulating a point on the intact hemisphere, the electrode was moved to a symmetrical point on the affected hemisphere. The distance between 2 points stimulated in succession in one hemisphere was at least 4 mm. The number of points explored varied from 80 to 120 per dog.

At least three investigators collaborated in observing motor responses elicited by cortical stimulation, and the results of each stimulation were analyzed and described in detail. The locations of the stimulated points were marked on enlarged photographs of the exposed cortical surfaces.

Table I

Comparison of the extent of lesions, lengths of postoperative survival periods and maintenance doses of anaesthesia used in individual dogs

Dog No.	Lesion			Postoperative survival period (in months)	Average maintenance doses of anesthesia applied during the experiments (in mg/kg/h)
	Transection of the left pyramid	Damage of the left medial lemniscus	Damage of other structures		
68—223	complete	complete	none	2.0	2.7
68—114	complete	none	none	4.2	2.8
68—323	complete	almost complete	ventralmost portions of the reticular formation	5.0	2.8
68—327	complete	small, about 1/3	none	6.0	3.5
68—74	partial, about 70%	none	none	4.5	2.4
68—103	complete	none	none	4.5	4.7
68—75	complete	none	none	5.3	5.7

At the termination of the experiment, the animal was given an overdose of anesthesia and perfused with 0.9% saline, followed by 10% formalin. The brain was then removed and rephotographed in standard views.

For each dog figurine maps (38) and threshold maps were constructed. The analysis of the effects of pyramidotomy upon cortically induced movements was limited to points located in the posterior sigmoid gyrus and the lateral two thirds of the anterior sigmoid gyrus, i. e., to the representation of movements of the extremities (10, 35, 36). Points in the rostral part of the supplementary motor area from which face movements are elicited were also eliminated. The statistical analysis of the results was made with the nonparametric Sign test, Wilcoxon test for matched pairs and the Kolmogorov-Smirnov test.

The histological control of the lesions was done on serial transverse sections of the medulla and mesencephalon stained alternately with Nissl and Heidenhain methods.

RESULTS

Lesions. The results of histological verification of the lesions are shown in Table I. In all the dogs but one the left pyramid was completely transected. In dog 68–74 the lesion was partial, sparing about 30% of fibers in the lateral and medial parts of the pyramid.

In 3 out of the 6 dogs with a complete pyramidotomy the lesion was confined essentially to the pyramid itself (No. 68–114, 68–103 and 68–75). In the remaining animals the lesion was too deep, destroying to various extents the medial lemniscus and in some cases (No. 68-323) encroaching upon the ventralmost portions of the reticular formation. The medial lemniscus was as a rule damaged, if the lesion was placed caudal to the trapezoid body.

Neurological status. The neurological deficiencies observed in the operated dogs were, in general, similar to those described by other authors (22, 28). The day after the surgery, the operated animals were able to walk, but the affected limbs slipped on the floor. During the first few days after surgery, the animals also occasionally put the affected forefoot dorsum down. With time, these deficiencies gradually diminished, although a tendency to slip laterally with the affected limbs, especially when turning to the opposite side, and delayed correction of passively imposed malpostures were observed even 4–6 mo after the pyramidotomy. These deficiencies were more pronounced in the forelimb than in the hindlimb and also in dogs in which the medial lemniscus was additionally destroyed.

The visual placing reactions were usually absent for the first 2 or 3 postoperative weeks; they returned, thereafter but remained defective. When tested with both limbs free, the affected limb might not show any placing reaction at all, or the reaction was less prompt than in the normal limb. With the normal limb restrained, the operated animals regularly placed the affected limb, although the reaction was sluggish.

Contact placing was more impaired than visual placing. The reactions of the affected limbs returned only in some dogs and, if present, they required a stronger stimulation and were performed less promptly than on the normal side. The magnet reaction (27) was also defective and did not return to normal; when the animals were lifted off the floor the affected limbs lost contact with the floor earlier than the normal ones.

