FUNCTIONAL ORGANIZATION OF CORTICAL MOTOR AREAS
IN ADULT DOGS AND PUPPIES

Teresa GÓRSKA

Department of Neurophysiology, Nencki Institute of Experimental Biology, Warszawa, Poland

Abstract. In adult dogs and puppies ranging in age from 1 day up to 3 months the functional organization of the motor cortex has been investigated with 50 or 60 cycle a-c stimulation under Nembutal anesthesia. In adult dogs two separate, somatotopically organized motor areas have been differentiated (i) the “precentral” motor area (MI) which occupies mainly the rostral half of the gyrus sigmoideus posterior, and (ii) the supplementary motor area (MII) located in the lateral two-thirds of the gyrus sigmoideus anterior. In addition, stimulation of the somatosensory area I (S1) in the caudal half of the gyrus sigmoideus posterior elicited somatic movements. Stimulation of MI produced low threshold, relatively simple movements of the contralateral extremities. Movements obtained from S1 were similar, but had much higher thresholds. Stimulation of MII yielded high threshold, complex and often bilateral movements. In puppies up to 3 weeks of age cortical stimulation elicited bilateral movements which showed no definite projection pattern. From the 4th week of life a somatotopic organization and contralateral representation of the body began to appear and then gradually to evolve in the direction of the adult pattern. At the end of the 3rd month movements in puppies were essentially similar to those of adult dogs. However some minor differences were still present, suggesting that the process of maturation of cortical motor areas were not yet completed at this age.

INTRODUCTION

Since Fritsch and Hitzig’s (18) discovery that electrical stimulation of the pericruciate region produced movements of the body musculature in the dog, numerous investigators have used the electrical stimulation technique to analyze the extent and the organization of the motor cortex in various species (see 33). Systematic studies of this problem have led
to differentiation of two separate, somatotopically organized excitable areas in the primate frontal lobe: the precentral motor area (M₁) lying in front of the central sulcus, and the supplementary motor area (M₁₁) on the medial wall of the hemisphere (80, 81, 87). Besides these two areas, mainly motor in function, an independent, somatotopically organized motor outflow has been found to exist in the somatic afferent area I (S₁) in the postcentral gyrus as well as in the second somatic sensory area (S₁₁) on the upper bank of the sylvian fissure (3, 68, 76, 81, 88).

In subprimate forms the general arrangement of the sensorimotor region into four somatotopically organized areas appeared to be essentially similar to that in primates (81). The precentral motor area (M₁) and the somatosensory area I and II have been mapped in various species including the porcupine, rat, rabbit, guinea pig, cat and raccoon (30, 46, 77, 81, 89). Fewer data are available, however, on the supplementary motor area in subprimate forms. In the porcupine (46) and rabbit (81) the supplementary motor area lies on the medial wall of the hemisphere, as in monkey (81, 82, 87) and man (14, 56, 57). On the other hand, in the raccoon the supplementary motor area is located more laterally, extending on the gyrus sigmoideus anterior (36). In other subprimate mammals the localization of this area has not yet been investigated.

In the dog only the somatic afferent areas I and II have been mapped in detail (29). Their localization and somatotopic arrangement are similar to those of the cat (81). Area S₁ occupies mainly the caudal parts of the posterior sigmoid and coronal gyri. The leg, arm and face are represented in a mediolateral sequence; while in the anteroposterior direction the apices of the limbs and the snout are represented rostrally and the axial musculature caudally. Somatosensory area II (S₁₁) is located in the rostral part of the anterior ectosylvian gyrus between the suprasylvian and ectosylvian sulci. The face area is situated rostrally, the hindlimb area caudally. The proximal musculature and the back are represented more ventrally near the anterior ectosylvian sulcus, and the distal parts of the limbs and the snout more dorsally near the suprasylvian sulcus.

The pattern of representation in the cortical motor areas has not yet been extensively studied in the dog. Moreover, discrepancies in opinion exist as to the extent of the electrically responsive cortex in this species (10, 18, 60, 79). Although there is general agreement that stimulation of the cortex in the rostral part of the gyrus sigmoideus posterior produces movements of the body, the excitability of the caudal part of this gyrus and of the rostral and medial parts of the gyrus sigmoideus anterior has been called in question. A rough somatotopic arrangement of the motor cortex into neck, arm and leg subdivisions has been described, but no systematic studies of this problem have been carried out.
The aim of the present study was to analyze in detail the extent and the organization of the cortical motor areas in the dog. This seemed to be an important problem since the dog is a common laboratory animal, often used for studying motor functions after various cortical lesions. This paper analyzes the results of stimulating the posterior and anterior sigmoid gyri, i.e., the representation of the limbs and trunk. The effects of stimulation of the coronal gyrus, i.e. the face representation will be described elsewhere. Preliminary results of this study have been already published (84, 85).¹

In addition the present paper deals with the postnatal development of the cortical motor representation in the dog. Although this problem has been investigated by several authors using electrical stimulation of the cortex (51, 53, 61, 70) their results were largely controversial. Two main questions have been discussed: first, at what time, at birth or only later, does the motor cortex become electrically excitable, and a second, what is the sequence of appearance of movements of particular parts of the body, i.e., hindleg, foreleg and face, in the course of postnatal development of the motor cortex? Moreover, all these studies have usually focused on the first few weeks of the animal’s life; they do not give, therefore, a full and systematic description of changes in motor responses elicited by cortical stimulation over a long period of time. It will be shown that although stimulation of the motor cortex of the dog can at birth produce movements of various parts of the body, for a long period of time these responses differ from those obtained in adult animals. It seems, therefore, that the general picture of organization of cortical motor areas in adult specimens reflects the organization of motor systems which develop relatively late in ontogenesis and are superimposed on a less differentiated arrangement of cortical motor areas which developed earlier (22, 23).

MATERIAL AND METHODS

Adult dogs. Twenty six adult mongrel dogs, ranging in weight from 5 to 11 kg were used. In 10 animals the dorsolateral surface of the cortex was explored between the ansate, lateral and coronal junction caudally and the presylvian sulcus rostrally, and between the midline and the coronal sulcus laterally. In the rest of the animals, the buried

¹ Experiments on adult dogs have been partly done in the Laboratory of Neurophysiology, University of Wisconsin Medical School, Madison, Wisc., USA, and then finished at the Nencki Institute of Experimental Biology, Warszawa, Poland.
cortex was examined, i.e. the medial wall of the hemisphere, the anterior and posterior banks of the cruciate and presylvian sulci and the superior and inferior banks of the coronal sulcus. Each of these parts of the cortex was explored in at least three animals.

Experiments were carried out under Nembutal (sodium pentobarbital) anesthesia, administered intraperitoneally. The initial dose was 40 mg/kg of body weight, whereas maintenance doses of anesthesia ranged from 1.8-6.4 mg/kg/hr, the average dose being 3.1 mg/kg/hr. The rectal temperature was kept between 37-39°C with a water heating pad or an infrared lamp. The respiratory rate varied from 8 to 18 per minute.

