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MYELOARCHITECTONIC DIFFERENTIATION OF THE CEREBELLAR CORTEX [1]

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(Received May 7, 1966)

This paper was prompted by our research on the myeloarchitectonics of the cerebral cortex (Kreiner 1961) which revealed the existence of three types of cortical areas: the gyral, paragyral and fissural cortex. The aim of this paper was to analyse the differences between various regions of the cerebellar cortex, particularly those situated on the ridge of the cerebellar gyri and the bottom of cerebellar fissures.

The observations were done on four series of dog brains, one series of monkey and one of rat brain. The series were stained according to the methods of Weigert-Wolters, Klüver, Nissl and Schulze and sectioned in the parasagittal plane.

OBSERVATIONS

The cerebellar cortex is often considered to be one of the anatomically best known organs. In every textbook of neuroanatomy one can find a scheme of its architectonics based on the beautiful analysis of Köl-liker (1896), Ramon y Cajal (1904) and Déjérine (1901). The classic authors distinguished three layers: the molecular, the ganglionic, and the granular layer, and described their fine structure in detail.

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[1] This study is part of research project supported by N.I.H. under the agreement No. 287707 with the Department of Neurophysiology, Nencki Institute of Experimental Biology, Warsaw, Poland.

[2] I am much indebted to Miss Anna Nowak who made the preparations and drawings for this paper.

Our observations fully corroborate the correctness of this scheme. Nevertheless, we have found essential differences between the architectonics of various portions of the cerebellar cortex situated in the depth of the fissures and on the ridge of the gyri. The differences correlate with considerable differences of the thickness of the granular layer. Thus, within the cerebellar cortex five myeloarchitectonical types can be distinguished: the gyral type, the minor gyral type, the parietal type, the fissural type, and the minor fissural type.

The *gyral* type of the cerebellar cortex (Fig. 1) is found on the top of the primary and secondary cerebellar gyri. It is the type most com-

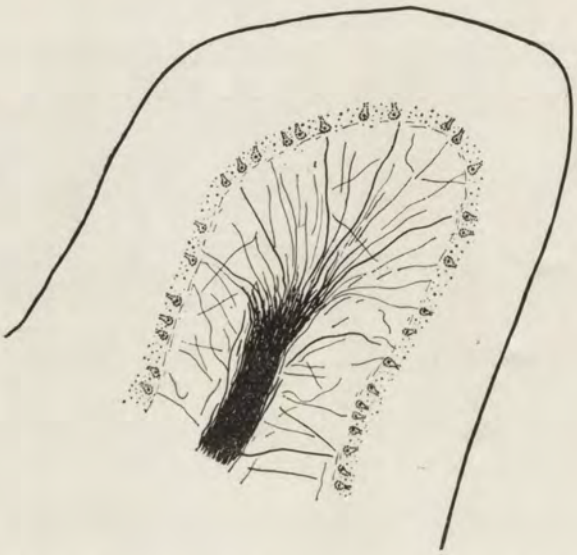

Fig. 1. Gyral type of the cerebellar cortex of the dog.
Semischematic, Weigert stain

monly studied by the classic neuroanatomists, and its architectonics is best known.

The gyral cerebellar cortex occupies the ridge of a cerebellar gyrus, forming a kind of cap. In the interior of this cap the white matter is located. It appears to be a well defined lamina composed nearly totally of thick and medium sized myelinated fibers. These run parallel and begin to disperse radially when entering the gyral area. The medium sized and thick fibers enter the granular layer (about 250 μ thick), and nearly reach the layer of Purkinje-cells. Among these radial fibers one can observe sparse tangential fibers, much thinner than the radial ones.

At the surface of the white matter the tangential fibers are more densely arranged; they run in various directions and make a loose plexus.

Another plexus of myelinated fibers is seen immediately below the layer of Purkinje-cells (plexus infraganglionaris, C l a r a 1959). This plexus is composed of fine fibers running in various directions except in the parasagittal plane. The plexus is joined by fine radial fibers, and in many places penetrates between the Purkinje-cells and touches the fine supraganglionar plexus. The latter is composed of fine or very fine fibers rather densely arranged. These fibers run parallel to each other and to the ridge of the gyrus, and only very few branch off into the molecular layer. The molecular layer (160–250 μ thick) contains fine fibers rarely, except the cortex of the central lobulus and the ligula.

Fig. 2. Minor gyral type of the cerebellar cortex of the dog. Semischematic, Weigert stain

The *minor gyral* type of the cerebellar cortex (Fig. 2). is found in small, not typical gyri situated on the wall of full gyri. They are hidden in the depth of the fissures. They are often not delimitated from the neighboring cortex by any distinct groove and become thus cryptogyri (K r e i n e r 1961).

The most typical, striking peculiarity of this type of cerebellar cor-

tex is the absence of the white matter in its interior, in the form of a medullar lamina. This kind of gyri is attached to the side of the white matter lamella of a full cerebellar gyrus. The radial fibers in this type of cortex branch off the white matter perpendicularly or sharply bend away. Making an arch the fibers join the surface of white matter in both directions, proximad and distad. This seems to indicate the existence of fibers connecting the minor gyral area with the proper gyral cortex as well as with the white matter in the center of the cerebellum.

The radial fibers of the minor gyral cortex are medium sized or thick. They penetrate through the granular layer close to the perikaryons of the Purkinje-cells without grouping into fascicles.

The tangential fibers are nearly all grouped at the surface of the white matter or just below the Purkinje-cells. The infragranular plexus at the surface of the white matter is very distinct. It is composed of thick fibers running usually parallel to the ridge of the gyrus, i.e., in the frontal plane. Many of these join the white matter or bend into radial fibers, while the others enter the neighboring areas of fissural or parietal cortex. The infraganglionic plexus is very well developed. It is composed of medium sized and fine fibers situated below the Purkinje-cells. These fibers continue in many places into the radial fibers, especially into the finer ones. The plexus enters between the Purkinje-cells and its fibers surround these cells. On the slope of the gyrus, among the fibers of the plexus there are some thick and medium sized fibers similar to the radial fibers.

The perikaryons of the Purkinje-cells are arranged in a single layer rather densely. On the other side of the Purkinje-cells the supraganglionic plexus is seen. It is composed of numerous fine and some thick fibers running parallel to the ridge of the gyrus. Some connections of this plexus with the infraganglionic plexus can be observed. Among the fibers of the supraganglionic plexus some small cells are found.

Within the molecular layer there are only few myelinated fibers running singly, most of them in the radial direction. The cytoarchitectonics does not differ essentially from the gyral type.

The *parietal type* of the cerebellar cortex (Fig. 3) can be found on the walls of fissures. It differs strikingly from the gyral cortex by the smaller thickness of the granular layer, which amounts, on the average, from 130 μ to 150 μ while the thickness of the molecular layer remains in this type of cortex rather unchanged, being on the average about 450 μ.

The myeloarchitectonics in this type of the cerebellar cortex differs considerably from that observed in the gyral areas. The myelinated fibers are thick, medium sized and fine. Most fibers are running tangentially or obliquely, with the radial fibers being least numerous. The white

matter of this kind of cortex is represented by the medullar lamina of a gyrus and the fibers which run within it, are parallel to the surface

Fig. 3. Parietal type of the cerebellar cortex of the dog. Semischematic, Weigert stain

of the cortex. Some of them branch off and then run nearly tangentially at a sharp angle for considerable distance. Finally they bend towards the Purkinje-cells standing about 45–60 μ apart and probably join them. The other elements are medium sized and fine fibers running among the granula in various directions. Some of them join the infraganglionic

Fig. 4. Fissural type of the cerebellar cortex of the dog. Semischematic, Weigert stain

plexus which appears less dense than that of the gyral areas. Only few of its fibers penetrate into the molecular layer. The supraganglionic plexus is well developed. It is composed of numerous fine and some thick fibers running parallel to the axis of the gyrus.

The *fissural type* of the cerebellar cortex (Fig. 4) is hidden at the bottom of the fissures. Its granular layer is strikingly thin, amounting, on the average, only to 70–120 μ, while the thickness of the molecular layer does not differ significantly from that observed in gyral or parietal type of cerebellar cortex. Consequently, the ratio between both layers appears very different in the distinguished types of the cerebellar cortex.

The myeloarchitectonics of the fissural type of the cerebellar cortex resembles somewhat that of the parietal type. The radial fibers are very few and most of the fibers run tangentially towards the neighboring portions of the cortex. Only some of them bend slightly towards the ganglionic layer of the Purkinje-cells. In the deep part of the cortex, close to the white matter, there are many thick fibers running along the bottom of the fissure.

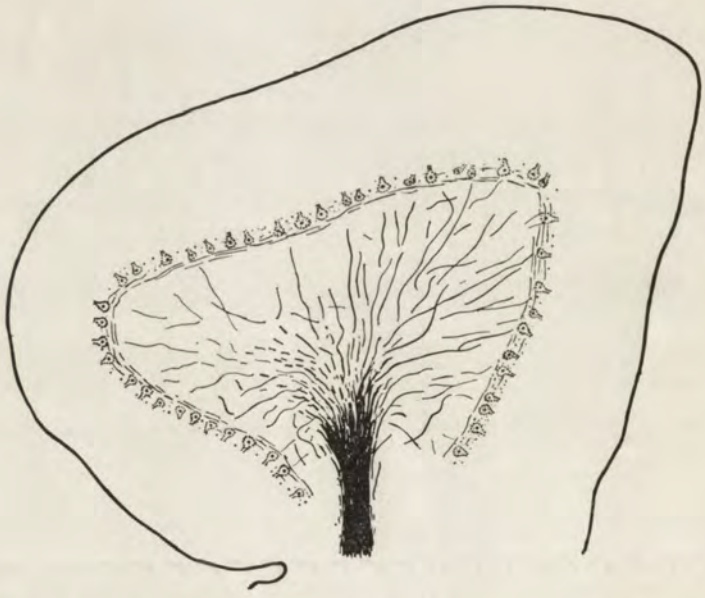

Fig. 5. Minor fissural type of the cerebellar cortex of the dog. Semischematic, Weigert stain

The infraganglionic plexus is rather poor containing only few fibers. However the supraganglionic plexus is well developed comprising many

fine and thick fibers. The perikaryons of the Purkinje-cells are present as well as in other parts of the cerebellar cortex. They are found about 50-60 μ apart. The cytoarchitectonics does not differ from the general scheme.

The *minor fissural type* of the cerebellar cortex (Fig. 5) can be found situated between two gyral areas on the top of some cerebellar gyri. In this position the minor gyral area occupies either the bottom of a very shallow furrow or a space without any morphological furrow, thus becoming a real cryptosulcus. The granular layer in this type of the cerebellar cortex is narrower than in the neighboring gyral areas and the Purkinje-cells appear less densely arranged.

The myeloarchitectonics of the minor fissural type differs considerably from the gyral areas. The number of myelinated fibers is much smaller. The radial fibers, very typical for the gyral type, are diffuse and run obliquely towards the Purkinje-cells. Some of them join the infraganglionic plexus which does not differ considerably from that of the fissural area. The medium sized and fine tangential fibers are more numerous in this area. Some of them continue into radial fibers of the gyral fields, others run parallel to the ridge of the gyrus.

The above description concerns the brain of the dog, but we have observed very similar structure in the brains of the monkey, and the rat. This seems to indicate that the described types of cerebellar cortex are present also in other mammals.

SUMMARY

Five architectonic types of the cerebellar cortex are described: the gyral type, the minor gyral type, the parietal type, the fissural type, and the minor fissural type. The types differ in myeloarchitectonics and in the ratio of thickness of the granular and the molecular layers. They are analogus to the types of cerebral cortex described previously by the author.

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MYELOARCHITECTONICS OF THE SEPTUM IN THE BRAIN OF THE DOG

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(*Received May 15, 1966*)

By the term "septum" I mean the cerebral region situated beneath the corpus callosum in the medial and, partly, medio-ventral wall of the brain hemisphere. It extends from the cortex frontalis and nucleus olfactorius anterior orally to the hippocampal commissure caudally. Laterally this region borders upon the lateral ventricle, ventrally it is bounded by the olfactory tubercle in its oral part and by the area preoptica more caudally. In literature the area of the septum has been given various denominations. I list them here as synonyms: corpus paraterminalis (Smith 1903, Goldby (1934) corpus paracommissurale (Smith 1896, 1897), area parolfactoria (Johnston 1913, Crosby 1917), pars precommissuralis septi (Herrick 1910, Hines 1923), fasciculus annularis anterior (Ziehen 1897, 1901, Retzius 1898), septum-lamina terminalis (Winkler and Potter 1911, 1914), pars precommissuralis septi + pars fimbrialis septi (Craigie 1925, Kappers 1908), septum precommissurale + septum postcommissurale (Fox 1940), and septum (Bleier 1961, Lohman 1963).

The septum consists of two parts, the area precommissuralis and the area postcommissuralis or the pars fimbrialis, which may be regarded as homologous with the septum pellucidum in the anatomy of man.

In mammals, most of the septal area is occupied by two main nuclear masses: the nucleus medialis and the nucleus lateralis. The relations of these two nuclei are in principle similar to those found in reptiles. Another fairly large nucleus, the n. tracti diagonalis Brocae, constitutes the caudo-ventral portion of the precommissural septum.

In addition to the two main nuclei, some smaller nuclear accumulations were described in the septal area of mammals. These are the nucleus septo-hippocampalis, the n. dorsalis, the n. triangularis and the n. septo-fimbrialis, which is the caudal portion of the nucleus lateralis, lying above the anterior commissure.

MATERIAL AND METHOD

Histological material from 5 dog brains fixed in formalin and alcohol was used for study. The brains were embedded in celloidin or paraffin and sectioned at 20–50 μ in the three cardinal planes. Sections were stained with cresyl violet by the Nissl method, with Luxol Fast Blue by the Klüver-Barrera and Weigert-Wolters methods and with the silver method of Landau. Observations were carried out using a magnifying glass (8–10x) to establish the general anatomical situation and under the microscope to trace in detail the myeloarchitectonic structure of the region under study. Drawings were made from frontal sections of the dog brains at a magnification of 10 times to facilitate these observations and to serve as a basis for the model of the septal nuclei.

OBSERVATIONS

The nuclei which occur in the area of the dog septum are grouped in two cords, a cord of medial nuclei and a cord of lateral nuclei.

In the first of them, I have included the nucleus septo-hippocampalis, nucleus dorsalis, nucleus medialis, nucleus tracti diagonalis Brocae and nucleus triangularis. The cord of lateral nuclei consists of the remaining nuclei of the septum, i.e., the nucleus lateralis, nucleus septo-fimbrialis, and nucleus accumbens.

The myeloarchitectonics of the septal nuclei will be presented in detail in the order established in the foregoing division.

A. Medial nuclei

1. The nucleus septo-hippocampalis (Fig. 1, 2, 7, 10, 12) is closely associated with the precommissural hippocampus, i.e. with the oral extension of the hippocampus. This nucleus lies almost in the medio-sagittal line, touching its fellow of the opposite side medio-caudally in the oro-medio-dorsal part of the septum.

The nucleus septo-hippocampalis was described as a comparatively small cellular mass by Young (1936) in the rabbit, Humphrey (1936) in the bat and Fox (1940) in the cat. Hines (1923) claims to have identified it in the human embryo.

Orally the nucleus septo-hippocampalis is closely connected with the precommissural hippocampus. Dorsally it reaches to the lateral nucleus, medially it borders with its oral part upon the rostrum corporis callosi, and more posteriorly upon its own counterpart of the opposite side. The nucleus septo-hippocampalis adjoins the lateral nucleus laterally and the large medial nucleus ventro-caudally.

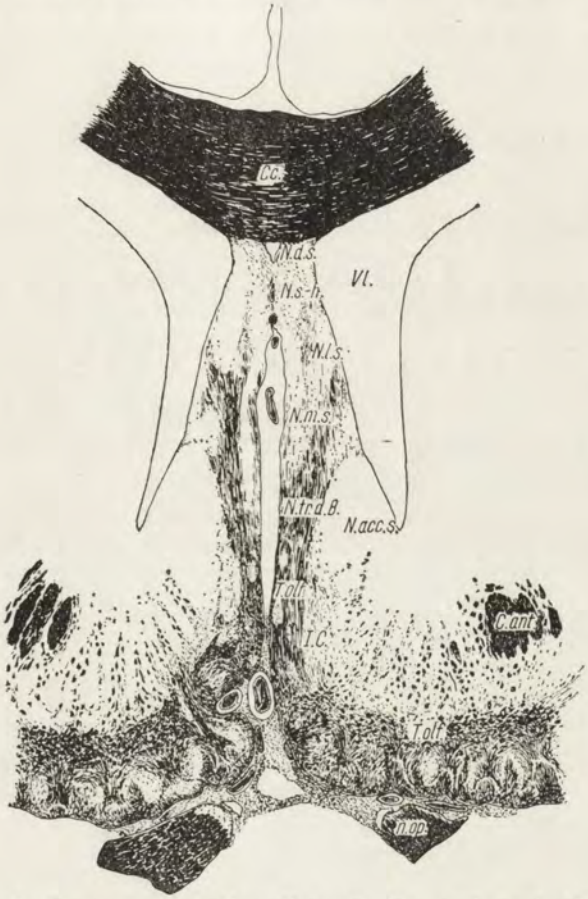

Fig. 1. Transverse section through the oral part of the septum of the dog, Weigert-Wolters preparation, sec. No. 108c. 12x.

Orally, medially and laterally the nucleus septo-hippocampalis is definitely bounded by the bundles of fibres of the fornix precommissuralis, surrounding it on these borders. In its dorsal and ventral portions this nucleus adjoins its fellow of the opposite side.

Owing to the fact that the nucleus septo-hippocampalis resembles a lens in shape, nerve fibres enclose it medially and laterally, forming a kind

of sheath. Caudally, this nucleus is not demarcated distinctly from the medial nucleus, which appears in the median line and somewhat more ventrally.

The nucleus septo-hippocampalis extends oro-caudally, its length being about 1200 μ and its dorso-ventral dimension scarcely about 200 μ. As has already been mentioned this nucleus has a lenticular shape. The equator of the lens, which has a relatively sharp margin, lies in a plane slightly oblique to the medio-sagittal plane so that the dorsal margin of the nucleus is nearer to this last plane, whereas the ventral one is shifted somewhat laterad.

Myeloarchitectonics. The inner part of the nucleus septo-hippocampalis is rather poor in fibres. Instead, the nucleus is surrounded by bundles of fibres on both the medial and the lateral side. Some, though not very numerous, of the surrounding fibres penetrate into the nucleus.

The fibres bounding the nucleus septo-hippocampalis laterally are comparatively thick and stain blue [1]. They pass oro-dorso-laterally from the caudo-ventro-medial side. In the ventral portion of the nucleus these fibres occur somewhat more densely than in the dorsal portion, where they are more scattered and arranged like a fan. Some of the fibres surrounding the nucleus septo-hippocampalis laterally enter its ventral portion and next run in the dorso-oral direction. In the dorsal part of the nucleus, they leave it and rejoin the fibres surrounding it laterally. The fibres bordering the nucleus septo-hippocampalis medially are similar in appearance to those described above. Their thickness is analogous and they also stain blue. These fibres run from the caudo-ventro-medial side in the oro-dorso-lateral direction, being more compact in the dorsal part and arranged more loosely ventrally. At both the dorsal and ventral margins of the nucleus the fibres which surround it laterally and medially join and mingle with each other.