The hopping reactions usually returned during the first postoperative month but also remained defective. They were sluggish and less frequent on the affected side, especially in the forelimb. When backward stepping on both hindlimbs was tested, the animals usually stepped back first with their normal leg.

In contrast to the effects of removal of the cortical sensori motor area (32), dogs with sectioned pyramids did not show any clearcut extensor posture nor any increased resistance to passive manipulation. The knee jerks were of similar amplitude and easily obtained on both sides.

Effects of pyramidotomy on the type of movements induced by cortical stimulation. Movements induced by cortical stimulation of the normal and affected hemispheres are illustrated in Fig. 1, which shows a figurine map of motor responses obtained in dog 68–114, stimulated 4 mo after the surgery. Table II gives a comparison of numbers of points eliciting various hind- and forelimb movements upon stimulation of the intact and affected hemispheres in four dogs with complete unilateral pyramidotomy (first 4 dogs listed in Table I).

Sectioning the pyramid in the dog did not abolish the possibility of eliciting a variety of movements from the affected hemispheres, nor did it change the general pattern of motor representation with the hindlimb represented medially and the forelimb laterally (Fig. 1). No clearcut effects of pyramidotomy were found with respect to hindlimb movements. Movements of thigh protraction and knee flexion predominated in both hemispheres and the number of points from which they were elicited was similar in the intact and affected hemispheres. Other hindlimb movements appeared too seldom or too irregularly (e. g. mainly in 1 out of 4 dogs) on stimulation of the dorsolateral surface of the cortex to draw any conclusions concerning their changes after pyramidotomy, even though the total number of points yielding these movements in the intact and affected hemisheres showed some significant

($P \leqslant 0.05$, Sign test) surgery effects (Table II). A detailed analysis of the effects of pyramidotomy upon cortically induced hindlimb distal movements require further experiments with stimulation of the medial wall of the hemishere and the posterior bank of cruciate sulcus, from which these responses are most frequently elicited (10).