The skin, bone and dura were removed from the region to be stimulated, usually over the left hemisphere. When necessary the left eye was also enucleated. Cortical surfaces lying within sulci were stimulated after subpial aspiration of opposing gyri. In order to study the medial wall, a part of the opposite hemisphere was removed. Special care was taken to avoid trauma to the tissue to be stimulated and to prevent blood loss. The exposed brain was kept moist with warm physiological saline, and a chamber constructed of saline-saturated cotton was erected over the exposed cortex to prevent drying of the pial surface.

The animals' body was supported horizontally with limbs pendant to allow maximal freedom of movement. The head was fixed rigidly in a special headholder, and the entire body was clipped to facilitate observation of movements. A movable electrode carrier was attached to the headholder. The position of the electrode tip could be specified in three rectangular coordinates, which were calibrated in millimeter units on the electrode carrier.

Monopolar stimulation was used throughout. A 0.5 mm diameter stainless steel wire insulated except for the tip served as the stimulating electrode. The indifferent electrode was attached to a saline soaked cotton ring on the scalp. 50 or 60-cycles sine wave current was delivered through a high impedance device, the amount of current (RMS values) being preset and read directly in milliamperes. Each stimulus lasted 2.5 sec, and a minimal interval of 2 min was allowed to elapse between successive stimulations regardless of whether or not a detectable response resulted (87). Each point was stimulated several times in order to determine the threshold value of stimulation producing a visible movement and to analyse movements recruited with suprathreshold stimulation. Usually the maximal stimulation of a given point did not exceed 150% of its threshold value. Only in case of high threshold points (2.4 ma and higher was this rule not followed, as the maximal current strengths applied in adult dogs were 3.0 ma.

Exploration of the cortex was carried out in 2 mm steps. The distance between successively stimulated points was no less than 4 mm in order
to minimize facilitation. The points stimulated were marked on an enlarged photograph of the exposed cortex according to the vascular pattern.

At least three investigators collaborated in observing the motor responses. The results of each stimulation were analyzed and described in detail. Time, cortical point stimulated; current employed, temporal sequence and relative strength of movements elicited were all recorded for each stimulation.

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

**Puppies.** Thirty two puppies, from 1 day up to 12 weeks of age, were used. They were divided into the following age groups: 1st, 2nd, 3rd, 4th, 6th, 8th, 10th and 12th weeks. In order to minimize the variability of the results due to differences in age within each group, only puppies of a certain age were taken for experiments. For example, data for the 1st week of life were collected only from puppies 1 day and 3-4 days old, for the 2nd week from puppies 10-13 days old, for the 3rd week from puppies 16-18 days old and so on.

In each group of puppies the dorsolateral surface of the cortex within the limits described for adult animals and the medial wall of the hemisphere were stimulated. At least two successful experiments with mapping the dorsolateral surface and one with mapping the mesial aspect of the hemisphere were performed in each age group. The cortical surfaces lying in the depths of sulci were not explored in puppies.

Nembutal administered intraperitoneally was also used in puppies for anesthesia as in adult dogs. The initial doses ranged from 20-40 mg/kg of body weight depending on the animal’s age and were preceded by atropine (0.1 mg/kg) and Fenactil (1.0 mg/kg). Supplementary doses of Nembutal, 3 mg/kg, were administered when necessary in order to prevent spontaneous movements.

The surgical procedure and the stimulation methods in puppies were similar to those in adult dogs. A more detailed description of the treatment of puppies during the experiments is given elsewhere (22).

**RESULTS**

**Part I. Motor effects of cortical stimulation in adult dogs**

**Extent and somatotopic arrangement of the motor cortex**

Figure 1 shows the location and the extent of the electrically excitable cortex in the dog in relation to the external morphology of the brain.
The hatched area in the Figure represents the region from which movements of trunk and limbs could be elicited. This region occupies the whole gyrus sigmoideus posterior together with its extension on the mesial surface of the hemisphere and the lateral two-thirds of the gyrus sigmoideus anterior. The responsive cortex extended rostrocaudally from the posterior bank of the presylvian sulcus to the ansate, lateral and coronal junction. Mediolaterally it extended from the splenial sulcus to the coronal sulcus, including its superior bank.²

Stimulation of the medial third of the gyrus sigmoideus anterior between the medial end of the presylvian sulcus and the midline, and

² Stimulation of the inferior bank of the coronal sulcus yielded mainly facial movements, which are not included in the present study.
of the medial part of the anterior bank of cruciate sulcus was ineffective in producing movements of the body musculature, at least with intensities of current used in this experiment (up to 3.0 ma). Stimulation of this region evoked eye movements and pupillary dilation. Similar effects were obtained upon stimulation of the medial wall of the hemisphere in front of the cruciate sulcus.

Within the electrically responsive area, hindlimb movements were represented more medially, and forelimbs laterally. A detailed analysis of cortical representation of various movements of the body is given below.

**Hindlimb movements.** Movements of the hindlimbs were elicited from the mesial aspect of the hemisphere behind the cruciate sulcus, the medial half of the gyrus sigmoideus posterior, the whole posterior bank of cruciate sulcus, the lateral two-thirds of its anterior bank, and a small strip of cortex in the anterior sigmoid gyrus just in front of the cruciate sulcus (Fig. 2).

The cortical representation of various movements of the hindlimb and their frequency of occurrence upon cortical stimulation were, however, not equal. The movement most often obtained was flexion of the knee (Fig. 2D). Its cortical representation overlapped the representation of all other hindquarter movements. Other movements relatively frequently encountered were thigh protraction (Fig. 2A) and ankle dorsiflexion (Fig. 2E). Both these movements were elicited from relatively large cortical areas, with thigh protraction most frequently elicited upon stimulation of the cortex near the midline, and dorsiflexion of foot on stimulation of the medial wall of the hemisphere and the posterior bank of cruciate sulcus. Other movements of the hindlimbs such as thigh retraction and abduction (Fig. 2BC), knee extension (Fig. 2G), ankle ventriflexion, and movements of the toes (Fig. 2F) occurred only rarely and were elicited from much more limited cortical regions. Movements of the tail (Fig. 2I) were represented mainly on the medial wall of the hemisphere.

The extensive overlap of the cortical loci yielding various hindquarter movements seen in Fig. 2 was only partly due to the fact that in this Figure both threshold and suprathreshold responses have been presented. Threshold stimulation of cortical points relatively rarely yielded a hindlimb response limited to one movement only. Most frequently two movements in two joints were elicited, which however, often differed in their strength and sequence of appearance. Suprathreshold stimulation caused an increase of the amplitude of these responses and usually recruitment of a new movement. In Fig. 2 the cortical loci yielding the
Fig. 2. Cortical motor representation of various hindquarter movements in the dog. Each part of the Figure (A–I) shows the extent of cortical regions yielding a different movement of the hindquarters. The density of symbols in a given cortical area represents the frequency of occurrence of a movement, i.e., the percentage of dogs in which this movement was elicited upon stimulation of a point located in this area. Both threshold and suprathreshold responses are included in the analysis. In order to show the cortex in the depths of sulci, the brain is diagramatically represented as if it were “rolled out”. The interrupted line passing through the postcruciate sulcus denotes the boundary between the motor and somatosensory cortex; (b), bottom of sulcus. Other abbreviations as in Fig. 1.

given movement on threshold stimulation overlap the area of its maximal frequency of occurrence.