Relatively thin, somewhat wavy and not very numerous fibres running from the caudo-dorsal and medial sides in the oro-ventro-lateral direction enter the medio-ventral portion of the nucleus septo-hippocampalis. They accumulate in the ventral part of the nucleus, but some of them pass farther laterad in the direction of the nucleus lateralis. These fibres do not form any distinct bundles and are scattered very loosely.

A well-defined system of fibres sinks into the nucleus septo-hippocampalis at its dorsal border. It extends medially to the fibres surrounding the nucleus laterally. The fibres of this system are thin, less intensely stained blue and have even border-lines. They run superficially from the caudo-medio-dorsal side in the oro-ventro-lateral direction and mingle

[1] Whenever I refer to staining in this part of the paper, I mean the Weigert staining method, unless it is stated otherwise.

with the fibres surrounding the nucleus laterally to pass to the nucleus lateralis next.

Fairly numerous thick fibres enter the caudal portion of the nucleus septo-hippocampalis at its ventral border. They are arranged more loosely, stain dark blue and have even outlines. They run oro-dorso-medially from the caudo-ventro-lateral side. In the dorsal part of the nucleus these fibres mingle with the fibres of the previous system.

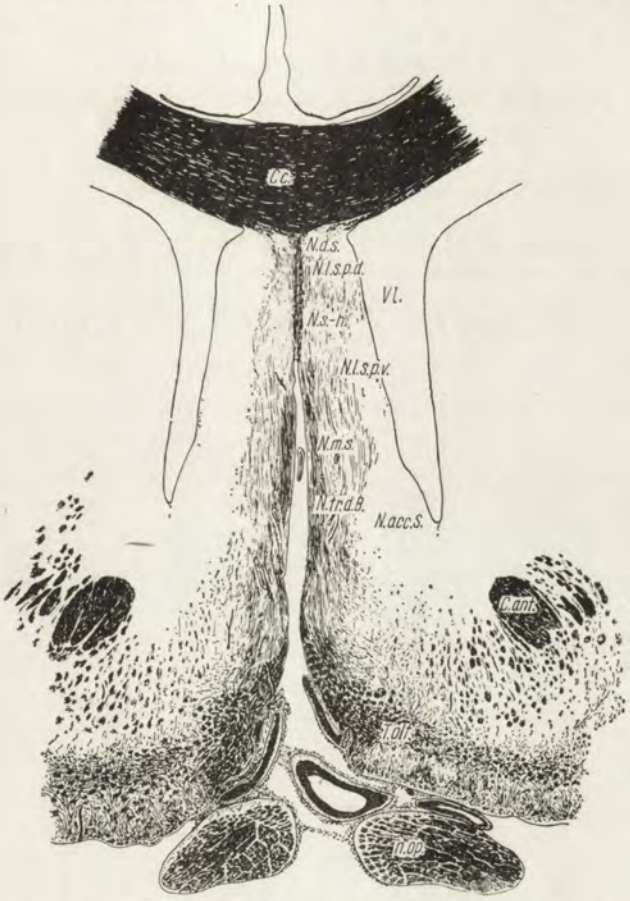

Fig. 2. Transverse section through the medial part of the septum of the dog, Weigert-Wolters preparation, sec. No. 119c
12x

Cytoarchitectonics. It has already been mentioned that the nucleus septo-hippocampalis has no well-defined boundary with the medial nucleus, situated more ventro-caudally. For nearly its whole length the nucleus septo-hippocampalis is in direct contact with the precommissural hippocampus, which lies ventro-medially to it.

Two types of cells may be distinguished in the nucleus septo-hippocampalis. The first type includes relatively large cells, which resemble those of the precommissural hippocampus in morphology. The cells of the second type are fairly well-staining and their size is about one-quarter of the size of the previous ones. The cells are for the most part round or oval in section and comparatively compactly arranged.

2. *The nucleus dorsalis septi* (Fig. 1, 2, 7, 10, 12,) is sited in the dorso-oral part of the medial nuclei group. This nucleus is relatively small, but distinctly marked among the other nuclei of the anterior part of the septum. It extends from the ventral extremity of the genu corporis callosi orally to the plane marked out somewhat posteriorly to the nucleus septo-hippocampalis. The dorsal nucleus appears dorsal and somewhat caudal to this last nucleus and, as it were, fills the gap between the ventral portion of the corpus callosum (its genu) and the dorsal portion of the lateral nucleus. Orally the dorsal nucleus is bounded by the ventral portion of the genu corporis callosi, ventrally it borders for a fairly great extent upon the nucleus septo-hippocampalis and farther upon the medial nucleus. Ventro-laterally and laterally it adjoins the nucleus lateralis and medially constitutes a part of the medial surface of the septum. On the dorsal side this nucleus neighbours upon the corpus callosum. The nucleus dorsalis is fairly well demarcated from the neighbouring nuclei by the fibres of the fornix precommissuralis, which is especially true of its caudal part.

The nucleus dorsalis has the shape of a fairly short ovoid, somewhat flattened dorso-ventrally. It extends oro-caudally for about 1900 μ. Loo (1931) wrote about the dorsal nucleus in the opossum. Andy and Stephan (1959, 1961) also described this nucleus in Galago and in the Soricidae as a large accumulation of cells in the dorsal part of the septum. In these animals, it stretches for the whole length of the septum, pushing the lateral nucleus ventro-laterally into the neighbourhood of the nucleus tracti diagonalis Brocae. The dorsal nucleus would also correspond to the nucleus septo-hippocampalis in the studies by Young (1936), Humphrey (1936) and Fox (1940). On the basis of my observations I may state that within the septum of the dog the nucleus dorsalis and the nucleus septo-hippocampalis occur as two distinct elements, independent of each other. They occupy the medio-oro-dorsal portion of the septum. It should be emphasized that the dorsal nucleus of the dog has a dorso-medial position and not a lateral one as in Galago or shrews, for in the dog it borders laterally upon the lateral nucleus, which farther caudally takes its place.

Myeloarchitectonics. Myeloarchitectonic observations show that the nucleus dorsalis, like the nucleus septo-hippocampalis, is an area

fairly poor in fibres, but it is bordered by bundles of fibres, which form as if a "sheath", particularly distinct in the central and caudal regions of the nucleus. At least two systems of fibres may be distinguished in the area of the dorsal nucleus.

The first system is made up of relatively thick fibres, loosely arranged and stained dark blue, with even outlines. The fibres of this system run obliquely from the dorso-caudo-medial side and tend oro-ventro-laterad. This system extends more or less uniformly throughout the area of the oral portion of the nucleus dorsalis and in the caudal region of this nucleus its fibres accumulate in the ventro- and dorso-medial portions. It is rather a system of passage and only a small number of its fibres end in the dorsal nucleus. A clear majority of the fibres reach the dorso-medial part of the lateral nucleus, where they scatter. The system under description joins the fibres of the fornix precommissuralis, which pass dorsally to the nucleus dorsalis. The fibres run parasagittally, diverge ventro-medially and reach to the medial surface of the septum.

The second system, also loosely arranged, consists of thick fibres, which stain dark blue. They pass oro-ventro-medially from the dorso-caudo-lateral side. Part of them run in the opposite direction. As in the previous system, the fibres are relatively uniformly dispersed in the oral portion of the nucleus dorsalis. Approximately at half the length of the nucleus the fibres of this system accumulate on the medial side and farther caudally they scatter uniformly again. Like the first system, this system is transitory and loses anly few fibres in the area of the nucleus dorsalis. Most of the fibres tend evntrad to the nucleus medialis.

Cytoarchitectonics. As regards cytoarchitectonics, the nucleus dorsalis resembles the lateral nucleus. The cells of which this nucleus is made up are fairly small, averaging about 8 μ in diameter. They are comparatively compactly arranged (which results in the formation of a kind of fibrous sheath enclosing the nucleus) and contain relatively faintly stained protoplasm with a fairly distinct and rather transducent cellular nucleus. These cells are mostly globular or ovoid in shape.

3. The nucleus medialis (Fig. 1–3, 7, 9, 12) is a large formation within the medial nuclei of the septum (Young 1936, Humphrey 1936, Fox 1940, Andy and Stephan 1959, 1961; Bleier 1961, and others). Its oro-caudal dimension is about 4900 μ.

Orally, the nucleus medialis lies ventrally to the caudal portion of the nucleus septo-hippocampalis, that is, it appears slightly posterior to the genu corporis callosi. A little more caudally the nucleus medialis takes the place of the nucleus septo-hippocampalis and expands dorsad. As a result it becomes a neighbour of the dorsal nucleus. Laterally and dorso-laterally the medial nucleus borders for its whole length — with

the exception of the oral portion, which adjoins the dorsal nucleus — upon the lateral nucleus. Ventro-laterally it is contiguous to the nucleus accumbens and medially its oral portion is bounded by the facies medialis septi. On the ventro-caudal side the medial nucleus touches the nucleus tracti diagonalis Brocae. More caudally, as this last nucleus increases in size, the medial nucleus becomes displaced farther laterad. In consequence, the nucleus tracti diagonalis Brocae is situated medio-ventro-caudally to the medial nucleus, which extends caudally up to the anterior commissure.

Fig. 3. Transverse section through the septum and the oralmost part of the area preoptica of the dog, Weigert-Wolters preparation, sec. No. 131a, 12x

The nucleus medialis is fairly well demarcated from the nucleus septo-hippocampalis by the fibres of the fornix precommissuralis. The boundary of the nucleus medialis with the lateral nucleus is rather indistinct and

fluid and so is its boundary with the nucleus tracti diagonalis Brocae. Some authors, e.g., F o x and B l e i e r, assume that the so-called magnocellular portion of the nucleus medialis belongs to the nucleus tracti diagonalis Brocae. Basing myself on my own observations, I also lean to the opinion of these authors (the division of the nucleus medialis into the parvicellular anterior part and the magnocellular posterior part

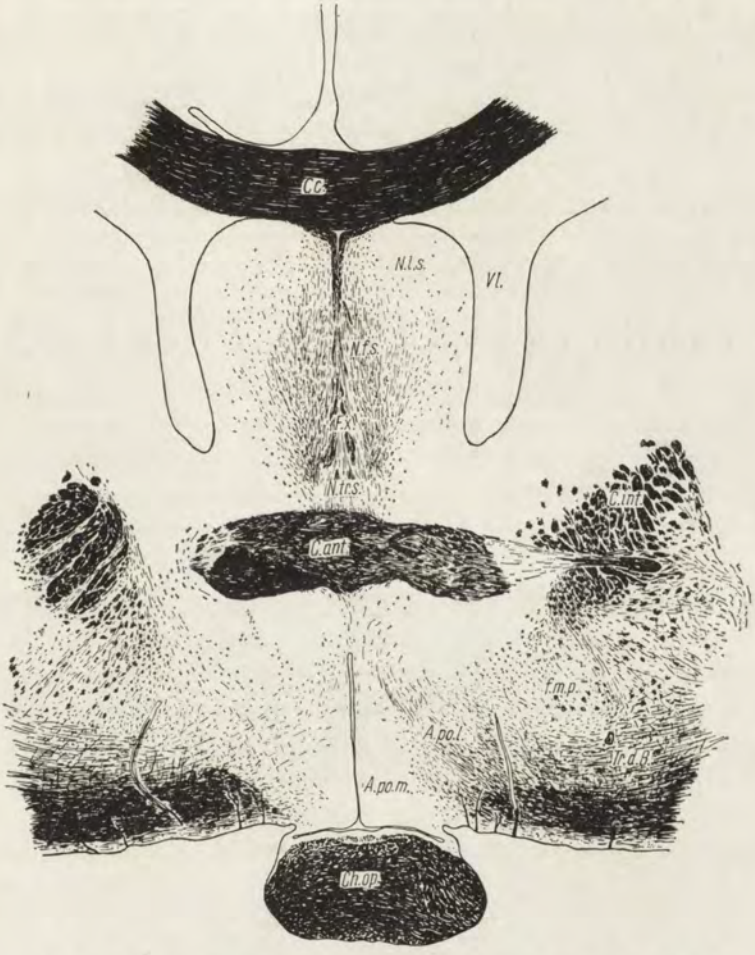

Fig. 4. Transverse section through the septum of the dog at the level of the arcus commissure anterioris and of the area preoptica, Weigert-Wolters preparation, sec. No. 141c, 12x

has been introduced by L o o (1931) on the basis of his observations on the septum of the didelphid). In the face of the foregoing, the nucleus medialis of the dog consists only of the parvicellular part.

The nucleus medialis has the shape of an irregular mass, which in general outlines resembles a prism. This mass is turned with its base, lying in the frontal plane, to the oral side. The caudal pole of the prism is truncated and fairly gently rounded. In the orodorsal part of the base there is a fairly distinct depression, in which the nucleus septo-hippocampalis rests. The axis of the medial nucleus is somewhat oblique to the sagittal plane of the brain, from which it departs laterally on the ventral side. This lateral deviation of the nucleus is caused 1° by the expansion of the nucleus tractus diagonalis Brocae in the medio-dorsal direction, and 2° by the there running bundle of fibres, which belongs to the fornix superior (situated on the medial side of the septum) and tends to the nucleus tracti diagonalis Brocae.

Myeloarchitectonics. In respect of myeloarchitectonics the area of the nucleus me dialis is fairly rich. Consequently, I managed to trace several basic systems of fibres in it.

The first of these systems passes in the dorso-oral and lateral directions beneath the corpus callosum. It consists of fairly thick fibres with even border-lines, stained dark blue. The system is, as a rule, loosely arranged, being somewhat denser on the lateral side of the medial nucleus. It spreads in the dorso-lateral portion of the nucleus, where it runs among the cells, which are arranged in unobtrusively marked bands.

The fibres of this system for the most part disappear within the medial nucleus, but part of them reach the dorsal portion of the nucleus tractus diagonalis Brocae, which closely adjoins the medial nucleus.

The system is more pronounced in the oral portion of the nucleus medialis than in its caudal regions. The situation presented above is similar to those described by Crosby (1917) in the alligator, Loo (1931) in the opossum and Johnson (1957) in the mole. These authors are of the opinion that this is an efferent projection from the oro-dorsal portion of the medial nucleus to the hippocampus.

The second system of fibres distinguished in the medial nucleus is included in the group of dorsal systems of this nucleus. The fibres of this system come from the fornix superior and penetrate into the medial nucleus at its dorso-medio-caudal border to pass ventro-oro-laterally next. Within the medial nucleus they scatter and together with a delicate "grundfasern" network form a kind of baskets round the nerve cells. This system, like the previous one, consists of fairly thick fibres, which stain very dark blue and have mostly even outlines, though there are also some undulate fibres among them. The arrangement of the fibres is also rather loose, the density of the system being somewhat greater on the medial and lateral sides of the nucleus. More laterally, part of the fibres

of this system leave the medial nucleus and enter the medial portion of the nucleus lateralis.

The third system, which penetrates into the oro-dorsal portion of the nucleus medialis from the medial side, is not so clearly visible. It is made up of fibres which for the most part run just below the nucleus septo-hippocampalis and partly also pass through its ventral portion. The fibres

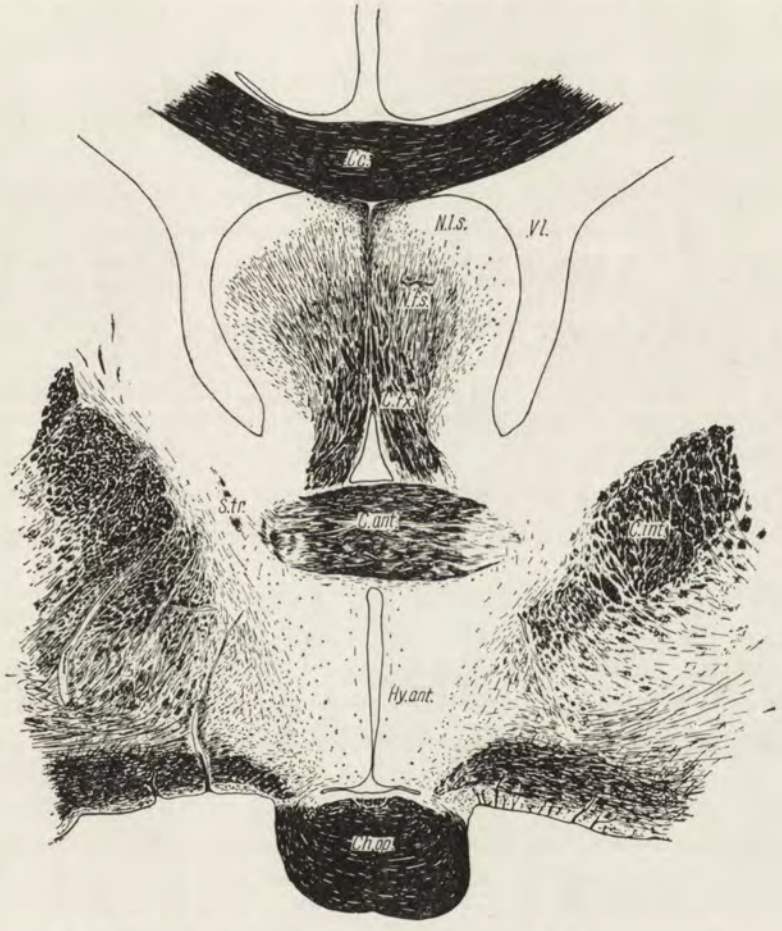

Fig. 5. Transverse section through the pars postcommissuralis septi of the dog, Weigert-Wolters preparation, sec. No. 146a, 12x

of this system come from the stria medialis Lancisii and run from the oro-medial side in the ventro-caudal direction. They mostly end in the oro-medial portion of the nucleus medialis, among the cells and the fibres of the systems described above. A small part of the system of fibres

coming from the stria medialis Lancisii traverses the nucleus medialis and goes on laterad towards the medial portion of the nucleus lateralis. The fibres of this system are very loosely distributed and thin (they are about half the thickness of the fibres in the previous systems). They stain pale blue and have a slightly wavy course. Right below the genu corporis callosi they come into contact with the stria medialis Lancisii, being its projection to the nucleus medialis and also, indirectly, to the nucleus lateralis.

The system of fibres arising from the tuberculum olfactorium and extending from the oro-ventro-lateral side in the dorso-medio-caudal direction belongs to the group of ventral systems of the medial nucleus. This system is composed of two types of fibres, medium-sized fibres stained dark blue and having even outlines and thin ones, stained pale blue and also with even and sharply marked border-lines. The system is relatively loose. It runs on the lateral side of the tractus diagonalis Brocae and reaches the oro-ventro-lateral portion of the medial nucleus. Upon entering the nucleus, the fibres scatter to form a kind of delicate fan nearly all over its area. This is the system of fibres of the tractus tuberculo-septalis; it connects the polymorphic layer of the tuberculum olfactorium with the nucleus medialis and has been described by different authors in various mammals.

In addition, fairly loosely arranged fibres, which stain dark blue and run dorso-caudally from the oro-ventral and medial directions, reach the nucleus medialis at the oro-ventro-medial border. These fibres scatter and terminate in the medio-ventral portion of the medial nucleus. They most likely belong to the tractus olfactorius medialis.