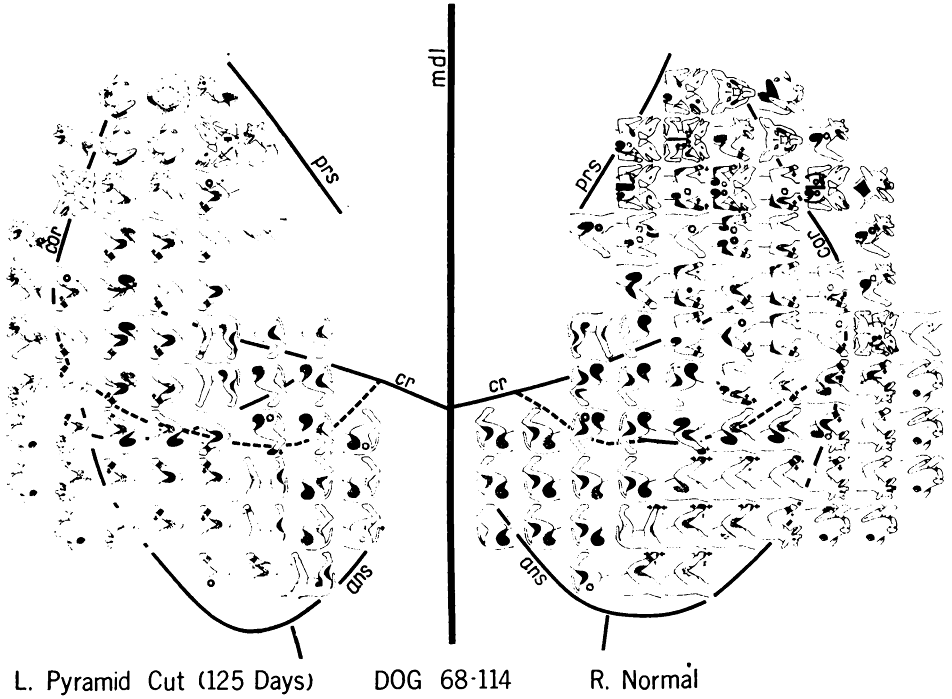

Fig. 1. Figurine map of movements elicited by stimulation of the posterior and anterior sigmoid gyri in both hemisperes in a dog 125 days after complete section of the left pyramid. On each figurine, regions of the body in which movements occurred or the musculature activated on stimulation of a given point are depicted by shading. With respect to wrist or toes movements, or rotatory movements of the limbs arrows denote the direction of the movements. The relative strength of movement is depicted by the density of shading: solid black signifies strongest and earliest responses, hatching intermediate and dots weakest responses, usually recruited with stronger stimulation. Contralateral and bilateral movements are represented on one-sided and two-sided figurines respectively. The dashed line on the posterior sigmoid gyrus marks the boundary between the "precentral" motor (M_I) and somatosensory I (S_I) areas (26). In order to maintain the appropriate orientation of individual figurines within the pattern of representation of the body, the contralateral movements in area S_I are represented in contralateral figurines, while in the remaining areas on ipsilateral figurines (33, 38). Abbreviations: mdl, midline; prs, presylvian sulcus; cr, cruciate sulcus; cor, coronal sulcus; ans, ansate sulcus.

TABLE II

Comparison of numbers of points eliciting in dogs various hind- and forelimb movements upon stimulation of symmetrical points in the motor cortex ($S_I + M_I + M_{II}$) in intact hemispheres (N) and hemispheres with complete section of the medullary pyramid (*P*). Bold type indicate statistically significant differences (Sign test). Data for the first 4 dogs listed in Table I, in which totally 157 pairs of symmetrical point were stimulated

Hindlimb movements

Hip				Knee				Ankle				Toes			
Protraction		Retraction		Flexion		Extension		Dorsiflexion		Ventriflexion		Dorsiflexion		Ventriflexion	
N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P
27	17	3	2	34	43	1	5	**10**	**2**	1	3	0	0	**3**	**10**

Forelimb movements

Shoulder				Elbow				Wrist				Toes			
Protraction		Retraction		Flexion		Extension		Dorsiflexion		Ventriflexion		Dorsiflexion		Ventriflexion	
N	P	N	P	N	P	N	P	N	P	N	P	N	P	N	P
12	14	40	35	77	79	17	9	64	74	**33**	**11**	7	2	**22**	**3**

Bilateral movements (in M_{II})

N	P
33	**11**

Out of movements of the forelimb, those performed in more proximal joints, like protraction and retraction at the shoulder, flexion and extension of the elbow were also found not to be affected by pyramidal lesions (Fig. 1 and Table II). The same holds true for dorsiflexion of the wrist and of the foretoes, the former category of movements being one of the most frequently elicited upon stimulation of cortical motor areas (cf. 10). On the other hand, movements of wrist ventriflexion and, particularly, of flexion of the foretoes were markedly impaired after pyramidotomy.

As illustrated in Fig. 1 (cf. also 10) stimulation of several points in the lateral part of the posterior sigmoid gyrus in the intact hemisphere yielded movements of foretoes, mainly their flexion together with adduction. In contrast, stimulation of symmetrically located points in the hemisphere with the pyramid cut, failed to induce in dog 68–114 any foretoes movements. Similar results were obtained in the majority of other dogs. Out of the 4 dogs analyzed in Table II, sporadic flexor movements of foretoes upon stimulation of the affected hemisphere were obtained only in one animal, which has the longest (6 months) period of postoperative survival (No. 68–327, Table I). When present, these movements appeared, however, upon suprathreshold stimulation and often as clonic afterdischarges. The decrease of the total number of points yielding toes ventriflexions upon stimulation of the affected hemispheres was highly statistically significant (Table II, $P < 1 \times 10^{-4}$, Sign test).

Movements of wrist ventriflexion were less affected after pyramidotomy than foretoes flexion. They could be elicited in all the dogs but one (No. 68–114) upon stimulation of the lateral part of the posterior sigmoid gyrus in the affected hemispheres, but the number of points from which they were evoked was reduced by 20–70%. Comparison of the total number of points yielding ventriflexion of the wrist showed a significant decrease in the affected hemispheres ($P < 0.01$, Sign test, Table II).