The hindlimb movements were in the majority of cases contralateral (Fig. 2, dots). Bilateral movements (triangles) and ipsilateral movements (squares) were observed only occasionally and solely upon stimulation of the lateral parts of the posterior and anterior banks of the cruciate
sulcus. When present, they appeared merely as movement of thigh retraction (Fig. 2B), knee extension (Fig. 2G), ankle ventri- and dorsi-flexion (Fig. 2E, H), movements of the toes (Fig. 2F), and were associated with some trunk movements (see below). Stimulation of the medial aspect of the hemisphere, the posterior sigmoid gyrus and the medial half of the posterior bank of the cruciate sulcus yielded contralateral hindlimb movements exclusively.

**Forelimb movements.** As is illustrated in Fig. 3, forelimb movements were elicited from a region comprising the lateral half of the gyrus sigoideus posterior, the lateral two-thirds of the gyrus sigoideus anterior, the posterior bank of the presylvian sulcus, the superior bank of the coronal sulcus and the lateral halves of the anterior and posterior

![Diagram of cortical motor representation of various forelimb movements in the dog.](image)

Fig. 3. Cortical motor representation of various forelimb movements in the dog. For explanation see Fig. 2.
banks of the cruciate sulcus. Medially the forelimb representation partly overlapped the hindlimb representation (see Fig. 2). Stimulation of this zone elicited both fore- and hindlimb responses.

Similarly to the hindlimb movements, the various forelimb movements, were not represented in the cortex to an equal degree. The most frequently obtained were elbow flexion (Fig. 3D) and wrist extension (Fig. 3H). They could be obtained from a relatively large cortical area. Retraction of the arm (Fig. 3B) had the largest cortical representation overlapping the whole forelimb area but was less frequently encountered than elbow flexion and wrist dorsiflexion. Other forelimb movements such as arm protraction (Fig. 3A) and abduction (Fig. 3C), elbow extension (Fig. 3G), wrist flexion (Fig. 3E), flexion and extension of the digits (Fig. 3FI) were observed less frequently and from more limited cortical regions. The movements of flexion of digits and of the wrist had the most restricted cortical localization.

Comparison of cortical loci yielding various movements of the forelimb shows a better spatial differentiation than in the case of hindlimb movements. This can be most easily seen when the cortical representation of movements in the proximal and distal joints are compared. The former are represented more medially and rostrally, and the latter more laterally and caudally (see Fig. 3BCEF). The spatial differentiation between the cortical loci eliciting responses at adjacent joints was much less pronounced.

In contradistinction to hindlimb movements, which were almost exclusively contralateral, bilateral and sometimes ipsilateral forelimb movements were relatively frequently encountered. As is shown in Fig. 3, the forelimb movements elicited from the gyrus sigmoideus posterior were entirely contralateral (dots) except for a strip of cortex lateral to the cruciate sulcus. On the contrary, bilateral and ipsilateral responses were elicited from the gyrus sigmoideus anterior, the posterior bank of the presylvian sulcus, the rostral part of the superior bank of the coronal sulcus, as well as the lateral parts of the anterior and posterior banks of the cruciate sulcus. The amount of bilateral responses varied depending on the kind of movement. Elbow extension was in the majority of cases bilateral. In other movements, such as arm retraction, protraction and abduction, elbow flexion, extension of the wrist and the toes bilateral responses occurred less frequently. Movements of flexion of the wrist and digits were only contralateral.

Another difference in movements obtained from the gyrus sigmoideus anterior as compared with the gyrus sigmoideus posterior was their more complex character. The degree of overlap between cortical areas yielding movements at different joints was much more pronounced in
the anterior than posterior sigmoid gyrus (Fig. 3). In the latter the thresh-
old stimulation of a given cortical point elicited movements in one or
two, which usually differed in their strength and sequence of appearance.
On the other hand, in the gyrus sigmoideus anterior, threshold stimulation
elicited more complex movements, of one or both forelimbs. The move-
ments elicited from this area consisted, in general, of complex synergies.

Moreover, some movements of the forelimb seemed to be better
represented in the gyrus sigmoideus anterior than the posterior. For
example, arm protraction was never obtained on stimulation of the gyrus
sigmoideus posterior, but it had a large representation in the gyrus
sigmoideus anterior (Fig. 3A). Arm abduction, elbow extension, wrist
dorsiflexion and extension of the digits were better represented in the
anterior sigmoid gyrus than in the posterior (Fig. 3CGHI). On the other
hand, flexion of the elbow, wrist and digits (Fig. 3D–F) were mainly
represented in the gyrus sigmoideus posterior. These differences suggest
a spatial differentiation between the representations of flexor and ex-
tensor muscles of the forelimb, the former being mainly represented in
the gyrus sigmoideus posterior, and the latter in the gyrus sigmoideus
anterior.

Trunk movements. Figure 4 shows cortical loci yielding upon stimula-
tion visible movements of the upper (Fig. 4A) and lower (Fig. 4B) por-
tions of the trunk. Since movements of the neck could not be directly
observed in the present study due to fixation of the animal’s head (see
Methods) and any attempts to move the head resulted in this situation in
torsion of the pectoral girdle, both of these movements were included in
one category.

Fig. 4. Cortical motor representation of trunk movements in the dog. For explana-
tion see Fig. 2.
The majority of cortical points eliciting trunk movements were hidden in the depths of the cruciate, coronal and presylvian sulci (Fig. 4). Only in the rostral parts of the gyrus sigmoideus anterior, was stimulation of the free cortical surface effective in producing trunk movements, which, however, were restricted to its upper part solely. On the contrary, stimulation of both banks of the cruciate sulcus and the superior bank of the coronal sulcus produced torsion of the upper and lower parts of the trunk. Torsion of the pelvic trunk was obtained mainly from the posterior bank of the cruciate sulcus. The response consisted of twisting the lower trunk to the contralateral side. On the anterior bank of the cruciate sulcus the representation of the upper and lower trunk overlapped. Stimulation of this region elicited torsion of the upper trunk toward the contralateral side, while the lower part turned to the ipsilateral side. Similar movements were obtained upon stimulation of the superior bank of the coronal sulcus.

Movements of the trunk were only exceptionally elicited at threshold values of stimulation. Usually they were recruited with suprathreshold stimulations, often as high as 150% of threshold value for that cortical point. When present, they were always accompanied by complex movements of both fore- and/or hindlimbs, which were elicited with lower values of stimulation.