As I have already mentioned, the nucleus medialis is closely associated with the nucleus tracti diagonalis Brocae, having a ventro-medial position. These nuclei are connected by relatively thin fibres, staining pale blue and scattered nearly throughout the depth of the nucleus medialis without forming a distinct system. Owing to this the nucleus medialis has an actual connection with the cellular elements of the nucleus tracti diagonalis Brocae and through these, indirectly, also with the fibres of the medial forebrain bundle.

Moreover, fairly thick fibres, loosely arranged and stained very dark blue, pass through the nucleus medialis tending to the nucleus tractus diagonalis Brocae. They are directed oro-ventrally and grouped rather on the medial side of the nucleus medialis. In all probability, they are fibres of the fornix precommissuralis and only travers the nucleus medialis on their way to the nucleus tracti diagonalis Brocae.

I should also mention a comparatively poorly marked system of fibres, which are very loosely arranged and come from the dorso-caudo-lateral

side. It is composed of thin and medium-sized fibres, staining dark blue. These fibres emerge from under the corpus callosum, enter the septum and reach the ventro-lateral and central portions of the medial nucleus. They seem to join the stratum subcallosum vel tapetum.

I also managed to ascertain the existence of a delicate texture of the "grundfasern" type in the nucleus medialis.

Cytoarchitectonics. As far as cellular structure is concerned, the medial nucleus consists of comparatively large cells, the diameter of which amounts on the average to about 11 μ. These cells are mostly oval or pyriform, with the fairly intensely stained protoplasm and a distinct nucleus and nucleolus. The cells of the nucleus medialis are disposed uniformly throughout its area and have a tendency to be arranged so that their long axes are directed dorso-ventrally. They resemble the cells occurring in the lateral nucleus only that their protoplasm stains more intensely and they exceed these last cells in size.

4. *The nucleus tracti diagonalis Brocae* (Fig. 1–4, 12) is an accumulation of grey matter connected with the bundles of nerve fibres termed the tractus diagonalis. The term "nucleus et tractus diagonalis" has been introduced into the neuroanatomical nomenclature by Broca in his work "Studies on the olfactory centres", Rev. d'Anthr., 1879 (after Young). The term was not practically used for a long time, until Johnston (1915) and Crosby (1917) applied it again in their neuroanatomical papers.

The tractus diagonalis Brocae is also referred to as the fasciculus olfactorius hippocampi, fasciculus septo-amygdalicus and fasciculus substantiae perforatae anterioris (after Gastaut and Lammers 1961). It is included in the group of pathways of the base of the rhinencephalon, and its nucleus, lying for the most part in the septum, is numbered in the cord of medial nuclei of the septum. In this last group it is distinguished for its large size and characteristic shape. It is a large magnocellular nucleus, lying against the medial surface of the septum and the medio-basal surface of the hemisphere. It borders the anterior commissure anteriorly, runs in the proximity of the medio-sagittal plane of the brain and swings latero-caudally and somewhat laterally below the anterior comissure.

Some authors, as Young (1936), Andy and Stephan (1959, 1961) and others, divide the nucleus tractus diagonalis Brocae into a dorsal part and a ventral part. As a plane of division they assume the plane which passes horizontally through the anterior comissure.

The dorsal part of the nucleus tracti diagonalis Brocae is placed in the septum. It occupies nearly the whole lower half of the septum and extends from the taenia tecta orally to the anterior commissure caudally. Oro-

dorsally it borders upon the ventral portion of the medial nucleus. Besides. the nucleus tracti diagonalis Brocae is bounded laterally by the medial and lateral nuclei and the nucleus accumbens and medially its dorsal portion is contiguous across the median line to the same portion of its follow of the opposite side. It thus presents a picture resembling an isosceles triangle in frontal sections. Just posterior to the dorsal portion of the nucleus tracti diagonalis Brocae is the anterior commissure with its bed nuclens.

Fig. 6. Transverse section through the caudalmost part of the septum of the dog, Weigert-Wolters preparation, sec. No. 150c, 12x

Beneath the plane of division (the horizontal plane passing through the anterior commissure) the nucleus tracti diagonalis Brocae is represented by its ventral part. This part spreads ventrally along the ventral surface of the hemisphere (the base of the hypothalamus). Partly it also passes through the fasciculus medialis prosencephali and next, laterally

and caudally, merges with the tuberculum olfactorium and globus pallidus, which is situated more dorsally.

The nucleus tracti diagonalis Brocae extends in the sagittal plane for about 5400 μ and is second to none but the lateral nucleus in size in the septum.

Generally speaking, the nucleus tracti diagonalis Brocae of the dog is like a boomerang with an additional arm. The broadest surface of the upper arm of this "boomerang" is almost vertical and lies in the sagittal plane, whereas the lower arm deflects latero-caudo-ventrally from the medio-sagittal plane. At the junction of these two arms there is a band of cells in the form of a stalk, which is the third arm of the "boomerang" and extends orally as far as the taenia tecta. Here it squeezes in between the taenia anterior and the tuberculum olfactorium as well as the regio retrobulbaris. This additional (third) arm belongs to the ventral part of the nucleus tracti diagonalis Brocae. The upper arm, which constitutes the dorsal part of the nucleus, is shorter than the lower arm, corresponding to the ventral part.

The shallow arch of the "boomerang" opens to the rear, i. e., towards the anterior commissure. The foregoing picture agrees with the description of this region given by Filimonov (1949), among other animals, for the dog.

The nucleus tracti diagonalis Brocae of the dog passes rather fluently into the surrounding formations so that its only sharp delimitation is the medio-basal surface of the cerebral hemisphere. A large island of Calleja adjoins the nucleus closely in the oro-latero-ventral region. It separates this nucleus, but not for its whole length, from the nucleus accumbens. The lateral portion of the nucleus tracti diagonalis Brocae is not very well demarcated from the nucleus medialis and nucleus lateralis; in this last case the demarcation line is formed by somewhat more compact fibres, which belong to the lateral nucleus (most of these fibres run in the ventral direction to the fasciculus medialis prosencephali). Ventrally the nucleus tracti diagonalis Brocae is bordered by the tuberculum olfactorium, which next, nearer to the anterior commissure, is replaced by this nucleus. The caudo-lateral boundary of the nucleus tracti diagonalis Brocae, which in this region lies in the area preoptica lateralis and anterior hypothalamus, is very vague and, in consequence, it is hard to determine its demarcation line exactly.

Myeloarchitectonics. Myeloarchitectonically, the nucleus tracti diagonalis Brocae is a rich area. Strongly myelinated fibres which run through this nucleus present themselves as a very compact bundle of relatively large size. This bundle passes through the septum tending to the subcortical nuclei and hypothalamus. The fibres of the diagonal tract

belong to the fornix precommissuralis and therefore they take rise in the hippocampus (they emerge from the commissura fornicis ventralis). This agrees with the views held by such authors as Young (1936), Fox (1940), Ramon y Cajal (1911) and Zeman and Innes (1963).

Within the nucleus the fibres have an unvariable arrangement. On its medial side there occurs a comparatively narrow bundle of fairly loosely arranged fibres, which constitutes a kind of marginal zone of the main bundle of very compact fibres running through the central and lateral parts of the nucleus tracti diagonalis Brocae. Similarly, another bundle of looser fibres can be seen on the lateral side of the nucleus.

In the dorsal portion of the nucleus, above the anterior commissure, the fibres run from the dorso-caudal side in the oro-ventral direction. They skirt the anterior commissure orally, forming an arch opened towards the commissure, turn laterally in relation to the medio-sagittal plane in the ventral portion of the nucleus tracti diagonalis Brocae, and run farther caudo-latero-ventrally.

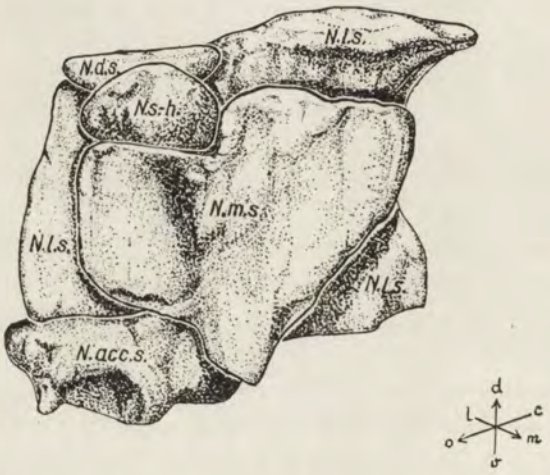

Fig. 7. Mutual relations of the nuclei of the septum of the dog visible from the oro-medial side. Wax-model reconstruction, 10x

The fibres which make up the tractus diagonalis arise partly in this very nucleus and partly in the hippocampus. It is difficult to determine on the basis of Weigert sections which of them are hippocampal fibres and which come from the cells of the nucleus tracti diagonalis Brocae. Fox, too, emphasizes that it is not possible in all cases to distinguish the fibres of passage from those connected with the septum by synapses.

Nevertheless, I attempted to solve this problem, basing on the observations made with silver preparations. These preparations reveal that in all probability the fibres coming to the nucleus tracti diagonalis Brocae from the hippocampus form synaptic connections with the cells of this nucleus or send off collaterals to its neurons.

The fibres of the diagonal tract vary in size, stainability and outlines. At least three types of fibres may be distinguished in respect of these qualities. Type I includes thick fibres, which are stained very dark blue with somewhat lighter margins and have relatively even — only sometimes distinctly wavy — outlines. Fibres of type II are of medium size, somewhat paler (bluish) in coloration, rather lighter in the region of the long axis and with even outlines. Type III is represented by thin fibres, staining pale blue and having smooth outlines.

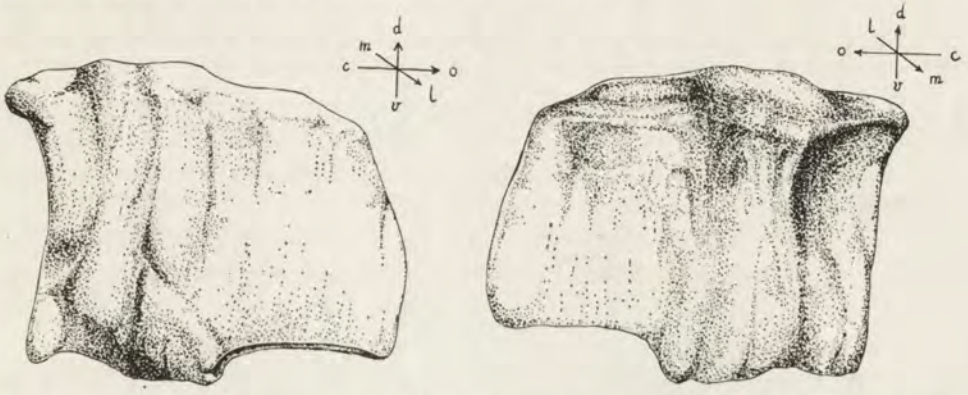

Fig. 8. Wax-model reconstruction of the nucleus lateralis septi of the dog, lateral (left) and medial (right) view, 10x

As has already been mentioned, the fibres of the medial portion of the diagonal tract are loosely arranged within its nucleus (marginal zone). They are mostly of type II, with an admixture of type III fibres, their course being rather short. The middle and lateral parts of the tractus diagonalis are compact and consist of a fairly large number of fibres of type I, which run for the nearly whole extent of the nucleus tractus diagonalis. Fibres of types II and III are also abundant here. In the lateral portion of the nucleus tracti diagonalis Brocae, which neighbours upon the nucleus lateralis, there are almost exclusively fibres of types II and III. In the dorsal portion the fibres extend in the sagittal plane. The abundance of fibres observed in this nucleus causes that its cells assume a rather zonular arrangement and are contained in "baskets" formed by these fibres. In the ventral portion the relations between the fibres and the cells are somewhat looser.

Most fibres of the tractus diagonalis emerge from the ventral portion of the psalterium. They run through the upper part of the septum in its median plane and then pass ventro-laterally to enter the nucleus tracti diagonalis Brocae. Here some of these fibres have connections with the neurons of this nucleus and the others, joined by fibres from the neurons of the tractus diagonalis and thus increasing in number, pass through the nucleus. They run farther in front of the anterior commissure, swing caudally and latero-ventrally under it, and in the end reach the ventral surface of the brain. Then this tract passes superficially through the posterior portion of the tuberculum olfactorium, to which it gives some of its fibres. In the same region the tractus diagonalis is traced through the ventral portion of the fasciculus medialis prosencephali, where some of its fibres terminate. Next it extends towards the lateral wall of the hemisphere and reaches the area prepyriformis and area preamygdaloidea.

This tract has also connections with the ventral extension of the globus pallidus and with the nucleus accumbens and area preoptica.

Cytoarchitectonics. The nucleus tracti diagonalis Brocae is composed of medium-sized, oval and irregular cells with an average diameter of 5–7 μ and a large number of large oval, triangular and fusiform cells ranging from 10 μ to 14 μ in diameter.

The medium-sized cells stain well with the Nissl or Klüver technique, their cytoplasm being rather light with a distinct nucleus and nucleolus. The large cells show a great stainability and have an evident perinuclear limbus as well as a large number of Nissl bodies in their cytoplasm.

The cells of the nucleus tracti diagonalis Brocae, especially the large ones, are furnished with distinct axons, which run more or less in the sagittal plane.

The cell bodies of this nucleus are arranged in a "stream", the breadth of which corresponds to the breadth of the tractus diagonalis. In the lateral and paramedial portions of the nucleus there are mostly medium-sized cells with a small admixture of large ones, whereas very numerous large cells occur in the central part.

On account of the large number of fibres the cells have rather a zonular arrangement with a sagittal course. On the ventral surface of the brain, in the ventral portion of the nucleus tracti diagonalis Brocae the large cells tend to accumulate in its lateral regions. A certain division of the cells can be seen in the region of the fasciculus medialis prosencephali, where part of them spread in the direction of the pyriform lobe and area anterior amygdalae and the others extend dorsally towards the globus pallidus.

Johnston (1923) and Young (1936) observed a similar arrangement of cells in the ventral part of the nucleus tractus diagonalis Brocae.

5. *The nucleus triangularis* (Fig. 4, 10, 12), or the supracommissural part of the nucleus periventricularis anterior, is the smallest of the nuclei of the medial cord and also of all the nuclei of the septum. This nucleus was denominated by Ramon y Cajal (1911) on account of its fairly distinctive shape and considered by that author to be an accumulation of cells of the bed nucleus of the hippocampal commissure. Humphrey (1936) also regards the triangular nucleus as belonging to the hippocampal commissure (in the bat). Loo (1931), Young (1936) and Fox (1940) hold similar opinions.

Bleier (1961), who describes the cat hypothalamus in detail, disagrees with the above-mentioned authors as to the membership of the triangular nucleus. She states that the nucleus described by Ramon y Cajal, Humphrey, Loo, Young, and Fox as the triangular nucleus of the septum, being an accumulation of grey matter placed in the medio-sagittal plane dorsally to the anterior commissure, is a part of the nucleus periventricularis anterior. She supports her opinion by the fact that there are obvious connections between this accumulation of grey matter and the nucleus periventricularis anterior seen in medio-sagittal sections through the cat hypothalamus. For this reason she did not think fit to use the term "nucleus triangularis".

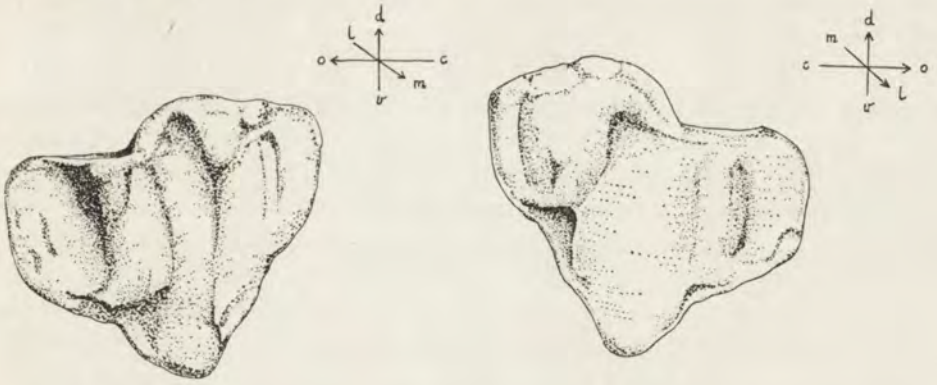

Fig. 9. Wax-model reconstruction of the nucleus medialis septi of the dog, medial (left) and lateral (right) views, 10x

My observations seem to confirm Bleier's opinion, for the precommissural part of the nucleus periventricularis anterior, corresponding to the triangular nucleus of Ramon y Cajal, Fox or Humphrey, very closely resembles the nucleus periventricularis anterior in its cyto- and myeloarchitectonic structure, which is a fairly conclusive evidence for its belonging to this nucleus. Both these anatomic formations

are composed of the same cellular elements and very similar fibres, which are almost the same size and have a similar arrangement and course.

The nucleus triangularis lies dorsal to the anterior commissure, between the columnae fornicis descendentis, which bound this nucleus dorsally and on both sides. Orally it borders upon the nucleus tractus diagonalis Brocae and the lumen of the third ventricle opens just caudal to it.

In shape the triangular nucleus resembles a pyramid, the base of which rests on the dorsal surface of the anterior commissure. The posterior wall of the pyramid lies in the frontal plane which at the same time limits the third ventricle anteriorly. The two other walls meet orally at an acute angle and show a slight depression to the inside of the nucleus.

The oro-caudal extent of the triangular nucleus, which as has already been mentioned, is the smallest of all the septal nuclei, does not exceed 100 μ. This nucleus can be seen in only a few sections of the frontal series.

In the oral portion of the nucleus and just anteriorly to it there are relatively numerous loops of capillaries. This picture resembles the situation observed in the area preoptica, which also rather corroborates both Bleier's and my view that the triangular nucleus belongs to the nucleus periventricularis anterior.

Myeloarchitectonics. A myeloarchitectonic examination shows that the nucleus triangularis, as I shall call this nucleus not to raise more confusion in the terminology, is not very rich either in nerve fibres or in systems that may be distinguished in it.

The first system observed in this nucleus is made up of both thicker and thinner fibres, which stain blue fairly intensely. It is comparatively very loose and its fibres pass from the dorso-caudo-medial side in the oro-ventral direction, some of them swinging laterally just close to the anterior commissure in the lateral regions of the nucleus. The thicker fibres of this system are arranged more densely in the lateral portion of the triangular nucleus and come into contact with the columnae fornicis descendentis, owing to which the central portion of the nucleus is rather devoid of fibres of this type. These fibres disappear dorsally among the fibres belonging to the fornix precommissuralis, whereas ventrally they run in front of the anterior commissure and enter the nucleus periventricularis anterior.

The thinner fibres of this system are grouped in the central part of the nucleus their course being, as a rule, the same as given above for the thicker fibres.

The cells of the nucleus triangularis accumulate rather centrally and are arranged in vertical bands entwined by thin fibres that has just been discussed.

The other system traced in this nucleus is poorly marked and penetrates its basal portion. It consists of relatively thin fibres, which are not very numerous and stain very pale blue. These fibres run oro-ventro-caudally, sloping at rather an acute angle to the horizontal plane. Laterally they touch the bed nucleus of the stria terminalis and medially enter the nucleus triangularis to scatter in its basal portion.