The effects of pyramidotomy on distal forelimb movements were limited to dogs with complete section of the pyramid. In the dog with partial pyramidal lesion (No. 68–74, Table I) stimulation of the affected hemisphere yielded easily foretoes flexion and the number of points from which these responses were obtained was similar in both hemispheres. The same holds true for movements of wrist ventriflexion.

Another effect of sectioning the pyramid was a reduction of bilateral movements elicited upon stimulation of the supplementary motor area (M_{II}). In the normal dog stimulation of the posterior sigmoid gyrus, i. e., the S_I and M_I areas, elicits, in general, only movements of contralateral extremities, whereas stimulation of the anterior sigmoid gyrus, i. e. the supplementary motor area, yields also bilateral movements (10). Such ipsilateral responses require usually somewhat stronger stimuli and/or are preceded by movements of contralateral limbs. Figure 1 and Table II show that bilateral movements evoked from the supplementary motor area (M_{II}) were affected by pyramidal lesions. They appeared in all the dogs but one (No. 68–223) upon stimulation of the operated hemispheres, but their number was reduced by 20–85%. Comparison of the total number of points yielding bilateral movements showed a statistically significant decrease in the affected hemispheres ($P < 0.01$, Sign test, Table II).

Effects of pyramidotomy on thresholds of cortically induced movements. Threshold currents required to elicit movements were found to be considerably increased after pyramidotomy. Figure 2 gives a threshold map of currents used to elicit motor responses from each stimulated point on both hemispheres in dog 68–114. The thresholds of symmetrically located points in the hemisphere with the transected pyramid were much higher than on the intact side ($P < 0.0005$, $n = 42$ pairs, Wilcoxon test for matched pairs). In other dogs with complete pyramidal lesion, the differences in the thresholds between the two hemispheres

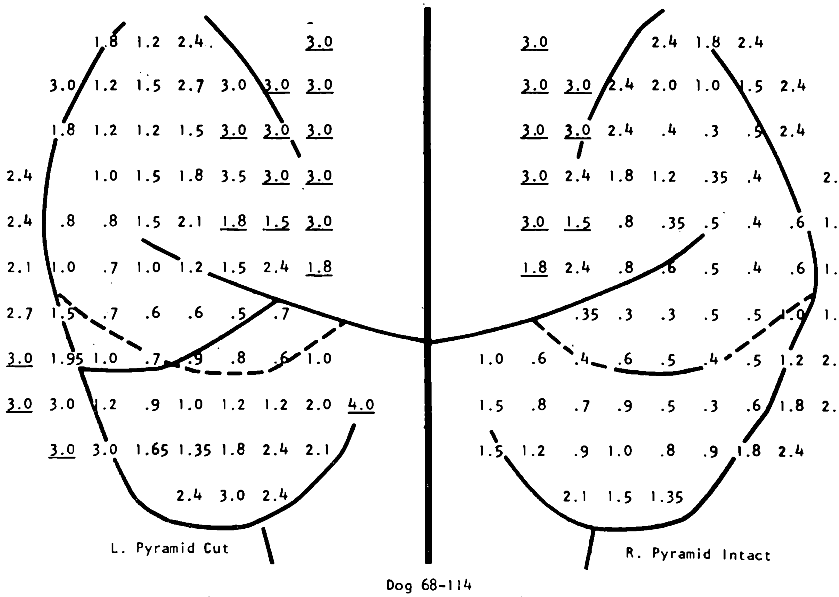

Fig. 2. Threshold values of stimulating currents used to elicit movements illustrated in Fig. 1. Figures underlined indicate no response.

were also statistically significant ($P < 0.0005$, dogs No. 68–223 and 68–323, $n = 27$ and 33 pairs respectively, and $P < 0.01$, dog No. 68–327, $n = 30$ pairs). Partial pyramidal lesion (dog No. 68–74, cf. Table I) likewise produced an increase in the thresholds of movements elicited from the affected hemisphere ($P < 0.005$, $n = 28$ pairs).