Torsions of the pectoral girdle were usually preceded and/or accompanied by bilateral movements of abduction, protraction or retraction at the shoulder together with elbow extension and wrist dorsiflexion (see Fig. 3). Turning of the upper part of the trunk toward the contralateral side was often associated with a protraction of the ipsilateral and retraction of the contralateral arm. Torsions of the pelvic trunk were accompanied by complex movement of hindlimbs which usually consisted of bilateral thigh retraction, together with knee extension and plantar flexion of ankle and toes. Sometimes the contralateral hindlimb flexed in all the joints, while the ipsilateral extended. These synergies explain why stimulation of the lateral part of the posterior bank of the cruciate sulcus produced such a great variety of hindlimb movements and why only from this area were bilateral hindlimb responses obtained (see Fig. 2).

The cortical loci from which trunk movements were elicited did not show any clear continuity (see Fig. 4). Their localization, however, suggests the existence of two cortical representations of the trunk. The first is located in the anterior and posterior banks of the cruciate sulcus, and the superior bank of the coronal sulcus; the second lies in the rostral parts of the anterior sigmoid gyrus along the presylvian sulcus and on its posterior bank.
The threshold for producing limb and trunk movements are shown in Fig. 5. Four classes of values were chosen: 0.5 ma and below, 0.6–1.0 ma, 1.1–2.0 ma and 2.1–3.0 ma, and the percent of responses of a given class was calculated as in Fig. 2–4.

As seen in Fig. 5A the area of highest excitability is situated laterally and caudally to the lateral end of the cruciate sulcus. It corresponds mainly to the forelimb representation yielding movements of distal joints (see Fig. 3). The lowest thresholds encountered in this area were of 0.2 and 0.3 ma. This area was surrounded by a higher threshold area ranging from 0.6–1.0 ma (Fig. 5B), the maximal percentage of responses within this class being grouped in the more medial parts of the gyrus sigmoideus posterior next to the cruciate sulcus, and on the dorsal part of its posterior bank. Stimulation of these parts of the cortex produced hindlimb movements, especially knee flexion (see Fig. 2).

In the remaining parts of the responsive cortex, i.e., the rostral parts of the gyrus sigmoideus anterior, the mesial aspect of the hemisphere,
the caudal parts of the gyrus sigmoideus posterior as well as in the cortex buried within the cruciate, presylvian and coronal sulci, the threshold value of stimulation ranged from 1.1–3.0 ma (Fig. 5CD). The highest values of stimulation were encountered at the outer margins of the excitable cortex near the presylvian and coronal sulci, and on the mesial wall of the hemisphere.

ANTERO-POSTERIOR DIVISION OF THE MOTOR CORTEX

Comparison of the motor effects of stimulation of the posterior and anterior sigmoid gyri suggests that this region can be divided, along its anteroposterior axis, into three separate areas, which correspond to the “precentral” motor area (M₁), the supplementary motor area (M₁₁) and the somatosensory area I (SI). The localization and the somatotopic arrangement of these areas is schematically represented in Fig. 6.

Fig. 6. Diagram of cortical motor areas in the dog. Abbreviations as in Fig. 1 and 2.

The “precentral” motor area occupies mainly the rostral half of the gyrus sigmoideus posterior, the posterior bank of the cruciate sulcus, and the adjacent cortex on the medial wall of the hemisphere. Rostrally it extends partly into the gyrus sigmoideus anterior and the lateral part of the anterior bank of the cruciate sulcus. Caudally this area abuts upon the somatosensory area I. This boundary was easily recognizable, since
stimulation thresholds suddenly increased 2–3 times, even over a distance of 2 mm, when passing from the M1 to S1 area, except for the medial wall of the hemisphere where these differences were not so clearly seen. Anteriorly the area M1 bounds with the supplementary motor area, the borderline between these two areas running along a line joining the rostral parts of trunk representation on the anterior bank of the cruciate sulcus and on the superior bank of the coronal sulcus (see Fig. 4). This line coincides with a line dividing areas of high and low excitability (see Fig. 5).

Within the precentral motor area the hindlimbs are represented medially, forelimbs laterally. Trunk and proximal parts of the limbs are represented rostrally, and distal parts of the body caudally, on the boundary between the M1 and S1.

Stimulation of the precentral motor area yielded relatively simple movements of the contralateral extremity, restricted at threshold stimulation to one or two joints. Only in case of stimulation of the trunk representation were the responses more complex and often bilateral.

The threshold values of stimulation in the precentral motor area were relatively low. In the forelimb region they usually ranged from 0.2–0.5 ma. In the hindlimb region they usually did not exceed 1.0 ma. The highest thresholds up to 2.0 and 3.0 ma, were encountered on the medial wall of the hemisphere and in the ventromedial parts of the posterior bank of the cruciate sulcus.

The supplementary motor area (MII) is situated in front of the precentral motor area (Fig. 6). It occupies the lateral two-thirds of the gyrus sigmoideus anterior, the posterior bank of the presylvian sulcus and a part of the anterior bank of the cruciate sulcus.

The somatotopic organization of this area is, in general, similar to that of the precentral motor area. Hindlimbs are represented medially, mostly hidden in the anterior bank of the cruciate sulcus; forelimbs are represented laterally. The trunk and proximal parts of the limbs are represented rostrally and the distal musculature caudally. The hindlimb representation in the supplementary motor area is relatively small, most of the MII being occupied by the forelimb representation.

The characteristic feature of the somatotopic arrangement of the supplementary motor area is a considerable overlap of representations of different movements and parts of the body, as well as a partial bilateral representation. Stimulation of this area elicited usually complex bilateral movements. Moreover, the data suggest that the extensor muscles are represented to a greater extent in the MII than in the M1 area. Also thresholds in MII were higher than in the M1 and ranged from 1.0 to
Moreover, the supplementary motor field was much more susceptible to narcosis than the precentral area. Higher doses of anesthesia much more easily depressed the excitability of this area as compared with M₁ and even rendered it completely inexcitable. The ipsilateral movements were the first to disappear.

In addition to the above described motor areas in the frontal lobe, stimulation of the caudal part of the posterior sigmoid gyrus, i.e., the somatosensory area I (S₁) (29) also produced motor responses. The somatotopic arrangement of the motor outflow in this area overlapped in general that of the sensory input. The hindlimbs were represented medially on the superior part of the gyrus sigmoideus posterior and the adjacent cortex on the mesial aspect of the hemisphere. Movements of the forelimb were elicited from the lateral parts of this gyrus. Movements of distal joints, i.e., of the wrist and fingers were elicited from rostral parts of this area on the borderline with M₁. No representation of the trunk has been found in this area, but it is possible that the maximal (3.0 ma) strength of stimulation was too small to elicit these movements.

Stimulation of S₁ elicited, usually, responses similar to those obtained from the precentral motor area, i.e., relatively simple movements of the contralateral extremity. The thresholds, however, were in the S₁ much higher than in M₁, the majority of points ranging from 1.1 to 3.0 ma (see Fig. 5).