The nucleus triangularis also comes into close contact with the bed nucleus of the anterior commissure, which neighbours upon it ventrally and ventro-laterally. Comparatively small numbers of very thin and fairly darkly stained fibres from this nucleus penetrate into the basal portion of the triangular nucleus. In frontal sections the course of these fibres is nearly parallel to the surface of the anterior commissure.

Cytoarchitectonics. As regards cytoarchitectonics, the nucleus triangularis is composed of fairly small cells, round and oval in section. They are relatively compactly arranged and on account of their fairly darkly stained cytoplasm form a uniform mass having the characteristic shape of a triangle in frontal sections.

In size and shape as well as in stainability of the cytoplasm the cells of the triangular nucleus are similar to those of the nucleus periventricularis anterior, which also lies in the medio-sagittal plane and extends in the form of a fairly compact band from the ventral surface of the anterior commissure to the top of the recessus supraopticus.

B. Lateral nuclei

Now I shall discuss the nuclei of the lateral cord, which includes two further nuclei of the septum, that is, the nucleus lateralis, the largest in the septum, and the nucleus fimbrialis (nucleus accumbens, vide Miodoński 1962).

6. The nucleus lateralis (Fig. 1–8, 12), being the largest of all the nuclei of the septum, belongs to the group of lateral nuclei. Because of its large size it was described by all the authors who investigated this region of the brain, i.e., by Crosby (1917), Young (1936), Loo (1931), Fox (1940), Johnson (1957, 1959), Andy and Stephan (1959, 1961), Herrick (1910) and Kappers (1908).

Orally the lateral nucleus appears laterally and somewhat dorsally to the nucleus septo-hippocampalis, at the level of the posterior part of the genu corporis callosi. Caudally it enlarges both dorso-ventrally and to the sides.

The lateral nucleus, together with the nucleus accumbens, borders the anterior corner of the lateral ventricle medially. Its oral portion is bounded by the nucleus septo-hippocampalis medially, the nucleus accumbens ventrally, the lateral ventricle laterally and the dorsal nucleus dorsally.

More caudally the lateral nucleus adjoins the medial nucleus medially — it forms an arch surrounding the medial nucleus dorsally and laterally — and the nucleus tracti diagonalis Brocae medioventrally. Ventrally it borders upon the nucleus accumbens and laterally, for its whole length, upon the lateral ventricle.

At the level of the anterior commissure the lateral nucleus is displaced still more laterally and somewhat dorsally by the columnae fornicis descendentis and the nucleus fimbrialis, which appears in this place.

The lateral nucleus is clearly demarcated from the nucleus septo-hippocampalis and nucleus dorsalis. Relatively well marked is also the boundary of this nucleus with the nucleus accumbens, situated ventrally to it and rather similar in its architectonics. These nuclei are separated from each other by a small depression, termed the sulcus limitans, in the surface bounding the lateral ventricle. The boundary of the lateral nucleus with the medial nucleus is the least distinct, whereas it is fairly well defined between its caudal portion and the nucleus fimbrialis at the level of the anterior commissure and farther to the rear.

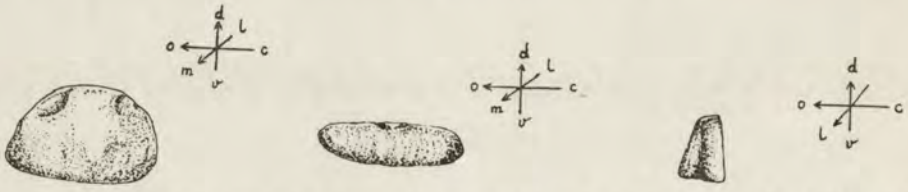

Fig. 10. Wax-model reconstructions of the nuclei: septo-hippocampalis (left) medial view, dorsalis septi (middle), medial view, triangularis septi (right) oro-lateral view, in the septum of the dog, 10x

On the basis of his observations on the structure of the septum in the opossum Loo (1931) divided the lateral nucleus into two parts, a dorsal and a ventral. Humphrey (1936) and Fox (1940), who studied this nucleus in the bat and cat, do not, however, accept this division because of the lack of any clear morphological differentiation. Other authors, e.g., Andy and Stephan (1959, 1961), who dealt with the same nucleus in Galago and the Soricidae, divided it into an external and an internal part.

I incline to Loo's opinion, since my observations show some differences in the myeloarchitectonic structure of this nucleus in the dog,

namely, its dorsal part is not so rich in fibres as the ventral part. These two parts also differ to some extent in their cytoarchitectonics.

The oro-caudal dimension of the nucleus lateralis reaches about 8200 μ. Oralmost this nucleus appears as a relatively narrow band of grey matter, squeezed in between the nucleus accumbens (situated ventrally), nucleus septo-hippocampalis and nucleus medialis on one side and the nucleus dorsalis (dorsally) and the lateral ventricle on the other side. More caudally the lateral nucleus increases rapidly both in width and in height.

In the plane lying just posterior to the dorsal nucleus the lateral nucleus forms a broad band, which in its dorsal portion is arcuately bent mediad over the medial nucleus. As a result, it fills up the whole dorsal and lateral part of the septum. The lateral nuclei of both sides of the brain adjoin each other along the median line in their dorso-medial portions, where they are separated only by the fibres of the fornix precommissuralis.

Generally speaking, the lateral nucleus resembles a broad and thick band, somewhat narrower in the oral portion and broadening caudally. As has already been said, the dorso-medial portion of this band is arched mediad in the form of a knee over the medial nucleus. Caudally, at the level of the anterior commissure and more posteriorly only the dorso-medial portion of the lateral nucleus can be seen in sections. It extends above the nucleus fimbrialis and finally ends somewhat anteriorly to the plane passing through the foramina interventricularis.

Myeloarchitectonics. A study of myelin sections shows the occurrence of some quantitative differences within the nucleus lateralis. The dorso-lateral portion, arched over the medial nucleus, is poorer in fibres than the ventral portion. I have also distinguished several systems of fibres and a delicate "grundfasern" network in the lateral nucleus.

The first system of fibres comes to the lateral nucleus from the dorso-medio-caudal side and runs farther in the oro-ventro-lateral direction. It comes from the medial nucleus and sinks into the medial portion of the lateral nucleus, which neighbours upon the medial. This is a very loose system composed of fairly thick fibres, which stain dark blue and have even outlines. It enters the nucleus lateralis rather caudally, i.e., just posteriorly to the plane passing through the dorsal nucleus.

The fibres of this system belong to the fornix precommissuralis. They scatter among the cells of the central region of the lateral nucleus and do not reach the ventricular surface of this nucleus.

The second system, which is much less pronounced, penetrates from the medial side into the oral portion of the nucleus lateralis and also into its ventral part. The fibres of this system run from the medio-oral

side in the ventro-caudal direction, coming to the lateral nucleus, similarly to those of the previous system, from the medial nucleus. They are thin and very loosely arranged fibres, staining pale blue and with slightly wavy outlines. These fibres disappear in the medio-ventral portion of the nucleus lateralis. They take rise from the stria medialis Lancisii and come here via the nucleus medialis.

The third system of fibres enters the nucleus lateralis from the caudo-dorsal and somewhat lateral side and passes oro-ventro-medially. This loose system consists of thick fibres, which have even outlines and stain dark blue, and of lighter and thinner, slightly undulating fibres. It ends in the dorsal part of the lateral nucleus, but partly also passes to its ventral part. In the medial portion of the ventral part of the lateral nucleus the fibres of this system mingle with those of the system described as the first. More caudally a part of this system runs on to the nucleus medialis.

Fig. 11. Wax-model reconstruction of the nucleus fimbrialis septi of the dog, frontal (left) and oro--lateral (right) views, 10x

Ventrally the lateral nucleus neighbours upon the nucleus accumbens; these two nuclei are separated from each other by the large island of Calleja orally, and farther to the rear by a delicate network surrounding the nucleus accumbens. A relatively small number of fine pale fibres with wavy outlines penetrate from the ventral part of the nucleus lateralis to the nucleus accumbens through this network. They are fibres connecting the lateral nucleus with the nucleus accumbens, described also by Fox (1940) in the cat and Johnson (1957) in the mole.

Most of the fibres grouped in the ventral part of the lateral nucleus run out of it in the ventro-medial direction and surround the nucleus accumbens dorso-medially and medially. Fox (1940) observed an identical situation in the cat. Several systems may be traced among these fibres. These systems are more or less clearly marked in spite of a great accumulation of fibres, which lie closely side by side.

One of the systems is composed of medium-sized fibres, which are stained relatively dark blue. It runs in the oro-ventral direction from the ventro-lateral part of the lateral nucleus and tends to the deep layers of the olfactory tubercle, i.e., to its polymorphic layer, where it terminates. It is the septo-tubercular system, described also by Fox (1940) in the cat and Lauer (1945) in the monkey.

Another system, which is however less distinct, consists of relatively thin fibres, stained fairly dark blue and disposed very loosely. It runs from the dorso-caudo-lateral side in the oro-ventro-medial direction. The fibres of this system leave the ventral part of the lateral nucleus and pass through the nucleus tractus diagonalis Brocae to the area preoptica lateralis and the central portion of the area preoptica medialis. A similar connection of these regions was found by Loo (1931) in the opossum.

A clear majority of the fibres which go out of the ventral part of the lateral nucleus run ventro-medially and reach the fasciculus medialis prosencephali. This system is arranged more compactly than the previous ones. It is made up of medium-sized fibres, staining fairly dark blue and having even outlines. These fibres run in the oro-ventral direction and somewhat medially, but more slantingly than those of the preceding system, i.e. the septo-preoptic.

The system under description runs partly together with the tractus diagonalis, lying on its lateral side. It enters the lateral hypothalamus and thus provides septo-hypothalamic connections. A similar pathway was described by Young (1936) in the rabbit, Johnson (1957) in the mole and Fox (1940) in the cat. A slight part of the fibres of this system mingle with the fibres of the stria terminalis.

It should also be emphasized that Fox and Herrick observed fibres running from the hypothalamus to the lateral nucleus of the septum and Guillery (1957) described degenerations in the lateral nucleus after lesions of the premammillary part of the hypothalamus in the rat.

I failed to find connections of the lateral nucleus with the temporal lobe (postauditory temporal cortex), which Simpson (1952) traced in the monkey.

All the three systems described above are placed fairly close beside each other, which is conditioned by a narrow passage left for them between the nucleus accumbens (laterally), the tractus diagonalis Brocae (medially) and the olfactory tubercle (ventrally).

Cytoarchitectonics. The cytoarchitectonic picture of the lateral nucleus shows some differences between the dorsal part and the ventral, that is, the dorsal part of the nucleus consists of more globular

and bigger cells (on the average 9–10 μ in diameter) than the cells of the ventral part, which are more loosely scattered. The ventral part is composed of smaller, ovoid or pyriform cells as well as of very small round cells (in this respect the ventral part is similar to the nucleus accumbens and nucleus medialis).

The cytoplasm of the cell bodies in the nucleus lateralis stains lightly, their nuclei being relatively well seen. The lighter coloration of the cells of the lateral nucleus distinguishes them from the more intensely stained cells of the medial nucleus.

7. *The nucleus fimbrialis* (Fig. 4–6, 11, 12) has almost the hindmost position in the septum. Only its oral portion accompanies, but for a short distance, the triangular nucleus, which is separated from it by the columnae fornicis descendentis. The fimbrial nucleus was described by Loo (1931) in the opossum, Young (1936) in the rabbit, Fox (1940) in the cat, Lauer (1949) in the panda, Johnson (1957) in the mole and guinea pig, and Andy and Stephan (1959, 1961) in Galago and shrews.

The nucleus fimbrialis is comparatively large and stretches to the sides rather than oro-caudally. Its oro-caudal dimension reaches 1000 μ in the dog.

Though the nucleus fimbrialis lies so far towards the back, it borders dorsally and somewhat dorso-laterally upon the dorso-medial part of the lateral nucleus and medially, but not for its whole extent, upon the columnae fornicis descendentis.

In the upper quarter of the height the nucleus fimbrialis adjoins its fellow of the opposite side along the median line. It, as it were, confines the columnae fornicis descendentis from above and behind. Laterally the fimbrial nucleus is bounded in its oral portion by the lateral nucleus and farther caudally by the lateral ventricle. Ventro-laterally it touches the bed nucleus of the stria terminalis. Orally the fimbrial nucleus is bordered by the lateral nucleus and the nucleus tractus diagonalis Brocae, whereas its caudal boundary is marked out by the ventral hippocampal commissure, the so-called psalterium ventrale.

The nucleus fimbrialis is an irregular mass, the shape of which is rather difficult to describe. Therefore in order to illustrate this shape more adequately, a wax model of this nucleus, magnified 10 times, has been produced.

Myeloarchitectonics. As far as myeloarchitectonics is concerned, the fimbrial nucleus is a fairly rich area. A distinct system of thick fibres, which stain dark blue and have somewhat wavy sharp outlines, can be seen in it. The fibres of this relatively compact system are arranged fan-like laterally to the columnae fornicis descendentis. In

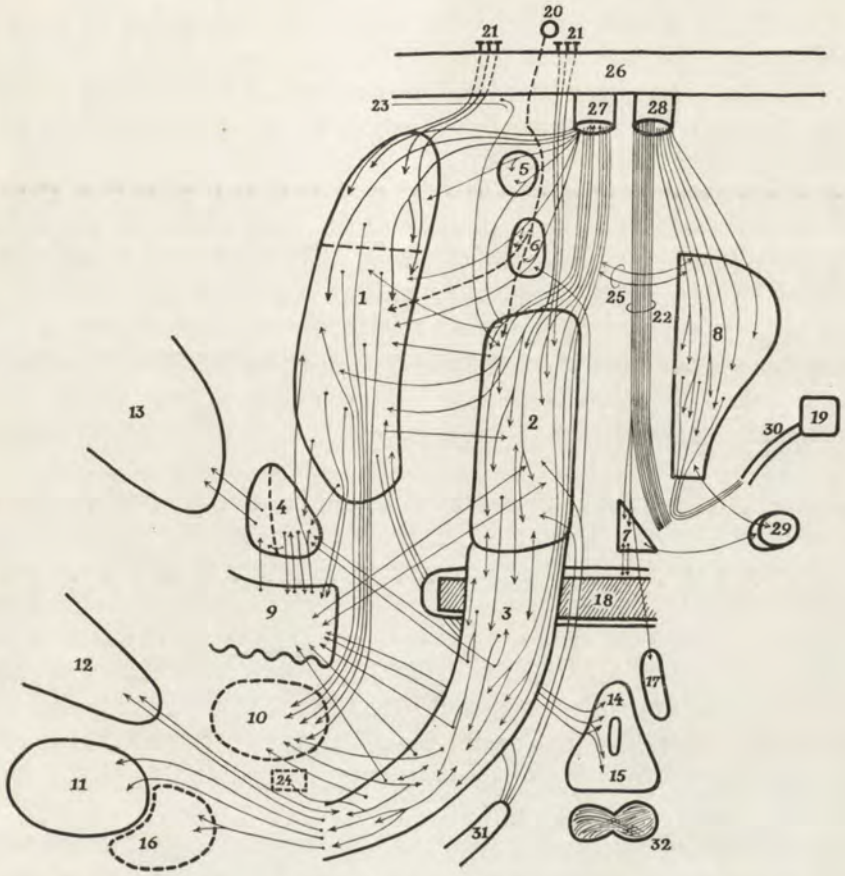

Fig. 12. Septal connections of the dog (schematic representation)

1, Nucleus lateralis septi; 2, Nucleus medialis septi; 3, Nucleus et tractus diagonalis Brocae; 4, Nucleus accumbens (septi); 5, Nucleus dorsalis septi; 6, Nucleus septo-hippocampalis; 7, Nucleus triangularis septi; 8, Nucleus fimbrialis septi; 9, Tuberculum olfactorium; 10, Fasciculus medialis prosencephali; 11, Amygdala; 12, Globus pallidus; 13, Nucleus caudatus; 14, Area preoptica; 15, Hypothalamus; 16, Cortex prepyriformis; 17, Nucleus periventricularis anterior; 18, Commissura anterior; 19, Nucleus habenulae; 20, Stria medialis Lancissi; 21, Fibrae perforantes corporis callosi; 22, Columnae fornicis; 23, Tapetum; 24, Substantia innominata Reicherti; 25, junctura fornix precommissuralis cum fornix postcommissuralis; 26, Corpus callosum; 27, Fornix precommissuralis; 28, Fornix postcommissuralis; 29, Stria terminalis et bed nucleus striae terminalis; 30, Stria medullaris thalami; 31, Stria olfactoria medialis; 32, Chiasma opticum

the medial portion of the nucleus the course of the fibres is nearly parasagittal. As the system passes towards the lateral side of the nucleus fimbrialis, the fibres diverge to the sides, assuming an oblique position (the axis of the course of the fibres runs from the ventro-medial side in the dorso-caudo-lateral direction).

The fibres of the system under description belong to the fornix postcommissuralis and take origin in the fimbria hippocampi. The course of

these fibres, as a rule, agrees with that of the columnae fornicis descendentis, i.e., they extend from the dorso-caudo-lateral side (in the lateral portion of the nucleus) to the oro-medial. This system of fibres, passing through the nucleus fimbrialis, is whole situated orally to the ventral hippocampal commissure.

Among the thick fibres of the foregoing system there are also thin and fine fibres, staining dark blue, of which some have the same course as the thick fibres, whereas the remaining ones run in the opposite direction, that is, from the caudo-dorso-medial side, and pass farther oro-ventro-laterally. The thin fibres which run in the same direction as the main system arise from the hippocampus and join the columnae fornicis descendentis. The other thin fibres more likely belong to the fornix precommissuralis, which they connect with the fornix postcommissuralis. Humphrey (1936) described a similar connection in the bat.

Another system found in the nucleus fimbrialis is made up of much thinner fibres (about a quarter of the breadth of the previous ones), which stain pale blue. They are loosely arranged and have smooth outlines. Unlike the system described above, this system includes a fairly small number of fibres and is not nearly as well seen. The course of its fibres is the same as in the first system. They run from the caudo-dorso-lateral side in the oro-ventro-medial direction, then turn under the lower corner of the lateral ventricle and cross the ventro-lateral region of the fimbriale nucleus. In all probability these fibres come from the supra-commissural part of the stria terminalis.

In the nucleus fimbrialis, just anterior to the ventral hippocampal commissure, a fairly distinct system of fibres departs laterally from the columnae fornicis descendentis. This system, like the previous one, consists of thin fibres, which are fairly compactly arranged and somewhat more darkly stained. These fibres pass dorso-caudo-laterally from the ventro-oro-medial side. They take rise from the fimbrial nucleus and columnae fornicis descendentis. More caudally they join the stria medullaris thalami. This system is homologous with the septo-habenular tract described in various mammals.

It should be mentioned that in the dog I also managed to find the presence of a very small nucleus of this tract (the nucleus tractus septo-habenularis) in the form of a few, rather large, hyperchromatic cells, lying among its fibres.