The increase in thresholds after pyramidal lesions was most pronounced in area M_I, which in the intact hemispheres has the lowest thresholds, especially in its lateral part, corresponding to forelimb representation (cf. 10; and Figs. 1 and 2). Figure 3 compares threshold currents used to elicit motor responses in the intact and affected hemispheres on stimulation of area M_I, S_I and M_{II} in the first 5 dogs listed in Table I. The increase in thresholds after pyramidal lesions was statistically significant in all these areas (Kolmogorov-Smirnov test). However, in area M_I the probability of equality of these two thresholds distributions was much smaller ($P < 5 \times 10^{-7}$) than in area S_I ($P < 5.2 \times 10^{-3}$) and M_{II} ($P < 1.5 \times 10^{-4}$), which shows that the area M_I was more affected by pyramidal lesion than the remaining parts of the explored cortex.

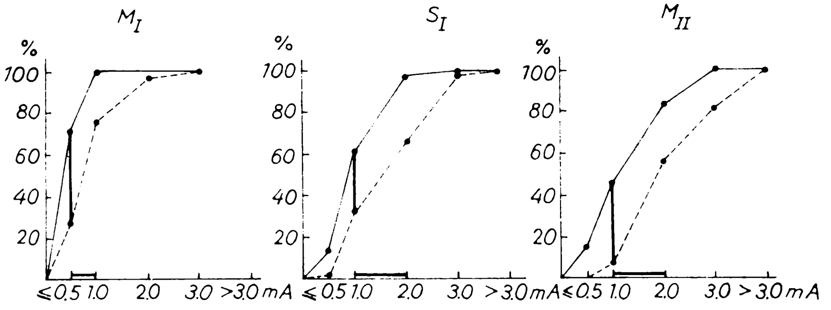

Fig. 3. Comparison of threshold current intensities required to elicit movements on stimulation of areas M_I, S_I and M_{II} in the intact (continuous line) and affected (interrupted line) hemispheres in dogs with unilateral pyramidal lesions. Abscissae, classes of thresholds. Ordinates: cumulative percentage of stimulated points. Horizontal lines denote classes of thresholds, which showed statistically significant differences in the percentages of stimulated points (Kolmogorov-Smirnov test). Vertical bars represent the maximal differences between the two cumulative distributions. The highest values of coefficient and the number of points compared in particular areas were the following: M_I, 2.72, $n = 77$; S_I, 1.62, $n = 55$; M_{II}, 2.09, $n = 55$.

The main effect of pyramidal lesion in area M_I was the abolition or significant reduction of the number of points with the lowest thresholds, lower than or equal to 0.5 mA. The percentage of points within this class of thresholds decreased from 72 in the intact hemispheres to 28 in the affected hemispheres. The latter points were present practically in two dogs only: one with partial pyramidal lesion (No. 68–74) and another with the longest period of postoperative survival (No. 68–327), while in the remaining three dogs they were either absent (No. 68–223) or encountered only at one or two stimulated points (No. 68–114 and 68–323).

In areas S_I and M_{II} the thresholds on the intact hemispheres were higher than in area M_I. Pyramidal lesion caused in these areas a shift of thresholds toward higher values, the vast majority of points having thresholds ranging between 1.1 and 3.0 mA, and the appearance of some points unresponsive to stimulation up to 3.0 mA. These latter points were mainly located in area M_{II}. It is also of interest to note, that although pyramidal lesions affected most the excitability of area M_I, this area after pyramidotomy had still the lowest thresholds, similar to thresholds in area S_I and lower than in area M_{II} ($P < 0.005$, Kolmogorov-Smirnov test) in the intact hemispheres. The lowest thresholds in area M_I after pyramidotomy were still encountered in its lateral part, corresponding to forelimb representation, similarly as on the intact side (cf. Fig. 2).