Movements elicited from M₁, M₁₁ and S₁ were classified at tonic. This means that they appeared with a relatively short latency and lasted up to the end of stimulation. The amplitude of responses usually increased during the course of the stimulation. Turning the stimulation off resulted in a quick relaxation of muscles. The responses were also relatively stable, that is, successive stimulations of the same point yielded essentially similar results. Only in the supplementary motor area was a tendency for maintaining the posture after the stimulation has been turned off sometimes observed. The responses evoked from this area were also slightly less reliable than those obtained from other motor areas.

**Part II. Motor effects of cortical stimulation in puppies**

The motor effects of cortical stimulation in puppies were largely different from those obtained in adult dogs. Although the anterior and posterior sigmoid gyri appeared to be electrically excitable by the first day of the animals' life, the adult pattern of cortical representation was not yet fully developed at the end of the third month. Two periods in the postnatal development of cortical motor areas were differentiated:
(i) from birth to the 4th week of life when movements in puppies were quite different from those elicited in adult dogs; and (ii) from the 4th week of life to the end of the 3rd month when movements in puppies' gradually took on the appearance of the responses in adult dogs. Movements elicited in both these periods of life are described below.

THE PERIOD FROM BIRTH TO THE 4TH WEEK OF LIFE

The main features of this period were lack of somatotopic organization of the cortex and lack of dominant representation of contralateral parts of the body. Stimulation of any part of the cortex within the sigmoid gyri and of the mesial aspect of the hemisphere yielded in puppies up to the 4th week of age usually only one stereotyped pattern of motor response, involving both fore- and hindlimbs at the same time.

Hindlimb movements were essentially limited to the retraction of the thigh, which in adult animals occurs relatively rarely and from a very limited cortical region (see Fig. 2). In the case of the forelimbs, the variety of movements was greater. The response most often observed was protraction at the shoulder, but movements of forelimb retraction, abduction and adduction were sometimes encountered. In distal parts of the limb, extension of the wrist and extension in metacarpal joints could be elicited; however, they never occurred individually, but always together with a movement at the shoulder (usually protraction). Other movements typical for adult dogs, such as thigh protraction, knee and elbow flexion, flexion of the wrist, usually could not be elicited by cortical stimulation in this period of life.

An additional difference between movements elicited in adult dogs and puppies in the first 3 weeks of their life concerns the character of their responses. In adult dogs movements elicited by cortical stimulation were tonic, and the responses obtained from the same cortical point on successive stimulations relatively stable. On the contrary, in puppies up to the 4th week of age these movements were, in general, neither tonic nor stable. The vast majority of movements were jerk-like, phasic or clonic. Tonic movements were only rarely observed. These responses were also variable, i.e., successive stimulations of the same cortical point produced quite different responses from stimulation to stimulation. For example, the first stimulation of a given cortical point could produce a jerk consisting of retraction of the hindlegs, the second a jerk-like protraction of the forelegs without any movements of hindlimbs, the third a jerk-like or phasic retraction of the hindlimbs with a clonic abduction and adduction of forelimbs. The movements obtained from the mesial aspect of the hemisphere did not differ in any respect from those elicited from the dorsolateral cortical surface.
THE PERIOD FROM THE 4TH WEEK TO 3 MONTHS OF LIFE

An essential change in movements evoked by electrical stimulation of cortical motor areas took place in puppies at the transition from the 3rd to the 4th week of their life. Beginning with the 4th week the somatotopic organization and contralateral representation of the body first made their appearance and then gradually evolved in the direction of the adult pattern. The repertory of movements became enriched, resembling that of adult animals. Besides, the movements became tonic and more stable on successive stimulations of the same cortical point. At the end of the 3rd month the overall picture of movements produced by electrical stimulation of the gyrus sigmoideus posterior and anterior was quite similar to that of adult animals. However, some minor differences were still present, suggesting that the process of maturation of the cortical motor areas was not yet completed at this age.

Beginning with the 4th week, stimulation of the posterior sigmoid gyrus yielded some movements restricted to the contralateral hind- or fore-extremity. This spatial differentiation of the fore- and hindlimb representation as well as the appearance of the contralateral representation of the body was first seen at the margins of the excitable cortex. Stimulation of the mesial aspect of the hemisphere and of the most medial parts of the gyrus sigmoideus posterior yielded movements limited to the contralateral hindlimb. Stimulation of the cortex near the coronal sulcus elicited responses of the contralateral forelimb. In between there was a large zone which continued to produce bilateral movements of both fore- and hindlimbs. In older animals this transverse zone yielding bilateral movements became gradually more and more restricted, and at the end of the 3rd month bilateral movements had almost completely disappeared from the gyrus sigmoideus posterior. They were mainly obtained on stimulation of the gyrus sigmoideus anterior, the latter being the region from which bilateral movements were elicited in adult dogs as well.

Bilateral movements obtained in puppies upon stimulation of the gyrus sigmoideus posterior were usually associated with trunk movements. In adult dogs, as described above, trunk movements were obtained on stimulation of the gyrus sigmoideus anterior; whereas stimulation of the cortical surface over the gyrus sigmoideus posterior did not yield, as a rule, any trunk movements at all. On the contrary, in puppies stimulation of the posterior sigmoid gyrus and of the mesial aspect of the hemisphere easily produced trunk movements, in addition to those elicited from the anterior sigmoid gyrus. The cortical loci producing trunk movements gradually decreased with age, being more and more limited to a transverse zone in the gyrus sigmoideus posterior between the fore-
and hindlimb representations. At the end of the 3rd month trunk movements had almost completely disappeared from the gyrus sigmoideus posterior. They were obtained from the rostral parts of the gyrus sigmoideus anterior, the picture resembling that of adult dogs.

The gradual decrease of the trunk representation was correlated with a slow enlargement of cortical areas yielding movements of the contralateral hind- and forelimbs. The latter seemed to dislodge the trunk representation. This process, however, was not quite symmetrical. The cortical loci from which hindlimb movements could be elicited extended in puppies more laterally than in adult dogs, partially occupying the place of the forelimb representation. At the end of the 3rd month the cortical representation of forelimb movements in the posterior sigmoid gyrus seemed to be still smaller than in adult dogs. Although stimulation of lateral parts of this gyrus in 12 weeks old puppies produced forelimb movements similar to those obtained in adult dogs, these movements were often accompanied by a hindlimb response, usually a knee flexion, which was easily recruited with suprathreshold stimulation. In adult dogs, suprathreshold (i.e., up to 150% of threshold value) stimulation of these parts of the cortex did not evoke hindlimb movements at all. This would suggest that the representation of the foreleg might have been not fully developed at this period.

The process of development of the adult-like somatotopic arrangement of cortical representation of particular parts of the body was accompanied by an enrichment of their repertory of movements. Beginning with the 4th week, movements of knee flexion and thigh protraction appeared and then predominated. Movements of the ankle, toes and tail were also obtained. In the forelimbs, the number of shoulder protractions elicited from the gyrus sigmoideus posterior began to decrease, while those of shoulder retractions increased. Movements of elbow flexion and then wrist and digit flexion were also obtained.