Cytoarchitectonics. The nucleus fimbrialis is made up of medium-sized cells, which are, however, smaller than the nerve cells of the dorso-caudal part of the lateral nucleus. The average diameter of these cells is about 7–8 μ. They are oval or slightly fusiform in shape and lie among the fibres of the fornix postcommissuralis in the form of rather

conspicuous bands, especially so in the medial portion of the fimbrial nucleus, whereas they are more dispersed in its lateral portion. Similarly, the cells are arranged fairly compactly in the medial region of this nucleus and more loosely in its lateral region, where they neighbour upon the bed nucleus of the stria terminalis and the bed nucleus of the anterior commissure. They differ from the cells of these last nuclei in size, the cell bodies in the nucleus fimbrialis being larger and somewhat more intensely stainable. Besides, their cytoplasm stains fairly well and the nucleus and nucleolus are distinct.

The cells of the nucleus tractus septo-habenularis compared with those of the nucleus fimbrialis are larger, hyperchromatic, oval or pyriform in shape and contain distinct Nissl granulations.

The general appearance of the cells of the nucleus interstitialis tractus septo-habenularis resembles that of the large cells occurring in the nucleus tracti diagonalis Brocae. The nucleus tractus septo-habenularis is a very small nucleus composed of a small number of cells, which are grouped close to the columnae fornicis descendentis at the place where this tract leaves the nucleus fimbrialis.

8. The nucleus accumbens as well as *the area preoptica* have been dealt with in a separate paper (Miodoński 1962 and 1963, respectively).

DISCUSSION

On the basis of my observations, the septum of the dog may be divided into two parts, the septum precommissuralis and the septum postcommissuralis. A similar division was adopted by Fox (1940), Craigie (1925), Lohman (163), Kappers (1908) and Crosby et al. (1962). In the dog, the precommissural septum is decidedly the larger part and forms about three-quarters of the whole mass of the septum. This division is at variance with that offered by Johnston (1913, Fig. 89), who distinguished the area parolfactoria and the primordium hippocampi in the septal area of different mammals. Andy and Stephan (1959, 1961) divide the septum in a different manner, namely, into four parts including the particular groups of septal nuclei, i.e. the dorsal, ventral, central, and caudal groups.

My observations concerning the dog septum show that its division into the pre- and postcommissural parts is the most adequate because it gives a fairly good general notion of the location of the septum within the telencephalon and the anterior commissure, being a large formation constantly present in the brains of mammals, is of great value as a topographic landmark. Moreover, the division of Andy and Stephan,

as has already been mentioned, refers to the location of the septal nuclei, whereas this division has been performed from the viewpoint of the topography of the septum.

Apart from the topographic division of the septum presented above, I have divided the septal nuclei of the dog into a cord of nuclei situated medially and a cord of lateral nuclei (two cords in either hemiseptum). In the dog the cord of medial nuclei includes the nucleus septo-hippocampalis, nucleus dorsalis, nucleus medialis, nucleus tracti diagonalis Brocae and nucleus triangularis. The cord of lateral nuclei consists of the nucleus lateralis, nucleus accumbens and nucleus fimbrialis.

The division of the septal nuclei into these two cords is supported by their myeloarchitectonic features. The myelinated fibres of the septum run principally in two groups: a medial and a lateral. A group of medial fibres separates the two above-mentioned cords of septal nuclei (on either side). The results of the studies carried out by Craigie (1925) on the rat, Fox (1940) and Snider and Niemer (1961) on the cat, and Lohman (1963) on the guinea pig corroborate the rightness of this division of nuclei in the dog septum.

I shall now compare the particular nuclei of the septum in the dog with the data given by other authors, who described them in various mammals. I shall discuss the nuclei of the medial cord first.

Both the nucleus septo-hippocampalis and the nucleus dorsalis of the dog have been described in the present paper (see the descriptive part). In the dog they are well-seen structures both in Weigert and silver sections and in preparations stained by the Klüver-Barrera method.

The septo-hippocampal nucleus is easy to identify in the oro-dorsal part of the dog septum. It shows associations with the septum as well as with the precommissural part of the hippocampus. The dorsal nucleus is also well-seen in the dog. Here it lies in the dorso-medial portion of the septum, stretched oro-caudally over a relatively short extent, without reaching the caudal regions of the septum, in which it disagrees with the descriptions given by most of the authors cited. None of them described both the septo-hippocampal nucleus and the dorsal nucleus in the septum at the same time, but they distinguished one of these nuclei only. The following authors described only the nucleus septo-hippocampalis: Craigie (1925) in the rat, Young (1936) in the rabbit, Fox (1940) in the cat, Humphrey (1936) in the bat, Lohman (1963) in the guinea pig, Lauer (1945, 1949) in the macaque and panda, and Johnson (1957) in the mole.

These authors assert that the septo-hippocampal nucleus comes from the precommissural hippocampus and extends far to the rear in the dorsal part of the septum, which last detail is not compatible with my

observations. They further state that the nucleus septo-hippocampalis corresponds in its topography and cytology to the dorsal nucleus such as described by Loo (1931) in the opossum. Similarly to Loo (1931), who distinguished only the dorsal nucleus in the opossum, Andy and Stephan (1959, 1961) describe the nucleus dorsalis in Galago and shrews as a large nuclear mass extending in the dorsal portion of the septum for its whole length. Besides, these authors divide this nucleus in their animals into an anterior, an intermediate, an external and an internal part. The internal part of the dorsal nucleus in this conception may be homologous with the dorsal nucleus of the dog in my division. The remaining parts of the dorsal nucleus of Andy and Stephan correspond to the dorsal part of the lateral nucleus of the dog. Some authors have not described either the septo-hippocampal nucleus or the dorsal nucleus (Adrianov and Mering (1959) in the dog, Snider and Niemer (1961) in the cat, Snider and Lee (1961) in the macaque, and Winkler and Potter (1911, 1914) in the rabbit and cat), which seems rather strange, for one of these nuclei was always found by other investigators in the same species.

The nucleus medialis of the dog is a large and distinct formation, conspicuous in both Weigert and Nissl sections. The structure of this nucleus described in this paper resembles that presented by such authors as Koelliker (1896) in the rabbit, Cajal (1904) in the rat, Johnston (1913) in different mammals, Herrick (1910) in reptiles and amphibians, Smith (1899) in marsupials, Fox (1940) in the cat, Humphrey (1936) in the bat, Bleier (1961) in the cat, Craigie (1925) in the rat, Kappers et al. (1936) in mammals, Young (1936) in the rabbit, Young (1926) in reptiles, amphibians and mammals, Lauer (1945, 1949) in the macaque and panda, Andy and Stephan (1959, 1961) in Galago and the Soricidae, Johnson (1957) in the mole, Johnson (1959) in the guinea pig, Snider and Niemer (1961) in the cat, Snider and Lee (1961) in the macaque, Fivkova and Marsala (1960) in the cat, rabbit and rat, Crosby et al. (1962) in mammals and man and Lohman (1963) in the guinea pig.

The greater part of these authors found that the medial boundary of the medial nucleus is rather poorly marked and they also emphasize the close association of the medial nucleus with the nucleus tracti diagonalis Brocae, these two observations being consistent with my findings concerning this nucleus in the dog.

Describing the medial nucleus of the opossum septum, Loo (1931) divided it into a magnocellular and a parvicellular part. The contemporary authors, Bleier and Fox as well as I, lean to the opinion that the

magnocellular part of the medial nucleus of Loo is a component of the nucleus tracti diagonalis Brocae. The great myelo- and cytoarchitectonic likeness between the magnocellular part of the medial nucleus and the nucleus tracti diagonalis Brocae would indicate this fact. They are so similar that practically it is impossible to distinguish them from each other.

Scarcely a few authors, as Winkler and Potter (1911, 1914) and Adrianov and Mering (1959), have not recorded the medial nucleus, though it is visible in their drawings and was described and presented in sketches in the same species, i.e., the cat, rabbit and the dog, by other authors.

In the dog the nucleus tracti diagonalis Brocae, belonging to the medial group of septal nuclei, does not differ in structure from the pictures of this nucleus given by various authors, who investigated it in mammals, e.g. Craigie (1925) in the rat, Loo (1931) in the opossum, Young (1936) in the rabbit, Humphrey (1936) in the bat, Johnson (1957) in the mole and (1959) in the guinea pig, Fox (1940) in the cat, Bleier (1961) in the cat, Ramon y Cajal (1940) in the rat, Lauer (1945, 1949) in the macaque and panda, Lohman (1963) in the guinea pig, Andy and Stephan (1959, 1961) in the Galago and the Soricidae, and Kappers et al. (1936) in mammals.

It should be emphasized that the division of the nucleus tracti diagonalis Brocae into the dorsal and the ventral part adopted by me and grounded on the topographic conditions connected with its course was also applied by other authors, namely, Young as well as Andy and Stephan.

As to the ventro-lateral ends of the tractus diagonalis Brocae in the dog, they generally behave like those described by Loo, Young, Humphrey and Fox, that is, the ventral part of the diagonal tract terminates for the most part in the area prepyriformis and area anterior amygdalae (vel substantia innominata Reicherti). In the dog, too, I have found connections of the tractus diagonalis Brocae with the globus pallidus, which were reported by Fox, Young, and Winkler and Potter.

The last nucleus of the medial cord is the nucleus triangularis, a small accumulation of cells situated in the supracommissural part of the septum. This nucleus was described by Ramon y Cajal, Humphrey, Loo, Young and Fox, who considered it to be the precommissural part of the hippocampal commissure.

Bleier (1961) disagrees with the foregoing opinion on the membership of the triangular nucleus. In her detailed description of the hypothalamus in the cat she states that the triangular nucleus is a part

of the nucleus periventricularis anterior of this structure. Her opinion is based on the fact that in the medio-sagittal sections of the cat hypothalamus the nucleus triangularis is evidently associated with the nucleus periventricularis anterior.

My observations of this nucleus in the dog induce me to accept Bleier's opinion, for in this animal the cyto- and myeloarchitectonic structure of this region, regarded as the supracommissural part of the nucleus periventricularis anterior by Bleier and corresponding to the triangular nucleus of Ramon y Cajal, Fox, or Humphrey, is very similar to the structure of the nucleus periventricularis anterior. Both these nuclei are composed of similar cells and fibres which are nearly the same thickness and show a similar arrangement and course in the dog. The occurrence of fairly numerous loops of capillaries resembling those of the area preoptica in appearance just anterior and somewhat ventral to the triangular nucleus also supports this opinion.

The largest nucleus of the lateral cord is the nucleus lateralis. It has been generally described in different mammalian species by Ramon y Cajal (1904), Loo (1931), Humphrey (1936), Young (1936), Kappers et al. (1936), Fox (1940), Lauer (1945, 1949), Bleier (1961), Snider and Niemer (1961), Snider and Lee (1961), Crosby et al. (1962), Lohman (1963) and Jeserich (1945). My observations concerning the structure of the lateral nucleus of the dog as a rule come very near the findings offered by these authors.

Within the lateral nucleus of the dog I have found some differences, which make it possible to divide it into two parts: a dorsal and a ventral. This division is compatible with the opinions of Jeserich (1945), Lauer (1945, 1949) and Loo (1931). On the other hand, Andy and Stephan (1959, 1961) distinguish an external and an internal part in the lateral nucleus. In my opinion the former division is more adequate because of the differences in the cyto- and myeloarchitectonic structure ascertained in the dog. In my case the eventual demarcation line would run horizontally and not dorso-ventrally, as it is marked out by Andy and Stephan. The division proposed by me seems also justified by the numbers of fibres coming to these two parts of the lateral nucleus, that is, the dorsal part receives fewer fibres than the ventral.

The dorso-caudal portion of the lateral nucleus, sited in the postcommissural septum, is closely associated with the nucleus fimbrialis and, consequently, Crosby, Humphrey and Lauer consider this last nucleus to be a part of the lateral nucleus. In my opinion the myeloarchitectonic differences between the dorso-caudal portion of the lateral nucleus and the fimbriale nucleus allow their discrimination,

though the similarity of these regions in so far as their cytoarchitectonics is concerned would corroborate the view of the above-mentioned authors.

The last nucleus in the dog septum discussed in this paper is the nucleus fimbrialis, described in different mammals by Johnson (1957, 1959), Fox (1940), Lauer (1945, 1949), Young (1936), Loo (1931), Andy and Stephan (1959, 1961), Lohman (1963) and Kappers et al. (1936).

Almost all these authors regard this nucleus as a caudal extension of the lateral nucleus, associated with the fornix postcommissuralis. My findings are consistent with their opinion. However, as this nucleus sends its fibres mainly towards the habenular nuclei, I think it should be treated as a distinct nucleus.

Unlike the authors cited above, Jeserich has not described the nucleus fimbrialis in the weasel.

Now I come to the relatively abundant connections of the septum (Fig. 12).

The bulk of the fibres which enter the septum come from the fornix and consequently from the hippocampus.

In lower mammals, i.e. in marsupials, the fornix divides in the region of the anterior commissure into two parts: one smaller or the fornix precommissuralis and another larger or the fornix postcommissuralis (Loo 1931, Powell et al. 1957). In higher mammals the situation has changed owing to the development of the corpus callosum. The intense expansion of the corpus callosum towards the back and also to the front brings about the stretch of the fornix in the caudo-dorsal direction, which is connected with the displacement of the hippocampus. As a result, the place where the fornix splits into the two components has been moved away from the anterior commissure and now it lies in the dorso-caudal region of the septum, just posteriorly to its supraforaminal portion (Fox 1940, Gastaut and Lammers 1961).

The following groups of fibres may be distinguished in the precommissural fornix: fibres emerging from the hippocampal commissure, fibres running on the dorsal side of the corpus callosum or the stria medialis Lancisii and, finally, fibres perforating the corpus callosum at unequal intervals. These last fibres pierce through the caudal portion of the corpus callosum more frequently than through its oral portion (according to some authors this relation may be reversed) and gather on its ventral surface.

The fibres emerging from the hippocampal commissure and those perforating the corpus callosum and gathering on its ventral surface correspond to the fornix superior of Koelliker (1896). The fibres of the stria medialis Lancisii run on the dorsal surface of the corpus

callosum in the oral direction, then turn round the genu corporis callosi and pass oro-ventrally as the marginal fascicle of Smith (1896).

Apart from the differences bearing upon the definition of the precommissural and postcommissural fornix between the lower and the higher mammals, in the higher mammals the bulk of fibres are those of the fornix postcommissuralis, and only a slight number of them penetrate into the septum. These fibres are homologous with the whole fornix ventralis distinguished by Smith (1892).

The fibres of the fornix precommissuralis, i.e. those coming from the ventral hippocampal commissure as well as the fibres perforating the corpus callosum run oro-ventrally through the septum. During their course through the septum they divide and go to the medial nucleus, the nucleus tracti diagonalis Brocae and partly to the medial surface of the lateral nucleus (Kappers et al. 1936, Humphrey 1936, Jeserich 1945); moreover, some fibres run to the area preoptica medialis (Loo 1931), the regio hypothalamica lateralis (Nauta 1956, 1958, Valenstein and Nauta 1959) and the regio hypothalamica medialis (Humphrey 1936).

The fibres which pass dorsally to the corpus callosum run together with the stria medialis Lancisii and next enter the oro-dorsal portion of the septum to reach the nucleus septo-hippocampalis (or the so-called extension of the hippocampus into the septum), the medial nucleus and the lateral (Johnson 1957; Humphrey 1936; Fox 1940).

The second largest bundle of fibres found in the septum is the tractus diagonalis Brocae, which is considered to be a pathway connecting the hippocampus and the septal area with the tertiary olfactory centres. The tractus diagonalis Brocae receives fibres from the fornix superior. These fibres, descending through the nucleus tractus diagonalis Brocae, gather the fibres coming from the large cells of this nucleus. Besides, they are joined with large cells by means of collaterals occurring in this nucleus. According to Johnson (1957) the tractus diagonalis receives fibres from the medial nucleus.

The fibres of the diagonal tract run orally round the anterior commissure and turn ventro-latero-caudally. They pass between the olfactory tubercle, which has an oral position, and the area preoptica. Just beneath the anterior commissure the tractus diagonalis Brocae gives part of its fibres to the ventral region of the medial forebrain bundle and to the posterior portion of the olfactory tubercle (Fox 1940, Johnson 1957, Young 1936, Humphrey 1936). The fibres which join the medial forebrain bundle run in it to the hypothalamus (Fox 1940, Johnson 1957, Humphrey 1936, Young 1936).

Extending farther latero-caudally towards the lateral wall of the

hemisphere, the fibres of the tractus diagonalis Brocae divide to reach the area prepyriformis and the area anterior amygdalae vel substantia innominata Reicherti (Johnson 1957, Fox 1940, Humphrey 1936, Loo 1931). It should also be emphasized that, before giving out its fibres to the above-mentioned regions, this tract has connections with the globus pallidus (Fox 1940, Winkler and Potter 1911, 1914).

The results of my studies concerning the nucleus tracti diagonalis Brocae and the diagonal tract itself in the dog coincide as a rule with the data quoted above. In addition, I managed to trace the connections of the nucleus tracti diagonalis Brocae to the nucleus accumbens and the area preoptica lateralis in the dog.

The connections of the remaining nuclei of the septum may be regarded as a third system of fibres.

The majority of the nuclei described in the septum, i.e. the lateral and medial nuclei, the nucleus accumbens and the nucleus tracti diagonalis Brocae, are connected with each other by a fairly abundant "network" of interconnecting fibres (Lauer 1945, 1949, Fox 1940). Besides the nucleus tractus diagonalis Brocae discussed above, the conneections of two other large septal nuclei, the medial and the lateral, are treated of rather in detail in literature. These two nuclei are considered by different authors to be afferent and efferent in relation to the hippocampus. This opinion is based on the suggestion expressed by Crosby (1917) in her paper on the forebrain of the alligator that the medial nucleus is a way-station for afferent impulses tending to the hippocampus, whereas the lateral nucleus is a similar way-station for efferent impulses coming from the hippocampus. Loo, Young and almost all contemporary investigators support this conception. The medial nucleus is regarded as an afferent nucleus in relation to the hippocampus. Andy and Stephan (1961) described both the efferent and the afferent projection of this nucleus, distinguishing dorsal and ventral projections within them.

The dorsal efferent projection of the medial nucleus to the hippocampus was described by Crosby (1917) in the alligator, Loo (1931) in the opossum and Johnson (1957) in the mole. Cairney (1926), too, wrote about fibres running from the medial nucleus to the hippocampus in reptiles. Degeneration studies are also believed to corroborate the presence of connections of this type. Morin (1950) described degenerations of fibres within the hippocampal fimbria and commissure following a lesion, which also involved the precommissural part of the septum, in the guinea pig. The lesion situated more orally without encroaching upon the septal area did not cause any degenerative changes

in it. Daitz and Powell (1954) noted degenerations in the posterior portion of the medial nucleus and partial degenerations in the nucleus tractus diagonalis Brocae as the result of the section of the hippocampal fimbria in the rat, rabbit and monkey. McLardy (1955) found cellular degenerations in the medial nucleus following the section of the fornix in the monkey. Rose and Woolsey (1943) write that in the rabbit the lesions of the telencephalon including the hippocampus induced degenerations of cells in the medial nucleus and the nucleus tracti diagonalis Brocae.

In the opinion of different authors, the ventral efferent projection of the medial nucleus is made up of the connections of this nucleus with the nucleus tracti diagonalis Brocae (Herrick 1910, Loo 1931, Young 1936, Guillery 1957), with the area anterior amygdalae and globus pallidus (Fox 1940, Lauer 1945) and with the medial forebrain bundle (Gurdjian 1925, Mettler 1943).