The increase in the thresholds of movements after pyramidal lesions diminished as a function of the length of postoperative survival time. Figure 4 compares the mean thresholds of symmetrical points in area M_I in the intact and affected hemispheres in five dogs with different periods of postoperative survival (Table I, first five dogs listed). The mean thresholds for the intact hemispheres were similar and ranged between

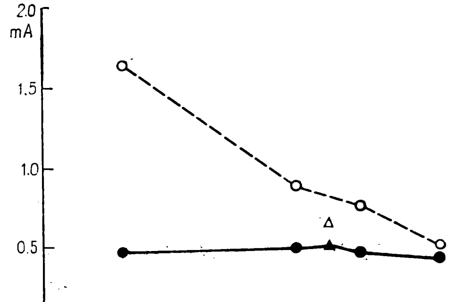

Fig. 4. Comparison of mean thresholds for movements evoked from M_I area in the intact (filled symbols) and affected (open symbols) hemispheres in dogs with unilateral pyramidal lesions stimulated at different (2-6 mo) times after pyramidotomy. Circles, data for dogs with complete transection of the left pyramid (No. 68-223, 68-114, 68-323 and 68-327 respectively); triangles, data for a dog with partial pyramidal lesion (No. 68-74). Abscissae: length of postoperative survival period. Ordinate: mean stimulation thresholds.

0.41 and 0.5 mA. On the side of the pyramidotomy, the highest thresholds (increase by 250%, $P < 0.005$, $n = 13$ pairs, Wilcoxon test for matched pairs) were found in the dog stimulated 2 mo after surgery, the lowest (increase by 21%, statistically nonsignificant) in the dog with the longest (6 mo) period of postoperative survival. The data for the remaining two dogs, stimulated 4.2 and 5.0 mo after the surgery, occuppied intermediate positions (increase by 79% and 68%, $P < 0.005$, $n = 20$ and 11 pairs respectively). These differences were not due to differences in the extent of medullary lesions, since the dog stimulated 5.0 mo after the surgery, had the deepest lesion (No. 68–323, cf. Table I) and nevertheless the increase in the thresholds on the affected side was in this animal smaller than in dogs with more limited lesions and a shorter time of postoperative survival (No. 68–223 and 68–114). They were neither due to differences in the of depth of anesthesia, since the dog stimulated 6 mo after the surgery (No. 68–327) received larger maintenance doses of Nembutal than other dogs, the data for which are shown in Fig. 4. These results suggest that the effects of unilateral pyramidal lesions on thresholds of movements elicited by cortical stimulation in the dog are mainly compensated within the first 6 mo after the surgery. Partial pyramidal lesion (No. 68–74, see triangles in Fig. 4) caused a less pronounced increase (by 25%, $P < 0.005$, $n = 14$) in the thresholds of the affected hemisphere than in other animals with complete pyramidal lesion and comparable periods of postoperative survival.

Effects of large doses of Nembutal upon cortically induced movements. The data presented above concerned only 5 out of 7 operated dogs, those in which relatively low maintenance doses of Nembutal (2.7–3.5 mg/kg/h) were used. In the remaining 2 dogs, the maintenance doses of anesthetic were much larger, approaching 5 and 6 mg/kg/h (No. 68–103 and 68–75, cf. Table I). Such large doses of Nembutal caused an increase in the thresholds of movements elicited from both hemispheres, but this effect was much more conspicuous in the hemisphere with the transected pyramid. Figure 5 shows the mean thresholds and the percentages of points producing movements on stimulation $\leqslant 3.0$ mA of area M_I in both hemispheres in 4 pyramidotomized dogs with similar periods of postoperative survival (4.2–5.3 mo) but different doses of anesthetic. Increasing the maintenance doses of anesthetic from about 3.0 (No. 68–114 and 68–323) to about 5.0 (No. 68–103) and 6.0 (No. 68–75) mg/kg/h caused in the intact hemispheres an increase in the mean thresholds from 0.45 and 0.49 mA to 0.76 and 0.91 mA, i.e., about 50 and 100% respectively. In the hemispheres with the pyramid cut the increase in thresholds was much higher. In the dog with about 5 mg/kg/h of anesthetic (No. 68–103), essentially only points located in the lateral half of area M_I were found to produce movements with current intensities up to 3.0 mA, and the mean threshold of these points was 2.55 mA. With higher doses of Nembutal, approaching 6 mg/kg/h (No. 68–75), the whole motor cortex, including area M_I, became completely unexcitable even with stimulus intensities up to 4.0 mA.