The postnatal changes in motor responses elicited by cortical stimulation were best seen in the gyrus sigmoideus posterior, i.e., in the M₁ and S₁ areas. They were less obvious in the gyrus sigmoideus anterior, i.e., the supplementary motor area stimulation of which produced in adult animals more complex and often bilateral movements. It is worth mentioning, however, that whereas in adult dogs stimulation of this area, as a rule, did not yield movements of the hindlimbs and of the pelvic trunk, these responses were easily obtained in puppies at a certain transient stage of development. Later on, they disappeared, giving way to the larger representation of the forelimbs and upper trunk characteristic for adults.

From the 4th week of life the character of movements in puppies
also had been changing. Instead of jerk-like, phasic or clonic responses, tonic movements gradually began to dominate. The responses became also more reliable on successive stimulations of the same cortical point. At the end of the 3rd month non-tonic movements and unstable responses were only sporadically encountered, the overall picture resembling closely that of an adult animal.

The postnatal changes in motor responses elicited by cortical stimulation were accompanied by a gradual decrease of current required to evoke movements. In puppies from the very beginning of their life, the precentral motor area had the lowest thresholds, while the supplementary and the somatosensory area I were less excitable, as in adult dogs. However, in puppies the current required to elicit motor responses in all these areas was proportionally higher than in adults. For example, in the majority of points in MI the threshold ranged from 0.6 ma to 2.0 ma, although some points with thresholds below 0.5 ma were also occasionally seen. Similarly, in MI and SI thresholds ranged from 2.0 to 5.0 ma, as compared with 1.0–3.0 ma obtained in adults. Although the excitability of all these areas increased with age, this process was not yet finished at the end of the 3rd month. In puppies 12 weeks old the current required to elicit motor responses was still slightly higher than in adults.

DISCUSSION

Extent and functional differentiation of the motor cortex in the dog

The present study shows that electrical stimulation of a large cortical region, involving the whole gyrus sigmoideus posterior, the adjacent cortex on the mesial aspect of the hemisphere, and the lateral two-thirds of the gyrus sigmoideus anterior produces in dogs movements of the extremities and the trunk. This area is in general larger than that described in the dog by other authors (10, 18, 60, 79) who either questioned the responsiveness of the caudal part of the gyrus sigmoideus posterior or of the rostral part of the gyrus sigmoideus anterior. It corresponds, however, with the data obtained in the cat (19, 81) and the raccoon (30, 36), both these species having a pattern of fissuration of the frontal lobe similar to the dog.

Comparison of movements and stimulation strength used to elicit responses from various parts of the sigmoid gyri suggest the existence of two separate cortical motor areas in the frontal lobe of the dog: (i) the “precentral” motor area (MI) located in the rostral part of the gyrus sigmoideus posterior and the caudal part of the gyrus sigmoideus anterior, and (ii) the supplementary motor area (MII) located in the
central and rostral parts of the gyrus sigmoideus anterior. In addition the somatosensory area I (S1) in the caudal part of the gyrus sigmoideus posterior (29) also appeared to have some motor functions, since its stimulation produced motor responses.

Stimulation of the precentral motor area yielded low threshold, relatively simple movements of the contralateral limbs, except for the trunk representation where bilateral and sometimes ipsilateral responses of the limbs were also obtained. Movements evoked from S1 were essentially similar to those elicited from M1, but required higher intensities of stimulation. Stimulation of the gyrus sigmoideus anterior, i.e., the supplementary motor area elicited high threshold, more complex and often bilateral movements.

The somatotopic arrangement of M1 and S1 areas in the adult dog was, in general, similar to other species (81). The hindleg was represented medially, on the mesial aspect of the hemisphere and the superior half of the gyrus sigmoideus posterior. The foreleg was represented in the lateral half of this gyrus. Apices of the limb were represented near the line separating M1 and S1; while the proximal musculature lay far away from this line. These relationships were more clearly perceptible in the forelimb than in the hindlimb region. In the supplementary motor area the pattern of representation was similar to M1, with distal musculature lying caudolaterally, and the trunk rostromedially, near the presylvian sulcus. The foreleg representation occupied the major portion of M1. The hindleg representation was small and almost completely hidden in the anterior bank of the cruciate sulcus.

The boundary between the M1 and S1 areas was delineated in the present study by a sudden increase of current required to elicit somatic movements. In the central part of the gyrus sigmoideus posterior this line ran through the postcruciate sulcus, while medially and laterally it passed more rostrally. This boundary corresponded fairly well with the posterior limit of the electrically excitable cortex in the dog as defined by Smith (60). This author has also studied the cytoarchitecture of this region in the dog and found that the boundary between his excitable and non-excitable cortex was congruent with the transition of cortex specific for Brodmann's area 4, which is characterized by the presence of large and giant pyramidal cells in the fifth layer and absence of the internal granular layer, into a markedly granular cortex of Brodmann's area 3. Both these areas were separated by a narrow transition zone characterized by the presence of the fourth granular layer as well as large and giant pyramidal cells in the fifth layer. Similar observations have been made in the present study (unpublished data). This picture is consistent with data obtained in other species (76) in which
a sharp increase of current required to elicit somatic movements was correlated with the transition of the agranular precentral cortex into the granular postcentral cortex.

Comparison of the rostral limit of the somatosensory area I defined in the dog by recording evoked potentials to tactile stimulation (29) and of the caudal limit of the precentral motor area as found in the present experiments, suggests a partial overlap between these two areas. A similar overlap has been also found on other species (3, 76, 81). In man “sensory experiences” have been elicited by stimulation of the precentral convolution (55, 56). Distribution of somatic afferents to the precentral as well as to the postcentral region has been also found by recording potentials evoked by electrical stimulation of cutaneous nerves and dorsal roots (50, 83).

The motor functions of the postcentral cortex have been questioned by various authors who confined the motor area to the precentral cortex (26, 33, 48). Movements elicited from this region have been attributed to spread of current or transcortical conduction (16, 48). Nevertheless postcentral responses have been described widely in various species including man (11, 15, 19, 55, 76, 80, 81). The existence of an independent motor outflow from the postcentral cortex has been more conclusively proven by Woolsey et al. (88) who obtained motor responses from this region after chronic ablation of the precentral and supplementary motor areas in macaques. This is compatible with anatomical data showing that in various species the pyramidal tract takes origin partly from the postcentral cortex (9, 12, 47, 52, 54, 58). The smaller number of corticospinal fibres originating from the postcentral cortex may account for the higher current required to elicit movements from the S\textsubscript{T} area as compared with the area M\textsubscript{I}.

The rostral extent of the precentral motor area and the localization of the supplementary motor area in the dog require a more detailed discussion. The present data suggest that the supplementary motor area in the dog is situated in front of area M\textsubscript{I} in the lateral two-thirds of the anterior sigmoid gyrus. The boundary between M\textsubscript{I} and M\textsubscript{II} passes slightly obliquely in front of the lateral end of the cruciate sulcus down to the rostral end of the coronal sulcus. This boundary was delineated in the present study on the basis of three criteria: (i) the presence of a double trunk representation, one situated in the depths of the cruciate and the coronal sulcus, and the other in the rostral parts of the gyrus sigmoideus anterior near the presylvian sulcus; (ii) differences in motor responses obtained from the posterior and anterior sigmoid gyri, and (iii) differences in current strengths required to elicit movements from these two areas. Moreover, the M\textsubscript{I} and M\textsubscript{II} areas differed in their sus-
ceptibility to anesthesia, the excitability of the supplementary motor area being affected much easier than that of the precentral motor area.