The dorsal afferent projection from the hippocampal commissure to the medial nucleus was described by Humphrey (1936) in the bat and Fox (1940) in the cat as fibres perforating the corpus callosum on their way to the dorso-medial portion of the medial nucleus.

Johnson (1957) traced the fibres which reached the medial nucleus from the hippocampus, via the fornix superior, in the mole. The stria medialis Lancisii also provides the medial nucleus with fibres.

The ventral afferent projection of the medial nucleus is fairly rich in connections. Crosby (1917) states that this nucleus receives fibres from the olfactory tubercle and the tractus olfactorius medialis. Loo (1931) described, among other things, the afferent connections from the nucleus olfactorius anterior and tuberculum olfactorium to the medial nucleus, where they terminate in its anterior portion, in the opossum. Fox (1940) found fibres which arise in the globus pallidus and reach the medial nucleus through the tractus diagonalis Brocae in the cat. Brodal (1948) writes about the same fibres in the rat and thinks that they end in the medial nucleus. Johnson (1957), like Fox, finds the fibres connecting the globus pallidus and tuberculum olfactorium with the medial nucleus, in which they are supposed to end, in the mole. Some authors hold that the medial nucleus receives some fibres from the medial forebrain bundle (Mettler 1943, Guillery 1957).

Nauta and Kuypers (1958) described degenerations of fibres reaching the medial nucleus and the nucleus tracti diagonalis Brocae following a lesion in the medial region of the tectum in the cat.

A comparison of the foregoing data with the connections of the medial nucleus described in the dog in this paper shows a far-reaching

coincidence. Moreover, in the dog I have found the presence of "grundfasern" in the form of a fine network throughout the medial nucleus as well as a system of transitory fibres, running from the precommissural fornix through the caudal portion of the medial nucleus to the nucleus tracti diagonalis Brocae.

The lateral nucleus, in contradistinction to what has been said about the medial nucleus, is regarded as efferent in relation to the hippocampus. Like the medial nucleus, it has a dorsal and a ventral afferent projection and only a ventral efferent one. The dorsal efferent projection of the lateral nucleus has never been decribed. Fibres running from the lateral nucleus to the medial forebrain bundle (Young 1936, Crosby 1917, Cairney 1926, Fox 1940, Johnson 1957) as well as to the area preoptica and the hypothalamus (Loo 1931) were found within the ventral efferent projection. Besides, Fox (1940) and Johnson (1957) described the fibres connecting the lateral nucleus with the nucleus accumbens and Lauer (1945) traced the fibres going to the tuberculum olfactorium within this projection.

The dorsal afferent projection of the lateral nucleus is considered to be the one conducting impulses from the hippocampus to this nucleus. Crosby (1917) reported the fibres coming from the hippocampus to the lateral nucleus in the alligator and Cairney (1926) represented this nucleus as an area receiving afferent fibres from the hippocampus in reptiles. Loo (1931) found the fibres of hippocampal origin which terminated in the latero-dorsal portion of the lateral nucleus in the opossum. Fox (1940), too, followed the hippocampal fibres to the lateral nucleus. Both he and Young (1936) described the fibres coming to this nucleus from the stria medialis Lancisii.

In the monkey, Lauer (1945) observed a system of fornical fibres, from the fornix precommissuralis, tending to the medial portion of the lateral nucleus and some fibres from the postcommissural fornix which scatter in its posterior portion. A similar system of fibres, which took rise from the fornix precommissuralis and reached the lateral nucleus, was found by Johnson (1957) in the mole. Degeneration studies carried out by Simpson (1952), McLardy (1955), and Valenstein and Nauta (1959), namely, the effects of lesions performed in the hippocampus and fornix, seem to confirm the connections discussed above.

The ventral afferent projection of the lateral nucleus was described by Herrick (1924) as fibres passing from the medial forebrain bundle to the lateral nucleus. Fox (1940) wrote about fibres coming to this nucleus from the hypothalamus. A degeneration work conducted by Guillery (1957) on rats would confirm the existence of the connections of the hypothalamus with the lateral nucleus, as he observed de-

generation of fibres within this nucleus following a damage to the hypothalamus.

The connections of the lateral nucleus in the dog described in the present paper agree with the data of other authors presented above. It should be emphasized that, as far as the septo-hypothalamic projection is concerned, I managed to distinguish three basic systems of connections, mainly to the hypothalamus but also to the tuberculum olfactorium and area preoptica, within it in the dog. It should be also added that in an earlier paper (1962) I did not point out to the existing connections between the lateral nucleus and the nucleus accumbens clearly enough. It was not before I used silver sections that I succeeded in tracing these connections.

The connections of the other nuclei of the septum, that is, those of the dorsal, septo-hippocampal, fimbrial and triangular nuclei as well as of the nucleus accumbens are not very abundant. Nevertheless, I shall discuss them in the order given above.

The dorsal nucleus shows some associations with the fornix dorsalis, which Ramon y Cajal (1911) described in the rat. In the opossum, Loo (1931) found fibres which arise in the dorsal nucleus and pass ventrally on either side of the sagittal plane towards the tractus precommissuralis. On the basis of his experiments conducted on monkeys Mettler (1943) represented the dorsal nucleus as a nucleus which sends its fibres to the hypothalamus.

In the dog, I detected two types of connections of this nucleus with the fornix precommissuralis. One system of fibres, of fornical origin, enters the dorsal nucleus and partly terminates in here but a large number of its fibres go on to the medial nucleus. The other system, resembling the first in structure, scatters, also only in part, in the dorsal nucleus, tending farther laterally to the lateral nucleus. The dorsal nucleus, especially its caudal portion, is surrounded by the fibres from the fornix precommissuralis, which fibres separate it from the adjoining formations.

Similarly, the nucleus septo-hippocampalis has connections with the fornix precommissuralis, described also by Lauer (1945) in the monkey, Young (1936) in the rabbit, Humphrey (1936) in the bat and Fox (1940) in the cat. In addition, they ascertained that the septo-hippocampal nucleus receives a number of fibres from the stria medialis Lancisii. In the rabbit, Young (1936) noted relatively numerous fibres which come to the nucleus septo-hippocampalis from the tuberculum olfactorium as well as from the hippocampus precommissuralis.

A comparison of the descriptions of the nucleus septo-hippocampalis and its connections with my observations shows that in the dog this

nucleus is well-defined and receives fibres from the stria medialis Lancisii and also some fibres from the deep layers of the tuberculum olfactorium and fornix precommissuralis. Moreover, the nucleus septohippocampalis has a "sheath" formed of fibres belonging to the fornix precommissuralis.

The nucleus fimbrialis is regarded by various authors as the caudal extension of the lateral nucleus. On the basis of his observations on this region in the opossum, Loo (1931) distinguished the nucleus fimbrialis as a separate unit from the lateral nucleus. He found that the posterior (supraforaminal) portion of the lateral nucleus, corresponding to the nucleus fimbrialis in his conception, sends fibres to the medial nuclei of the habenula through the stria medullaris thalami. Taking this fact into account, Loo isolated the supraforaminal portion of the lateral nucleus as the nucleus fimbrialis. Loo's opinion was supported by the descriptions published later by Young (1936), Fox (1940), Lauer (1945, 1949) and Humphrey (1936).

The fimbrial nucleus receives fibres from the fornix postcommissuralis and through the septo-habenular fibres sends its impulses to the habenula (Johnson 1957, Fox 1940, Lauer 1945). I also regard the nucleus fimbrialis as the caudal portion of the lateral nucleus. On account of its separate connections I have isolated it as a distinct unit from this nucleus. Besides, the presence of the connections of the nucleus fimbrialis, as a discrete system of fibres from the supracommissural part of the stria terminalis, has been found in the dog.

The triangular nucleus was described by Lauer (1945) as a nucleus receiving fibres from the fornix postcommissuralis, which fibres as a rule tend to the bed nucleus of the anterior commissure. Fox (1940), Crosby (1917) and Humphrey (1936) share this opinion. According to Fox the triangular nucleus has also some interconnections with the nucleus fimbrialis, which however has not been found in the dog.

In the dog the connections of the triangular nucleus consist in principle of two systems of fibres. One of them is composed of fibres belonging to the fornix precommissuralis. Some of these fibres end in the triangular nucleus and some reach the base of this nucleus, where they swing laterally to enter the bed nucleus of the anterior commissure. The other system, very poorly seen, is made up of very fine fibres and extends to the regions of the bed nucleus of the stria terminalis.

In literature, emphasis is laid on the presence of connections between the septum and the gyrus cinguli through the medium of some of the fibres which pierce through the corpus callosum and belong to the fornix precommissuralis. Gastaut and Lammers (1961) claim that part of these fibres end in the septum, whereas the remaining ones

run to the hypothalamus and also perhaps to the tegmentum mesencephali. According to these authors there are also septo-cingular fibres, which run in the opposite direction either together with the cingulo-septal fibres or with those of the cingulum tending to the tuberculum olfactorium.

Experimental and histological studies carried out recently by Stoll et al. (1951) and McLardy (1955) have revealed fibres connecting the septum with the temporal cortex. In McLardy's opinion, in the macaque the septo-temporal fibres would come from the ipsilateral medial nucleus, whereas the temporo-septal fibres would supply the ipsi- and contralateral lateral nuclei of the septum.

The regio septalis, included in the area of the "rhinencephalon" as one of its components, belongs to the palaeopallium (palaeocortex, s. cortex olfactoria) or the oldest part of the rhinencephalon, occurring as early as in the Selachia and Teleostei.

The palaeopallium was usually considered in conjunction with the archipallium as the heterogenetic cortex (Brodmann 1905) or as the allocortex (Vogt and Vogt 1919). In the classification of the cortex offered by Rose (1926) the septal region has been reckoned in the semicortex.

As the palaeocortex is not distinctly demarcated, both phylogenetically and ontogenetically, from the subcortical structure, Filomonov (1949) suggested that it should be termed the "cortex semiseparata".

Pribram and Kruger (1954) have recently proposed to classify the components of the rhinencephalon in three systems. The first olfactory system, associated directly with the olfactory bulb — reception of olfactory sensations — includes the tuberculum olfactorium, the area diagonalis, the area prepyriformis and the nuclei corticalis et medialis amygdalae. The second olfactory system, connected with the first, consists of the regio fronto-temporalis, the area septalis, the area subcallosa and the nuclei basalis et lateralis amygdalae. The third olfactory system, which is connected with the second, is composed of the formatio hippocampalis, the area entorhinalis and the gyrus cinguli.

In addition to associational functions of the olfactory type, the second and third systems show adaptation for other functions, as they are connected with the nuclei of the thalamus and hypothalamus and with the postauditory temporal cortex. Nowadays the second and third systems — the septum belongs to the second — are supposed to be responsible for elaboration of emotional states, for the olfactory sensation is admittedly very strongly associated with the emotional attitude, perhaps more strongly than it is found in the case of any other sensations.

This opinion seems to be supported by neurophysiological experiments, in which sensations of the olfactory type — reception of smell — was obtained only from the cortex prepyriformis and the cortex pyriformis intermedia, then from the components of the first system.

The studies of Olds and Milner (1954, 1956) and Brady and Nauta (1953) also indicate that the septal area constitutes an inhibitory system, because its destruction brings about increased activity of the animals. Moreover, the septal area is also supposed to be concerned with the responses which occur in the condition of fear and fright, because after its damage these responses are considerably weaker and the animals become less timid.

As regards its functionality, the rhinencephalon may be divided into two components, which are however very closely associated. One of them would include the rhinencephalic structures connected with the reception of olfactory sensation, that is, the olfactory bulbs and tract, the prepyriform cortex and the intermediate pyriform cortex, as centres of a low order for olfactory sensation, as well as the cortex entorhinalis and the hippocampus, as associational centres of a high order. The other component of the rhinencephalon would consist of the structures responsible for the elaboration and subjective experience of emotional states, i.e. the septum, the amygdala, the hypothalamus with the preoptic area and corpora mammillaria, the anterior nuclei of the thalamus and the cortex cinguli.

Having passed through the olfactory nerves, the impulses reach the olfactory bulb, from where they are conducted farther by the secondary neurons which form the olfactory pathways. Just anterior to the tuberculum olfactorium (vel substantia perforata anterior) these pathways split into two bands: the medial and lateral striae olfactoriae. The stria olfactoria medialis carries the "olfactory impulses" to the system elaborating the emotional states, namely, through the tuberculum olfactorium to the septum, which this band joins also directly. Along the pathways of the hypothalamus and the corpora mammillaria the impulses reach the anterior nuclei of the thalamus and through the point-to-point projection of these nuclei the gyrus cinguli.

The stria olfactoria lateralis conducts the "olfactory impulses" farther to the prepyriform cortex (operculum frontale) and through the intermediate pyriform cortex to the entorhinal cortex and the hippocampus, the associational centres of a high order. The fibres of this stria also carry the olfactory impulses to the amygdala.

Both parts of the rhinencephalon are closely connected with each other by the large system of the fornix, which comes from the hippocampus to the septum, hypothalamus, corpora mammillaria, and an-

terior and intralaminar nuclei of the thalamus. The gyrus cinguli, being connected with other regions of the neocortex, gives a projection to the hippocampus, closing the circuit between these two components of the rhinencephalon.

The complex of nuclei of the amygdala with its efferent pathway, the stria terminalis, was also considered to be an element connecting both components of the rhinencephalon. The stria terminalis reaches the preoptic area and hypothalamus and also, partly, the septal area. The recent studies of R. Miodoński (personal communication) on the amygdala of the dog seem to indicate that only a small part of the stria terminalis comes from this structure, whereas the bulk of this band takes rise rather in the hippocampus. This suggests that the olfactory sensation is strongly assocciated with the arousal of emotional states and that they are experienced in conjunction.

The rhinencephalic system, elaborating emotional states, exerts an influence upon the motor behaviour of the organism, which is manifested both in motor activity of the skeletal muscles (especially of the face) and in autonomic responses, e.g. the ruffling of hair, increase in blood pressure, increase in heart rate and dilatation of the pupil of the eye. The influence of the rhinencephalon on the motor activity of the skeletal muscles is particularly distinct in the mimic muscles of the face owing to the connections with the motor nuclei of the seventh nerve by the habenulo-interpeduncular tract, the medial forebrain bundle and the mammillo-tegmental tract, which reach the motor portion of the formatio reticularis descendentis.

The connections between the hippocampus and the putamen and caudate nucleus through the fornix and the intralaminar nuclei of the thalamus as well as the connections of the septum with the caudate nucleus may be responsible for the increase in the muscular tonus accompanying the emotional states.

The connections between the hippocampus and the postauditory temporal cortex, which is free from the influences of the thalamus, may govern the emotional attitude at the fixation in the memory of sensory experiences of the organism in conjunction with the olfactory sensation.

On the basis of an analysis of neurons by the Golgi method Leontovich and Zhukova (1963) have included the septum, or rather its internal part, in the system of the formatio reticularis. The hypothalamus (except the nucleus corpus mammilare mediale) with the preoptic area, the substantia innominata Reicherti and some parts of the thalamus have also been reckoned in this system. The inclusion of a part of the septum the cord of medial nuclei in my conception, in the formatio reticularis, together with the hypothalamus and preoptic area, which

are higher centres of vegetative responses, may throw proper light upon the part played by the septum in the emotional and vegetative responses of the organism.

SUMMARY

The term "septum" is here used for the regio situated beneath the corpus callosum in the medial wall of the brain hemisphere. It extends from the temporal cortex and anterior olfactory nucleus to the hippocampal commissure. The septal nuclei are grouped in two cords: a cord of medial nuclei and a cord of lateral nuclei. Medial nuclei: The septo-hippocampal nucleus (Fig. 1, 2, 7, 10, 12) is fairly strongly associated with the precommissural hippocampus and lies in the oral portion of the septum. It is a relatively small nucleus, rather poor in respect of myeloarchitectonics. Two systems of fibres coming from the precommissural fornix have been distinguished. They partly end in this nucleus and partly pass farther to the lateral nucleus of the septum. A system of fibres received from the stria medialis Lancisii was also noted.

The dorsal nucleus (Fig. 1, 2, 7, 10, 12) is sited in the oro-dorsal part of the septum and belongs to the smallest nuclei of this structure. It appears in the dog septum as a distinct anatomical unit, independent of the septo-hippocampal nucleus. Its myeloarchitectonics is poor. Two systems of fibres from the fornix precommissuralis were observed. They pass through the dorsal nucleus, to which they give some of their fibres. These systems are transitory ones and tend to the medial and lateral nuclei.

The medial nucleus (Fig. 1–3, 7, 9, 12) is a large, myeloarchitectonically rich nucleus, which extends for the nearly whole length of the precommissural septum. The following systems of fibres were noted: system of efferent fibres running through the fornix precommissuralis to the hyppocampus; system of afferent fibres which come from the fornix superior and scatter all over the medial nucleus, whereas a small number of fibres of this system go on to the adjoining lateral nucleus of the same side; system of very loosely arranged fibres, less well seen and coming to the medial nucleus from the stria medialis Lancisii; part of its fibres pass to the lateral nucleus; system of fibres running from the tuberculum olfactorium and scattering fan-like within the medial nucleus; system composed of not very numerous, loosely arranged fibres, taking origin in the stria olfactoria medialis; "system" of interconnecting fibres between the medial nucleus and the nucleus tracti diagonalis Broeae; system of fibres which originate from the precommissural fornix, pass transitorily through the medial nucleus and reach the nucleus tracti

diagonalis Brocae; system, which is indistinct owing to its poor stainability, made up of very loose fibres connecting the medial nucleus with the stratum subcallosum vel tapetum.

The nucleus tracti diagonalis Brocae (Figs. 1–4, 12) lies along the medial and basal aspects of the hemisphere. It is the second largest nucleus in the septal area. The fibres of this nucleus emerge from the commissura fornicis ventralis and, in all probability, come from the hippocampus.

The fibres of the tractus diagonalis Brocae surround the anterior commissure anteriorly and turn ventro-caudo-laterally next. They pass through the posterior part of the tuberculum olfactorium, where some of the fibres terminate (ventral part of the tract), and at the same level some of them (dorsal part) go to the medial forebrain bundle. Farther, the fibres of the tractus diagonalis Brocae reach the area prepyriformis and area preamygdaloidea vel substantia innominata Reicherti. Connections of the tractus diagonalis with the ventral part of the globus pallidus as well as with the nucleus accumbens of the septum and the preoptic area of the hypothalamus are also present in the dog.