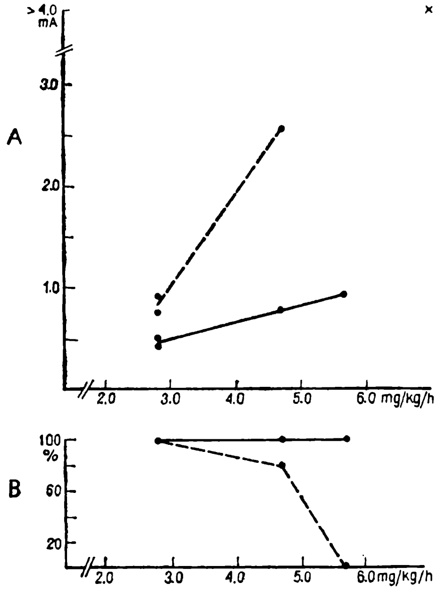

Fig. 5. Comparison of mean threshold current intensities (A) and of percentage of points at which stimuli $\leqslant$ 3.0 mA were effective (B) on stimulation of area M_I in the intact (continuous line) and affected (interrupted line) hemispheres in pyramidotomized dogs with a similar (4.2-5.5 mo) period of postoperative survival but different maintenance doses of Nembutal (data for dogs No. 68-114, 68-323, 68–103 and 68–75). Abscissae: average maintenance doses of Nembutal. Ordinates: *A*, mean threshold in mA; *B*, percentage of effective points, x in A denotes that in the dog 68–75 current intensities of 4.0 mA did not produce movements upon stimulation of the affected hemisphere.

DISCUSSION

The results of the present study support the behavioral evidence, showing that in the dog pyramidal lesions affect the motor performance to a relatively small degree (7, 9, 16–18, 22, 28, 30, 31). Movements elicited upon stimulation of the motor cortex of the hemisphere with the transected pyramid were, in general, very little changed as compared to those obtained from the normal hemisphere. No effect of pyramidal lesion was found with respect to movements performed in proximal joints, except for their increased thresholds, but these returned almost completely to normal values within the first 6 mo after the surgery. Out of movements performed in distal joints, ventriflexion of the wrist and flexion of foretoes were most markedly affected. The number of points from which the former responses were evoked was greatly reduced after pyramidal lesions, while the latter could not be, in the majority of dogs, obtained upon stimulation of the affected hemispheres. In behavioral experiments, transection of medullary pyramids in the dog also did not abolish relatively simple instrumental movements performed mainly in proximal joints (7, 9, 16–18), but only resulted in a transient increase of their latency and/or a decrease of their amplitude (9). On the other hand, tasks requiring movements of the wrist and of foretoes were found to be much more affected (14, 15).

Another effect of pyramidal lesions was the reduction of bilateral movements elicited upon stimulation of the anterior sigmoid gyrus, i.e., the supplementary motor area (M_{II}) (10). Since in the normal dog these movements are performed mainly in proximal joints and are often associated with trunk movements, their reduction after pyramidal lesions suggests that the supplementary motor area in the dog is the main source of origin of ipsilateral pyramidal projections, which mainly influence the motoneurons of the trunk and proximal muscels. In the cat the anterior sigmoid gyrus is also the source of origin of the ipsilateral corticospinal projection (1, 2) and stimulation of this region yields movements of the trunk and epaxial musculature (25, 33).