The rostral limit of the precentral motor field does not correspond to any of the published cytoarchitectural maps of the dog's cortex (1, 27, 40). It extends beyond the region of large or giant pyramidal cells which in the dog disappears at the level of the lateral extension of the cruciate sulcus (1, 40). However, the rostral limit of this precentral motor field coincides closely with the anterior margin of the electrically excitable area delineated in the dog by Woolsey (79). It also corresponds with the rostral boundary of the cortical region which was considered by Holmes and May (32) to be the source of the corticospinal tract in the dog. Although since that time numerous data have proved that the pyramidal tract also originates from the cortex lying more anteriorly, the precentral gyrus or its homologue in subprimate mammals is still considered a source of the vast majority of corticospinal fibers (9, 12, 52, 58). This is compatible with the results showing that area M1 had much lower thresholds and was much more resistant to anesthesia than other parts of the electrically excitable cortex.

The presence of the trunk representation in the rostral part of the precentral motor field constituted one of the criteria of differentiation between the precentral and supplementary motor areas. The trunk and neck representation in the depths of the cruciate and coronal sulci was discontinued on the cortical surface by an intervening arm area. Since the axial musculature seems to be less excitable than distal parts of the body, the current might have been too low to elicit movements of the axial musculature from the cortical surface. Contralateral flexion of the neck on stimulation of the cortex just in front of the lateral end of the cruciate sulcus has been described in the dog (79). In cats stimulation of the cortex hidden within the cruciate sulcus, near its lateral end, produced trunk movements (13) as in dogs.

In man the supplementary motor area lies on the mesial aspect of the hemisphere in front of the precentral foot representation (2, 56, 57). Stimulation of this area evokes complex motor synergies, involving both contra- and ipsilateral parts of the body, and the arrest of vocalization and speech. A similar localization of the supplementary motor area has been found in primates (81, 82, 87). Although in primates no ipsilateral movements have been obtained on stimulation of this area, the motor responses differed in several respects from those elicited from the precentral motor area. They were more complex, could be easily facilitated by repeated stimulation, were susceptible to the anesthesia and required higher intensities of stimulation.

In subprimate forms the supplementary motor area does not have
a uniform localization. In the porcupine and the rabbit it is located on the medial wall of the hemisphere (46, 81). On the other hand, in the raccoon it extends more laterally, occupying the medial two-thirds of the anterior sigmoid gyrus (36). In the cat, the gyrus sigmoideus anterior has been included into the precentral motor area, and the supplementary motor area has been hypothetically situated in the depths of the cruciate sulcus and on the medial wall of the hemisphere (81).

Although in the raccoon and the dog, the supplementary motor area occupies the gyrus sigmoideus anterior, its localization is not identical in both these Carnivore brains. In the raccoon area M_{II} is placed more medially than in the dog. It also involves cortical regions, such as the medial third of the gyrus sigmoideus anterior and the mesial aspect of the hemisphere in front of the cruciate sulcus, which in the dog is ineffective in producing motor responses, except for extraocular muscle action. These dissimilarities cannot be explained by differences in parameters of stimulation, since they were similar in both species (see 36). Other characteristic features of motor responses elicited from the supplementary motor area were, however, similar in the raccoon and the dog. Stimulation of this area in the raccoon resulted in a widespread coordinated bilateral activity, with hind- and forequarter movements organized along a caudorostral direction. The motor responses required higher intensities of stimulation and depended on the depth of anesthesia.

The functional differentiation of the anterior and posterior sigmoid gyri in the dog is supported by the results of experiments with partial ablations of the sensorimotor region (63–65). Bilateral lesions of the gyrus sigmoideus posterior were followed in dogs by a general motor disability, paresis and ataxia, loss of placing reactions, as well as transient absence of movements in the conditioned reflex situation. These symptoms varied in degree depending on the extent and the localization of the lesion in caudal (sensory) or rostral (motor) parts of the posterior sigmoid gyrus. On the contrary, bilateral ablation of the whole gyrus sigmoideus anterior evoked only very slight, if any, signs of paresis or ataxia, and no impairment in placing reactions nor in execution of skilled movements. A similar difference in motor deficits resulting from ablations of the precentral and supplementary motor areas has been found in monkeys (28, 73, 74). Lesions of the precentral area were followed by an immediate, severe impairment of voluntary movements, hypotonia and loss of placing and hopping reactions in extremities contralateral to the ablation. Although partial recovery of motor functions took place with time, slowness in execution of fine movements and impairment of placing and hopping reactions were persistently observed. On the other hand, bilateral ablations of the supplementary motor area produced in monkeys disturbances in
posture and tonus but no noticeable paresis and impairment of placing and hopping reactions.

The last problem to be commented upon concerns the concept of the so-called "premotor" cortex. This term usually designates a region in front of the precentral gigantopyramidal area, which has many cyto-architectural similarities with the precentral cortex, except for a smaller number of pyramidal cells and absence of giant pyramidal cells in the fifth layer. Campbell (8) has labelled this part of the cortex an intermediate precentral area, and Brodmann (5) designated it area 6. The premotor cortex has been considered as an integrative region controlling complex motor acts and its removal has been found to produce disturbances of skilled movements and "motor apraxia" (35, 38). The functional uniformity of the premotor cortex has been re-examined by Woolsey and his collaborators (87). On the basis of stimulation studies, in monkeys he has included the posterior parts of area 6 in the precentral and supplementary motor areas. Further ablation studies in monkeys (28, 73, 74) have supported the view that only those portions of area 6 which belong to the precentral and supplementary motor areas possess some motor functions. Ablations of the remaining parts of area 6 and of the frontal lobe resulted in no motor impairment, nor did they aggravate the motor deficits produced by previous lesions of the precentral and supplementary motor areas.

In the dog lesions of the whole gyrus sigmoideus anterior have been thought to produce "premotor symptoms" (65). They consisted of a pronounced dysreflexia in the conditioned reflex situation, an increased tendency to perseveration of all possible motor acts, hyperactivity, exaggerated orientation reaction to the conditional stimuli and an abnormal direct alimentary reaction. However, further analysis of this syndrome has shown that the crucial region for eliciting some of the "premotor" symptoms is located in the dog on the mesial aspect of the hemisphere (62, 66, 67). Since this region projects to the dorsomedial nucleus of the thalamus it has been classified as belonging to the prefrontal cortex (69).