The triangular nucleus (Fig. 4, 10, 12) is the smallest of the septal nuclei and lies dorsally to the anterior commissure, between the columnae fornicis descendentis. In the dog this nucleus bas been found to be a part of the nucleus periventricularis anterior. A system of thick and thin fibres coming from the fornix precommissuralis has been noted. The thick fibres are partly lost in the triangular nucleus, partly run to the anterior periventricular nucleus. The thin fibres scatter in the area of the triangular nucleus. Another ill-seen system is composed of a small number of thin fibres, which come into contact with the bed nucleus of the stria terminalis. Fibres connecting the triangular nucleus with the bed nucleus of the anterior commissure were also ascertained. Lateral nuclei:

The lateral nucleus (Fig. 1–8, 12) is the largest in the septum. It extends along the lateral aspect of the septum throughout its length. In the dog it has been divided into a dorsal part, poor in fibres, and a ventral part, abounding in them. "Grundfasern" occur throughout the lateral nucleus. The following systems of fibres have been distinguished: system of fibres which arise from the fornix precommissuralis and come to the lateral nucleus from the medial; system of less well-seen fibres from the stria medialis Lancisii; system of loosely arranged fibres from the fornix precommissuralis, coming directly to the dorsal part of the lateral nucleus; system of very fine fibres — best seen on silver preparations — tending to the nucleus accumbens; system of fibres connecting the tuberculum olfactorium with the lateral nucleus;

system of less well-seen, loosely arranged fibres passing from the ventral part of the lateral nucleus to the preoptic area; strong system of fibres, coming from the ventral part of the lateral nucleus, for the most part joining the medial forebrain bundle and partly reaching the hypothalamus.

The fimbrial nucleus (Fig. 4–6, 11, 12) belongs rather to small nuclei of the septum; nevertheless, it is rich in fibres. Three systems have been found in this nucleus. The first system, composed of thick fibres, which come from the postcommissural fornix and scatter fan-like in the fimbrial nucleus, and thin fibres, running among the thick ones. The thin fibres arise in the hippocampus and part of them connect the fornix precommissuralis with the fornix postcommissuralis. The second system runs from the supracommissural part of the stria terminalis. The third system is formed by the fibres of the tractus septo-habenularis, leaving the fimbrial nucleus.

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ABBREVIATIONS

a.po.,	area preoptica	N.l.s.p.d.,	nucleus lateralis septi pars dorsalis
a.po.l.,	area preoptica lateralis	N.l.s.p.v.,	nucleus lateralis septi pars ventralis
a.po.m.,	area preoptica medialis	N.ms.,	nucleus medialis septi
c.,	caudal	n.opt.,	nervi optici
C.ant.,	commissura anterior	N.s-h.,	nucleus septo-hippocampalis
Cc.,	corpus callosum	N.tr.d.B.,	nucleus tractus diagonalis Brocae
Ch.op.,	chiasma opticum	N.tr.s.,	nucleus triangularis septi
C.int.,	capsula interna	o.,	oral
d.,	dorsal	Rec.s.opt.,	recessus supra opticus
f.m.p.,	fasciculus medialis prosencephali	Str.med.th.,	stria medularis thalami
Fx.,	fornix	Str.ter. et n.str.ter.,	stria terminalis et bed nucleus striae terminalis
Hy.ant.,	hypothalamus anterior	T.olf.,	tuberculum olfactorium
I.C.,	insula Calleja	v.,	ventral
l.,	lateral	Vl.,	ventriculus lateralis
m.,	medial		
N.acc.s.,	nucleus accumbens septi		
N.ds.s.,	nucleus dorsalis septi		
N.l.s.,	nucleus lateralis septi		

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MYELOARCHITECTONICS AND CONNECTIONS OF SUBSTANTIA INNOMINATA IN THE DOG BRAIN

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An analysis of the myeloarchitectonics and anatomical connections of substantia innominata is the aim of this paper.

Serial sections obtained by cutting the dog brain in frontal, sagittal and horizontal planes were used. The sections have been stained by the Weigert, Nissl and Klüver-Barrera methods, as well as the Schultze silver method. Six series have been used in all.

Substantia innominata is a strongly myelinated area bordering posteriorly, on the amygdaloid complex and reaching, with its anterior division, the olfactory tubercle. Practically, the rostral portions of the amygdaloid complex make up a mediocaudal boundary of the substantia innominata. Medially, the substantia innominata touches the anterior parts of the hypothalamus and lateral preoptic area. The ventral part of the external capsule constitutes the lateral boundary of the substantia innominata. Dorsally, the substantia innominata contacts the ventral part of the nucleus lentiformis and ventrally, it contacts the pyriform and prepyriform cortex (Figs. 1 and 2).

Cytoarchitectonically, substantia innominata appears to be homogeneous. It is filled with loosely disposed cells which, in medial and ventral parts, become somewhat more concentrated. These cells are strongly stainable, fairly large and triangular or polygonal in shape. In the posterior part, there occur abundant collections of neurous, called massa intercalata (Figs. 5 and 6, MI).

Several systems of fibers from the hypothalamus, thalamus, amygdaloid complex, the adjacent cerebral cortex, putamen and globus pallidus pass through the substantia innominata. Four areas may be distinguished

on the basis of fibers belonging to different systems. The lateral area (Figs. 1, 2 and 4–6, LT), including lateral parts of the substantia innominata, is marked by the predominance of fibers coming from the amygdaloid complex, whereas the area principalis (Figs. 1, 2, 5, 6, PC) contains primarily those, coming from the medial forebrain bundle and inferior thalamic pedunculus and is situated medially to the lateral area. The sublenticular area (Figs.1–6, SL) is passed by fibers running from the lentiform nucleus to the remaining parts of the substantia innominata. The latter area contains many fibers, coming from the ansa lenticularis and occupies the dorsomedial part of the substantia innominata, adhering to the ventral

Fig. 1. Frontal section through the dog brain. Weigert stain. Note the connections of the inferior thalamic peduncle with the substantia innominata

boundary of the lentiform nucleus. The area diagonalis ventralis (Figs. 2 and 6, DV) is a lowermost part of the diagonal band of Broca. On account of its close relationship to the area principalis, it is considered, in the present paper, part of the substantia innominata. It is situated medially to the anterior parts of the area principalis.

Myeloarchitectonics

The area lateralis is part of the substantia innominata in which fibers predominate which run mediorodorsally (Figs. 4–6, LT). It has a shape of a formless pyramid with its apex pointing forwards and base resting on the anterior sections of the basal and lateral nuclei of the amygdala. It occupies dorsolateral parts of substantia innominata, dorsolaterally bordering on the ventral part of external capsule and ventrolaterally on

pyriform and prepyriform cortex. Anterior portions of the medial nucleus of the amygdala and, in front, area principalis (Fig. 6) make up a medial boundary of area lateralis, whereas the area sublenticularis forms its dorsomedial boundary.

Fibers, coming from the corpus amygdaloideum, are most numerously represented in the area lateralis. Several different systems may be distinguished among them.

The system, associated with the longitudinal association bundle (F o x 1943) constitutes a bundle of fibers which, in addition to the longitudinal association bundle, contains other similarly oriented fibers (Fig. 8). A part of them comes from the dorsal part of the basal amygdaloid nucleus and from the ventral parts of the central amygdaloid nucleus. They make up the proper longitudinal association bundle (M i o d o ń s k i 1965). In the anterior part of the basal amygdaloid nucleus, these fibers are joined by

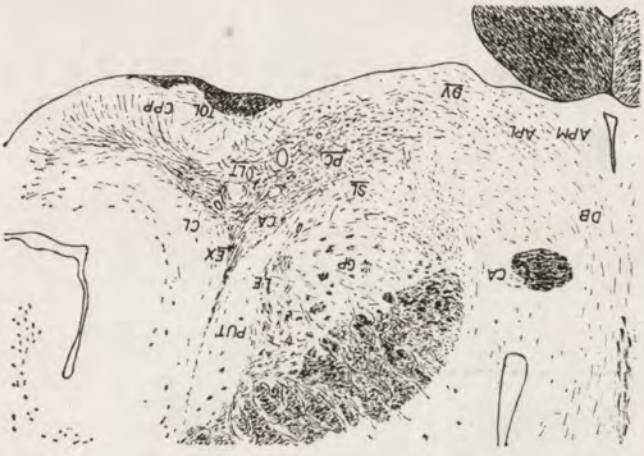

Fig. 2. Frontal section through the dog brain, Weigert stain. Note the connections of the substantia innominata with the diagonal band of Broca

others, coming from the ventral part of the basal amygdaloid nucleus. Fibers, coming from the hippocampal gyrus constitute the third component of this system. They reach substantia innominata after passing the basal amygdaloid nucleus (M i o d o ń s k i 1965). They run through the basal nucleus in the form of bundles parallel to its longitudinal axis.

In the caudomediodorsal parts of area lateralis, all components of the system form a uniform mass of fibers, running anteromediodorsally. They reach the dorsal parts of the area principalis and from there, through the area sublenticularis, the caudal parts of the globus pallidus. Some of these fibers penetrate as far as a region adjacent to the medial boundary of the

globus pallidus and reach the vicinities of the nucleus interstitialis striae terminalis (Figs. 3 and 4, IST).

Fig. 3. Horizontal section through the dog brain, Weigert stain. Note the system of fibers, passing from the substantia innominata to the posterior portions of the globus pallidus

Fibers, running anteromedially which predominate in the lateroventral parts of area lateralis, make up a system, associated with the medial forebrain bundle (Figs. 5, 6 and 8). This system consists of fibers, coming from the anterior parts of basal and lateral nuclei of the amygdala and of those, coming from the pyriform cortex. To join the medial forebrain bundle, these fibers pass from the lateral area to the area principalis where they turn caudomedially (Figs. 5, 6 and 8).

A part of fibers, coming out of the medial parts of basal and lateral nuclei of the amygdaloid complex and primarily those from the pyriform cortex, join the posterior part of the anterior commissure. These fibers,

visible only in the posterior parts of the lateral area, run anterodorsally, more and more converging. After joining a compact fiber bundle of the anterior commissure, they run anteromedially (Figs. 1, 2 and 8).

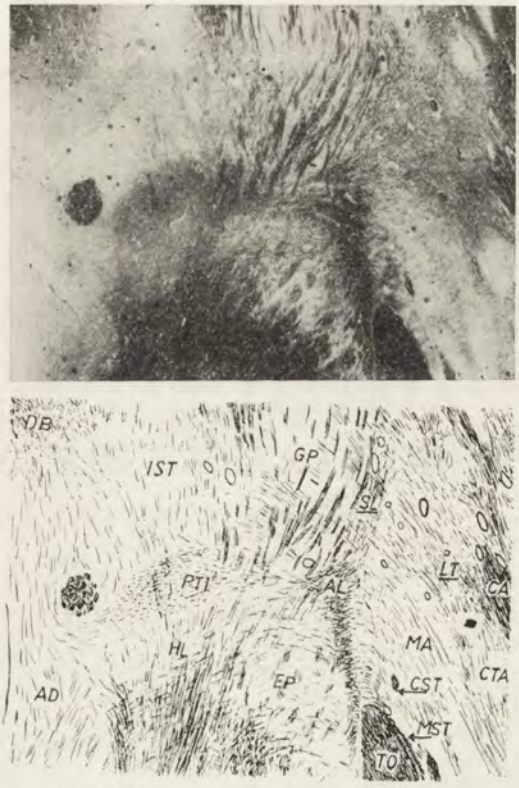

Fig. 4. Horizontal section through the dog brain, Weigert stain. Note the fibers, passing from the anterior portions of the amygdaloid complex, via the substantia innominata, the globus pallidus and the olfactory tubercle

The systems of fibers, described above, are also penetrated by fibers which run orally and oromedially. Some of them come from the basal nucleus, some others — from the lateral nucleus of the amygdala and, in the lateroventral parts of area lateralis, there also occur fibers coming from the pyriform cortex. After passing the lateral area, these fibers reach the anterior parts of the area principalis and, through them, the olfactory tubercle (Figs. 6 and 8, TUB).

In addition to fibers, related to the amygdaloid complex and pyriform cortex, there are other systems, represented in the lateral area. Fibers,

running ventroromedially, detach from the dorsal part of the external capsule and spread over the entire lateral area but they also may be seen in the area principalis (Figs. 1 and 2). It is difficult to determine, however, whether these fibers leave substantia innominata or not.

Fig. 5. Horizontal section through the dog brain, Weigert stain. Note the connections of the medial forebrain bundle with the fiber systems, coming from the basal and the lateral nuclei of the amygdala and from the pyriform cortex

A system, running parallel to the former, but leaving the ventral part of the external capsule, comes from the claustrum (Figs. 1 and 2, CL). These fibers are directed towards the area principalis and, presumably, they join the medial forebrain bundle.

Finally, medio-orally running fibers may also be seen in the latero-ventral parts of the area lateralis. After passing to the area principalis, these fibers turn medially, hereafter — mediocaudally and, finally, together with the medial forebrain bundle they reach the lateral nucleus of the hypothalamus. These fibers come from the prepyriform cortex (Fig. 2, CPP).

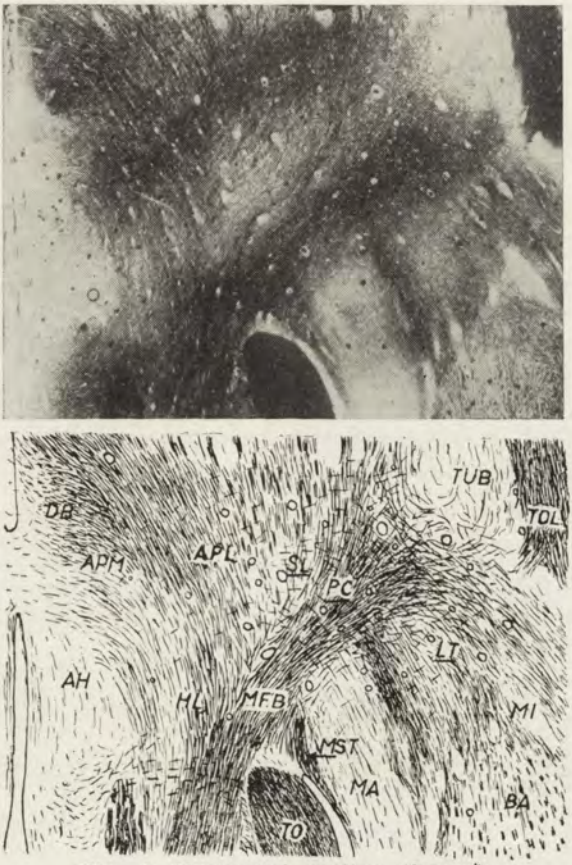

Fig. 6. Horizontal section through the dog brain, Weigert stain. Note the connections of the medial forebrain bundle with the olfactory tubercle, as well as — via the systems, visible in area lateralis (LT) — with the anterior portions of the amygdaloid complex and with the pyriform cortex

The area principalis (Figs. 1, 2, 5, 6 and 8, PC) is situated ventromedially to the area lateralis. Its posterior boundary is formed by the anterior parts of the medial and cortical nuclei of the amygdaloid complex and

the nucleus of the lateral olfactory tract. The area principalis adjoins the medial boundary of the area lateralis and, medially, the anterior sections of the hypothalamus and the lateral preoptic area. The area diagonalis ventralis makes up an anteromedial boundary of this region. Dorsally, the area principalis borders on the sublenticular area, whereas the surface of the brain makes up the ventral boundary of the area principalis.

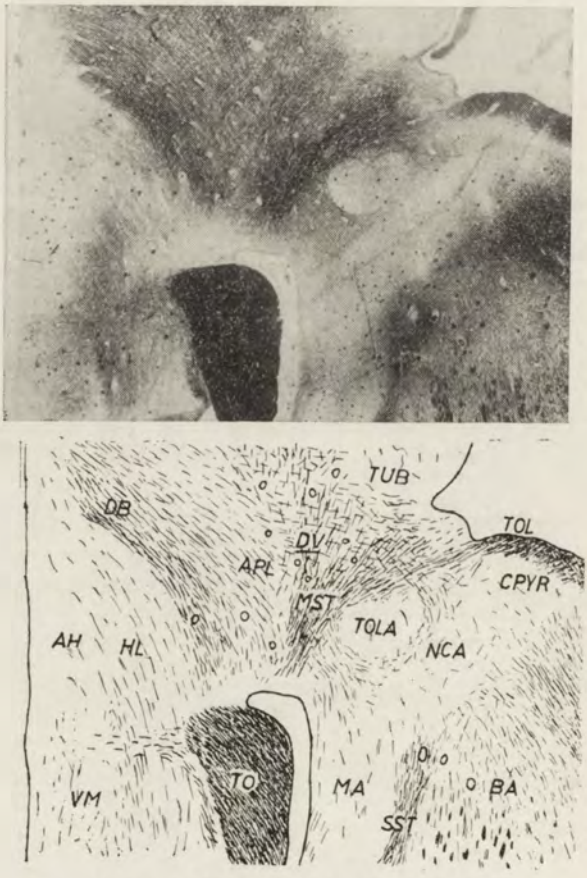

Fig. 7. Horizontal section through the dog brain, Weigert stain. Note the connections of the stria medullaris component of the stria terminalis (MST) with the lateral olfactory tract (TOL)

The area principalis directly adjoins the anteroventral parts of the brain stem and, therefore, fibers, coming from the hypothalamus, as well as from the thalamus and the habenula are numerously represented in this region.

A lateral branch of the medial forebrain bundle (Figs. 5, 6 and 8, MFB) penetrates, through the medial boundary, into the area principalis. Fibers, belonging to this system run anterolaterally and make up the main component of the fiber network of area principalis. Many of them reach as far as the anterior boundary of area principalis and pass to the olfactory tubercle. Some of them terminate in this place, some others extend further anteriorly and reach the caudal parts of the anterior olfactory nucleus. A part of fibers, coming from the medial forebrain bundle, turn laterally, passing to the area lateralis and, further on, in the direction of lateral and basal nuclei of the amygdala, as well as the pyriform cortex. Fibers, coming from the medial forebrain bundle, also reach, through area lateralis, the pyriform cortex (Fig. 2, CPP), their connections with claustrum and the external capsule being likely as well.

Fibers, coming from the inferior thalamic peduncle (Figs. 1, 3–5 and 8, PTI) abundantly occur in the dorsomedial parts of the area principalis. They come from the anterior parts of the thalamus and, in part, from the stria medullaris thalami. They run lateroventrally, dispersing all over the substantia innominata. Their further trace, cannot be determined to any reliable degree of certainty but their connections with the amygdaloid complex and olfactory tubercle are very likely. Some fibers, coming from the inferior thalamic peduncle, turn anterolaterodorsally and, after passing from the area principalis to the area sublenticularis, intermingle with fibers of the ansa lenticularis (Fig. 1).

The bundle of fibers, known as the stria medullaris component of the stria terminalis (Figs. 1 and 3–7, MST) enters posteriorly the mediocaudal parts of the area principalis. It comes from the stria medullaris from which it detaches at the anterior end of the thalamus and, together with the stria terminalis bundles, runs posteriorly. After encircling the internal capsule, it passes close to the amygdaloid complex, running near the surface of the optic tract and, finally, in the region of the optic chiasma, penetrates the mediocaudal parts of the substantia innominata (Miodoński 1965, 1966). Within the area principalis, the stria medullaris component of the stria terminalis runs anteriorly, beneath the fibers of the medial forebrain bundle, towards the olfactory tubercle. A part of its fibers, however, run orolaterally and join the lateral olfactory tract (Fig. 7, TOL).

A dense system of fine fibers, running medio-orodorsally (Figs. 4–6 and 8, MA) from the anterior parts of the medial nucleus of the amygdaloid complex penetrates the area principalis. The fibers enter the gaps between the fibers of the medial forebrain bundle and run towards the anterior parts of the hypothalamus and the preoptic area.