The increase in thresholds of movements after pyramidal lesions was most pronounced in the area M_I, which in the normal dog has the lowest thresholds, especially in its lateral parts, corresponding to forelimb representation (10). This is compatible with the data showing that in the dog the majority of pyramidal fibers takes origin from the rostral part of the posterior sigmoid gyrus (22, 23) corresponding to area M_I. This area is also characterized by the presence of the largest pyramidal cells in the 5th layer (11, 29). However, since after pyramidal lesions the movements from area M_I were still evoked at lower thresholds than from M_{II} and S_I areas, it might be inferred that this area is also the main source of origin of other nonpyramidal systems descending to the spinal cord. To what extent various pathways taking origin from that and neighboring cortical regions (19) are responsible for yielding movements upon stimulation of the motor cortex in the intact and pyramidotomized animals remains to be determined.

In all the experiments performed under Nembutal anesthesia, the depth of anesthesia is a very critical factor, which highly influences the excitability of the nervous system. In the present experiments the thresholds of movements elicited upon stimulation of the motor cortex in the intact hemisphere were found to be similar in various animals, if the maintenance doses of Nembutal ranged between 2.4 and 3.5 mg/kg/h. Under such conditions the threshold for the hemispheres with the transected pyramid were always higher than for the intact ones, but the differences between both hemispheres decreased as a function of the length of postoperative survival time. Larger maintenance doses of Nembutal increased the thresholds in the motor cortex of both hemispheres, but these effects were much more conspicuous for the hemispheres with the transected pyramid. With maintenance doses of Nembutal approaching 6 mg/kg/h, the motor cortex of the affected hemisphere became unexcitable even for very high (up to 4.0 mA) current intensities. The more pronounced effects of Nembutal on the thresholds of movements of the hemispheres with the transected pyramid can be explained by the fact that Nembutal is known to block transmission in multisynaptic pathways (6) and this effect is most accentuated when repetitive stimulation is used (4, 8). Since in the dog the corticospinal fibers terminate in the intermediate zone of the spinal cord (5), the effects of volleys in the pyramidal tract are mediated by at least disynaptic pathways. However, these pathways would involve less synapses than in the majority of other nonpyramidal systems originating in the motor cortex and thus the thresholds of the intact hemispheres were less affected by anesthesia than in the hemispheres with the transected pyramid. The decreased excitability of nonpyramidal systems under Nembutal anesthesia may also account for the fact that in awake animals, pyramidal lesions did not produce changes in thresholds of cortically induced flexor movements of limbs, but only an increase in their latency and a decrease in their amplitude (24), as was observed with regard to movements established using the instrumental conditioning technique (9).

The last problem to be discussed concerns the comparison of the role of the pyramidal system in motor control in the dog and other species. In the dog both behavioral and cortical stimulation effects of pyramidotomy were less pronounced than in the cat or the monkey. In the cat, for example, unilateral pyramidal lesions caused also an increase in the thresholds of movements elicited from the operated hemisphere which, however, persisted for two years after surgery (13) and these effects were correlated with a diminished motor skill displayed by the pyramidotomized cats in behavioral experiments (12). In the monkey the effects of pyramidotomy were much more pronounced than in the cat. Movements elicited from the hemisphere with the transected pyramid were much more stereotyped than those elicited from the intact hemisphere, and mainly limited to flexions of the knee, flexion of the elbow and pronation of the forearm (37). No digital movements could be elicited in either arm or leg except for the extension of the hallux and occasionally weak actions of fingers and wrist in which all digits flexed together. The increase in the thresholds of movements obtained from the operated hemisphere were much higher than in the dog or the cat and amounted even 1.5 years after the surgery to more than 100% (37). Behaviorally, the operated animals showed a marked impairment in actions requiring use of fingers. They were unable to pick up small items of food from a table top nor to extract them from holes due to lack of separate finger movements. No recovery of individual finger movements was observed in adult pyramidotomized monkeys for more than one year after surgery (3, 21, 37), whereas in monkeys, operated as infants, these movements did not appear for three years after surgery (20). These species differences show that in phylogenesis the pyramidal control of movements gains in importance and develops in parallel with digital skill.

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