As shown in the present study the supplementary motor area occupies in the dog the major portion of the gyrus sigmoideus anterior. Although the function of this region in the motor behavior of the dog remains to be reevaluated, its function seems to be different from the rest of the "premotor" cortex. Stimulation of the medial third of the gyrus sigmoideus anterior and the mesial aspect of the hemisphere just in front of the cruciate sulcus produced no somatic movements but only extraocular muscle action and pupillary dilation. An autonomic center for eyes on the mesial surface of the frontal lobe just in front to the cruciate sulcus has also been reported for the cat (59). Campbell (8) in his cytoarchitec-
tural maps for dogs and cats has assigned the medial part of the gyrus sigmoideus anterior to the frontal cortex, while the more lateral parts of this gyrus have been classified as belonging to the motor type. Also Kreiner (41) in his myeloarchitectonic studies of the dog cortex has differentiated the medial part of the gyrus sigmoideus anterior from its lateral parts. The former has been included into the precruciate gyrus, which lies mainly on the mesial aspect of the hemisphere. This area has strong connections both with the cortex on the medial wall of the hemisphere and the more lateral part of the gyrus sigmoideus anterior. It is likely, therefore, that it may constitute in the dog an intermediary link between the prefrontal cortex and the supplementary motor area.

POSTNATAL DEVELOPMENT OF CORTICAL MOTOR REPRESENTATION IN THE DOG

The most interesting result derived from the experiments with motor cortex stimulation in puppies of different age, seems to be the extent to which the cortical representation of various parts of the body changed in the course of postnatal development. During the first 3 weeks of life neither spatial differentiation of cortical loci yielding fore- and hindlimb movements nor any predominance of the contralateral representation of the body was observed. Beginning with the 4th week of age a gradual shift toward an adult pattern of motor representation was seen. Contralateral movements of fore- and hindlimbs first made their appearance and the cortical loci yielding trunk and bilateral movements of the extremities became slowly restricted. All these processes were associated with a gradual enrichment of the repertory of movements elicited by cortical stimulation, an increase in the excitability of the motor cortex, as well as a change in the character of motor responses from non-tonic and variable into tonic and reliable. At the end of the 3rd month the pattern of responses elicited from the anterior and posterior sigmoid gyri closely resembled that of adults, except for slightly higher current strengths required to elicit movements and some differences in the extent of cortical areas yielding fore- and hindlimb movements. The former was relatively smaller, and the latter larger than in adult animals.

These results suggest that the general picture of somatotopic arrangement of cortical motor areas obtained in adults reflects the functional organization of motor systems which develop relatively late in the animals’ life. These systems are superimposed on other systems, which are less excitable, less differentiated and develop earlier in ontogenesis. In adult animals, therefore, the somatotopic organization of the cortex does not exclude the possibility that other parts of the body are represented to some extent in the same cortical area. The motor response elicited on electrical stimulation would depend, therefore, on which part of the
body posesses the most numerous and most excitable elements in a given cortical region.

Although the hypothesis that all parts of the cortex exert some control over all parts of the body musculature requires further experimental evidence, some data in the literature strongly support it. For example in monkeys lesions of the hand area resulted in some degeneration in the lumbar region of the spinal cord and lesions of the foot area resulted in degeneration in the brachial segments (20, 42, 49). Similarly ablation of the arm area alone had less effect on arm function than if arm and leg areas were both removed (6, 37). On the other hand, Travis (73) found that if the precentral forelimb area was removed completely at an initial operation and the contralateral upper extremity was permitted to reach its maximal recovery, ablation of the hindlimb area on the same side as the original lesion yielded no additional impairment in the upper extremity.

The motor responses elicited in puppies in their first 3 weeks of life and those obtained in latter periods are compatible with Hines' (31) description of movements in fetal and infant monkeys. She distinguished two types of movements which could be elicited upon electrical stimulation of the precentral gyrus. One group of movements which she has called idiokinetic were contralateral, more or less discrete and showed a definite topographical projection pattern upon the precentral gyrus. The second group, called holokinetic, consisted of movements which were not discrete, frequently bilateral and showed no topographical pattern. The holokinetic movements were elicited in earlier ontogenetic periods than the idiokinetic ones. They were, according to the author, of extrapyramidal origin since they could be also obtained in adult animals after surgical division of the pyramids. The idiokinetic movements, on the other hand, were thought to depend on the integrity of the pyramidal tract.

In the dog the gradual shift toward an adult pattern of motor responses taking place from the 4th week of their life seems to be correlated, at least partly, with a process of maturation of the corticospinal tract. At the age of 3 weeks all tracts in the spinal cord of the dog appear to be myelinated except for the lateral corticospinal tract and the fasciculus gracilis, in which the process of myelinization is not completed until 6 weeks of age (17). The postnatal development of spinal terminations of the pyramidal tract lasts, however, much longer, achieving by the age of 3 months, a pattern of projection similar to, but not entirely as complete, as that found in the adult dog (7). Similar conclusions regarding the duration of maturation of the pyramidal tract could be drawn from measurements of conduction velocities of corticospinal fibres in puppies
of different age (39). They are consistent with the fact that the maturation of the motor cortex, as judged by the effects of its electrical stimulation, is not yet completed at the end of the 3rd month.

In macaques the process of maturation of the corticospinal tract is not yet finished at the age of 8 months (43), and these data correspond with the results of cortical stimulation showing that in infant monkeys the extent of motor cortex and the threshold current producing movements approach the adult value at the age of 1 year or more (4). These differences in time reflect differences in the degree of corticalization of motor functions in various species. They are in agreement with the data showing greater functional significance of the pyramidal tract in monkeys (45, 72, 78, 86) as compared with dogs (21, 34) and cats (24, 25, 44, 75, 78).

The question as to what extent the movements obtained by cortical stimulation are subserved by pyramidal and extrapyramidal systems cannot be answered satisfactorily at the present time. According to Hines (31) sectioning the pyramids abolished the idiokinetic movements, leaving the complex, undifferentiated and nontopographically arranged holokinetic movements intact. Similar results were obtained in cats by Tower (71). On the other hand, recent experiments on monkeys with unilateral section of the bulbar pyramids (86), have shown, that although movements elicited from the operated side were much simpler and required stronger stimulation, as compared with the normal side, they were still contralateral and showed a definite topographic pattern of projection. Further experiments have to be carried out in order to evaluate the contribution of the pyramidal and extrapyramidal systems in motor functions at various stages of postnatal development in the dog.

The author wishes to express her gratitude to Dr C. N. Woolsey for enabling her to perform part of the experiments in the Laboratory of Neurophysiology, University of Wisconsin Medical School, Madison Wisc., USA, and for providing her with the equipment necessary to continue the study. This investigation was supported by Project 09.4.1 of the Polish Academy of Sciences and by Foreign Research Agreement 05.275.2 of US Department of the Health, Education and Welfare under PL 480.

REFERENCES


25. GÖRSKA, T., JANKOWSKA, E. and MOSSAKOWSKI, M. 1966. Effects of py-


64. STEPIEN, I., STEPIEN, L. and KONORSKI, J. 1960. The effects of bilateral


Received 24 February 1973

T. GÓRSKA, Department of Neurophysiology, Nencki Institute of Experimental Biology, 3 Pasteur, 00-973 Warszawa, Poland.