The area sublenticularis (Figs. 1–6 and 8, SL) is a flat formation, adhering to the ventral boundary of the globus pallidus and contacting, with its lateral part, the base of the putamen. This region is an intermediary area between these two structures and the rest of the substantia innominata. Below, area sublenticularis passes, without any distinct boundary, into area principalis and lateralis (Figs. 1–2).

The area sublenticularis is best-developed in the caudal parts of substantia innominata, posteriorly it stretches as far as above the central nucleus of the amygdala but, anteriorly, it becomes ever thinner to disappear finally off the caudal boundary of the olfactory tubercle.

Fibers, running ventromedially and parallel to the lower surface of globus pallidus, predominate among other ones, filling the area sublenticularis. They come from the ansa lenticularis and from the inferior thalamic peduncle and, together, form a system, called, the ansa peduncularis (Klingler and Gloor 1960). These fibers partially enter the globus pallidus mostly, however, they terminate in the ventral parts of the putamen.

Lamina medullaris externa (Fig. 1–2, LE), a system of fibers, running downwards along the boundary between the globus pallidus and the putamen, is another type fibers, entering the area sublenticularis. They run ventromedially and, after passing from the area sublenticularis to the area principalis, disperse among other systems of fibers that occur in this region. Their further trace can hardly be determined.

Fibers, coming from the ventral parts of the globus pallidus and the putamen behave in a much the same manner as those, described above but a part of them, instead of reaching the area principalis, reach the area diagonalis ventralis (Fig. 2, DV).

A system of somewhat thinner and less stainable fibers, penetrates the gaps between the fibers, mentioned above. Their trace is also different. The place of origin of these fibers is located in the anterior parts of the amygdaloid complex. In addition to fibers, coming from the longitudinal association bundle (Miodoński 1965, Fox 1943), this system consists of other ones which are present in the basal and central nuclei of the amygdala, among them, the fibers, coming from the hippocampal gyrus. From the anterior parts of the amygdoloid complex, these fibers run anteromediodorsally, through the area principalis, to the area sublenticularis from where they penetrate the ventrocaudal parts of the globus pallidus and, within it, they turn yet more medially (Figs. 3 and 4). A part of them reach the medial boundary of the globus pallidus and, after passing it, the vicinity of the interstitial nucleus of the stria terminalis. The rest of them appear to terminate in the region of the globus pallidus.

Within the area sublenticularis, in particular in its dorsolateral part, there occurs a small concentration of large, intensively stained cells. They are triangular and, sometimes, polygonal in shape. These concentrations correspond to that, described in the literature as the basal ganglion of Maynert (Laursen 1955, Kappers et al. 1936, Emmers and Akert 1963). Among the fibers of the lamina medullaris externa they occur most abundantly.

The area diagonalis ventralis (Figs. 1 and 7, DV) is lowermost part of the diagonal band of Broca. Laterally, it passes — without any distinct boundary — into the area principalis, medially, joins the nucleus diagonalis angularis (Clara 1959), borders on the area sublenticularis and, ventrally, contacts the ventral surface of the brain, forming on it a clearly visible convexity. Posterior parts of this region touch the area preoptic lateralis, anterior ones — reach the olfactory tubercle.

Fibers that are visible in the area diagonalis ventralis come from somewhat more dorsally placed parts of the diagonal band of Broca. They run laterocaudally. Many of them turn caudally and, together with the medial forebrain bundle fibers enter the lateral nucleus of the hypothalamus. The fibers that run laterally form two bundles, the dorsal one entering the area sublenticularis, the ventral — the area principalis.

Fibers, entering the area sublenticularis, are less numerous and take a laterodorsal direction in which they are similar to most fibers observed in this region (Fig. 2). They seem to join the ventral parts of the putamen.

Fibers, passing from the area diagonalis ventralis to the area principalis are more numerous (Figs. 2 and 8). Some of them run, through the area principalis towards the ventral parts of the external capsule and pyriform cortex, others turn caudally and extend to the anterior nuclei of the amygdaloid complex. Most fibers, coming from the diagonal band of Broca seem, however, to terminate in the substantia innominata and mainly in the area principalis and in the medial parts of the area lateralis.

Connections of substantia innominata

The substantia innominata is situated between structures concerned with the olfactory function, the hypothalamus and other parts the diencephalon, as well as the amygdaloid complex (Fig. 8). Consequently, this region is crossed by the olfacto-hypothalamic and olfacto-epithalamic tracts, as well as by tracts which connect the olfactory tubercle with the amygdaloid complex. In addition to olfactory connections the sub-

stantia innominata is passed by the fibers which associate (link up) the amygdaloid complex with the hypothalamus and the amygdaloid complex with the globus pallidus. It is also passed by the fibers which link up the thalamus and the epithalamus and the lateroventral parts of the telencephalon. Furthermore, the substantia innominata seems to be a destination place of many fibers which leave the diagonal band of Broca.

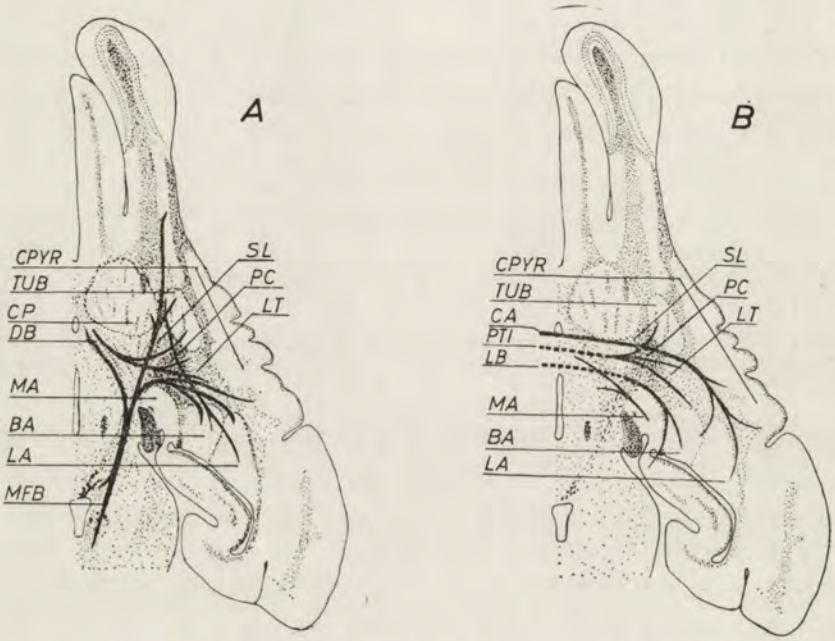

Fig. 8. Projection of larger tracts, passing through the substantia innominata, on the plane of Fig. 6. Smaller tracts, described in the text, have been omitted for the sake of clarity of the diagram. In particular the trace of fibers, coming from the external capsule connections with the claustrum, the trace of the stria medullaris component of the stria terminalis and its connections with the lateral olfactory tract were not considered. In addition, the diagram does not depict the connections of the substantia innominata with the putamen and with the lamina medullaris externa

Connections with the medial forebrain bundle. A compact system of fibers, running anterolaterally, which, within the lateral hypothalamic nucleus, detaches from the medial forebrain bundle, forming its lateral branch (Figs. 5, 6, 8), comes from the lateral parts of the hypothalamus and from the lateral preoptic area and enters the area principalis. These fibers represent the connections of the hypothalamus and the mesencephalic tegmentum with the anterobasal parts of the brain hemisphere. Most of these fibers run forwards and disperse in the olfactory tubercle,

while a smaller part of them reaches the mediocaudal parts of the anterior olfactory nucleus (L o h m a n 1963). They make up the olfacto-hypothalamic connections.

Many fibers, coming from the medial forebrain bundle turn laterally and pass across the area principalis and the area lateralis towards the prepyriform and pyriform cortex, as well as towards the claustrum and ventral parts of the external capsule (Figs. 2, 5 and 6). They form cortico-hypothalamic connections.

Fibers, running towards the anterior parts of the amygdaloid complex are the third group of fibers, coming from the medial forebrain bundle. Extending laterally, they pass from the area principalis to the area lateralis and, hereafter, turn caudally and disperse in the anterior parts of the basal and lateral nuclei of the amygdaloid complex (Figs. 5, 6 and 8). There is only a very slight connection of these fibers with the medial and cortical nuclei of the amygdaloid complex, whereas the central nucleus of the amygdala is a place they never reach.

Some fibers, coming from the medial forebrain bundle pass from the area principalis to the area sublenticularis. They may be connected with the globus pallidus and with the ventral parts of the putamen.

Connections with the amygdaloid complex. Substantia innominata limits the amygdaloid complex anteriorly and, therefore, all fibers leaving the amygdala and running medio-orodorsally, come out of the lateral amygdaloid nucleus, the putaminal nucleus (M a k s y m o w i c z 1963, M i o d o ń s k i 1965) and the basal amygdaloid nucleus. A part of them, passing the area lateralis of the substantia innominata, converge and join the posterior part of the anterior commissure (Fig. 1, 2 and 8). Others run anteriorly and medially towards the area principalis (Figs. 5, 6 and 8) through which they reach the olfactory tubercle which is a place where they probably terminate. The most dorsal ones seem to reach the caudato-putamen which is situated above the olfactory tubercle.

Fibers that deflect medially, passing the area principalis, take an identical direction with those of the medial forebrain bundle so that both these systems cannot be distinguished in the medial parts of the area principalis. These are fibers coming from the basal and lateral nuclei of the amygdaloid complex. They have been more accurately described above when the connections with the medial forebrain bundle were discussed.

A large system of fibers coming out of the basal and central nuclei of the amygdaloid complex which is called the longitudinal association bundle (F o x 1943, M i o d o ń s k i 1965) disperses in the dorsocaudal parts of the area lateralis. In addition, this system contains fibers which,

coming out of the hippocampal gyrus reach the substantia innominata through the dorsal part of the basal nucleus of the amygdaloid complex (Miodoński 1965). No single components of this system can be distinguished within the area principalis. This system, passing the area principalis, deviates medially and, through the area sublenticularis, enters the posterior parts of the globus pallidus. In horizontal sections, it is fairly well visible between the globus pallidus and the more caudally situated nucleus entopeduncularis (Figs. 3, 4 and 8). Some fibers, coming from this system reach the medial boundary of the globus pallidus and disperse in the adjacent region. The connections of these fibers with the bed nucleus of the stria terminalis (IST) are very likely.

Fibers, coming from the medial nucleus of the amygdala behave somewhat differently. This nucleus is situated more anteriorly than the remaining nuclei of the amygdaloid complex. It adheres to the caudal parts of the area principalis, while the medial forebrain bundle fibers run almost parallel to the anterior boundary of the medial nucleus of the amygdaloid complex (Fig. 6). Despite a near neighborhood of the medial nucleus of the amygdaloid complex and the medial forebrain bundle only few fibers within this nucleus seem to come from this pathway. However, there exists a system of numerous fine fibers, coming from the medial nucleus of the amygdaloid complex, which, running anteromedially, intersect the medial forebrain bundle, reaching the preoptic area and the anterior parts of the lateral nucleus of the hypothalamus (Figs. 5, 6 and 8).

Fibers, coming from the anterior sections of the cortical nucleus of the amygdaloid complex run anterolaterally, through the ventral parts of area lateralis and join the lateral olfactory tract (Fig. 7). Some of them come from the anterior parts of the medial nucleus of the amygdaloid complex, as well as from the nucleus of the lateral olfactory tract.

Connections with diagonal band of Broca. The diagonal band of Broca is a band of fibers and cells which onginates at the base of the medial nucleus of the septum (Lohman 1963) and, extending ventrally and laterally, runs towards the substantia innominata. A part of the diagonal band, occupying the ventromedial corner of the brain hemisphere, is sometimes called the angular diagonal nucleus and its lower part, associated with substantia innominata, the ventral diagonal nucleus (Clara 1959).

The area diagonalis discussed in the present paper, corresponds to the ventral diagonal nucleus, described by Clara. The fibers of the diagonal band of Broca, after passing the area diagonalis ventralis, run laterolateroventrocaudally and enter the area principalis (Fig. 2.). From this place they scatter all over the substantia innominata, reaching the area lateralis and the area sublenticularis. A part of the fibers from the area sublenticu-

laris reach the vicinity of the ventral boundary of the putamen and the fibers from the area lateralis come to the region of the anterior sections of amygdala and the pyriform cortex. Anteriorly, the fibers belonging to the diagonal band of Broca reach the boundary between the substantia innominata and the olfactory tubercle, whereas those runnig anterolaterally cross this boundary and come to the olfactory tubercle. Most fibers, coming from the diagonal band of Broca seem, however, to terminate in the substantia innominata.

Connections with the inferior thalamic peduncle and the stria medullaris. Fibers, coming from the anterodorsal group of the thalamic nuclei (Valverde 1963, Gastaut and Lammers 1961), as well as those from stria medullaris of the thalamus are concentrated in a system designated as the pedunculus inferior of the thalamus. Fibers from the thalamus cannot be distinguished from those from the stria medullaris of the thalamus (Figs. 1, 3–5 and 8).

Pedunculus thalami inferior, running lateroventrally, reaches the mediodorsal boundary of the area principalis from where its fibers scatter within the area sublenticularis and area lateralis. It is likely that its fibers reach the anterior parts of the amygdaloid complex, as well as the fibers running from the stria medullaris — to the olfactory tubercle.

Stria terminalis pars ad striam medullarem is a bundle of fibers that detach themselves from the stria medullaris on the anterior surface of the thalamus and join the stria terminalis (Miodoński 1965, 1966). Like the rest of the components, pars ad striam medullarem (the stria terminalis component of the stria medullaris) encircles the internal capsule and reaches the vicinities of the mediodorsal parts of the amygdaloid complex. However, whereas other components of stria terminalis deviate towards the amygdaloid complex, stria terminalis pars ad striam medullarem passes the amygdaloid complex, running anteriorly and medially in a close neighborhood of the laterodorsal boundary of the opic tract (Miodoński 1965, 1966). After reaching the mediocaudal part of area principalis, the stria terminalis pars ad striam medullarem runs anterolaterally towards the olfactory tubercle but part of its fibers distinctly join the lateral olfactory tract and, together with it, runs anteriorly (Fig. 7).

Connections with the globus pallidus and the putamen. Fibers, coming from the globus pallidus and the putamen, enter the substantia innominata through the area sublenticularis, those running ventromedially (Fig. 1 and 2) being the most numerous. They come from the ventral parts of the putamen, from the globus pallidus and from the lamina medullaris externa. Ventrally, they join the ansa lenticularis and pedunculus inferior of the thalamus. A part of them enters the area principalis and, more anteriorly, the ventral diagonal area (Figs. 1 and 2).

A system of fibers, running anteromedially from the area principalis to the area sublenticularis, makes up a connection of the anterior portions of the basal nucleus and the central nucleus of the amygdaloid complex, as well as of the hippocampal gyrus with the globus pallidus and areas adjacent to its medial boundary.

Connections with the anterior commissure. The posterior part of the anterior commissure (Figs. 1–4 and 8, CA) disperses in the anterodorsolateral parts of the area lateralis and is a place of origin of fine fibers that run posteriorly along the boundary between the lateral and putaminal nuclei of the amygdaloid complex (Miodoński 1965). As it runs posteriorly, this system deviates ventrally, enriching in fibers the ventral part of the external capsule. Fibers, coming from the anterior commissure, after passing the area lateralis, disperse primarily in the prepyriform and pyriform cortices, the lateral and putaminal nuclei, as well as — in part — in the basal nucleus of the amygdala. The rest of the amygdaloid nuclei do not connect with the posterior part of the anterior commissure.

Connections with the external capsule and claustrum. Fibers, coming from the external capsule are abundantly represented in the substantia innominata. Mostly, they come from the upper part of the external capsule and, running ventroromedially, disperse in a fanwise manner within the area lateralis (Figs. 1 and 2). A part of them join the fibers of the posterior part of the anterior commissure, whereas other parts run downwards, towards the pyriform cortex, towards the anterior sections of the amygdala and towards the area principalis.

A system of fibers, coming from the claustrum (Figs. 1 and 2) penetrates between the fibers of external capsule and reaches the area lateralis. They run mediorally, then medially and finally, they enter area principalis, probably joing the fibers of the medial forebrain bundle which make for the hypothalamus.

Connections with the pyriform and prepyriform cortex. Fibers, coming from the pyriform cortex run anterioly and dorsally (Fig. 1). Many of them, after passing the area lateralis, join the posterior part of the anterior commissure. Others turn dorsally and join the fibers of the external capsule. In addition, many fibers run anteriorly from the pyriform cortex towards the olfactory tubercle. Some fibers from the pyriform cortex join those from the medial forebrain bundle.

The prepyriform cortex is a place of origin of fibers which — like those from the pyriform cortex—join the external capsule and the olfactory tubercle. Likewise, it is also a place of origin of fibers, running medially through the area principalis towards its medial boundary where they

disappear among the fibers of the medial forebrain bundle, making for the hypothalamus (Fig. 2).

Connections with the olfactory tubercle, anterior olfactory nucleus and lateral olfactory tract. The olfactory tubercle is an area from which abundant fibers run posteriorly through the substantia innominata. The medial forebrain bundle, amygdaloid complex and the adjacent cortex are the main recipients of these fibers (Fig. 8).

Fibers, passing from the olfactory tubercle through the area lateralis, reach the basal and lateral nuclei of the amygdaloid complex, as well as the prepyriform and pyriform cortex. Fibers, making for the cortex take a lateroventral position to those, running to the amygdaloid complex.

Fibers from the olfactory tubercle, entering the area principalis, run mediocaurally (Figs, 5, 6 and 8) to join o lateral branch of the medial forebrain bundle, the pedunculus inferior of the thalamus or the stria medullaris component of the stria terminalis.

The lateral olfactory tract runs along the lateroventral boundary of the substantia innominata. Some of its fibers deviate medially and run through the ventral parts of the substantia innominata to the nucleus of the lateral olfactory tract, to the medial and cortical nuclei of the amygdaloid complex. A part of them joins the stria medullaris component of the stria terminalis.

Fibers, running posteriorly from the ventromedial parts of the anterior olfactory nucleus, after passing through the olfactory tubercle, penetrate the anterior parts of the area principalis where they join the fibers of the medial forebrain bundle (Lohman 1963) and, together with them, make for the hypothalamus.

DISCUSSION

The nomenclature, concerning the area situated in front of the amygdaloid complex and reaching to the olfactory tubercle is nonuniform and inaccurate. This area has usually been described in connection with adjacent structures and most frequently referred to as the anterior amygdaloid area (Crosby and Humphrey 1944, Lauer 1949, Johnson 1957a,b, Gastaut and Lammers 1961, Lohman 1963). Some investigators have called it the bed nucleus of the medial forebrain bundle or, simply, the medial forebrain bundle (Smith 1930, Young 1936, Valverde 1963). On account of its close neighborhood with the globus pallidus and the putamen, situated above it, this region has sometimes been called, the "sublenticular gray" or "basale Kerngruppe" (Kappers et al. 1936, Clara 1959).

The boundaries of the substantia innominata have been inaccurately

determined. It is in particular the boundary with the lateral preoptic area that displays — in different papers — a tendency to shift more or less lateral (Humphrey 1936, Crosby and Humphrey 1944, Lauer 1949, Bleier 1961, Lohman 1963). Sometimes, the name substantia innominata has been used to determine this region (Villiger 1946).

Substantia innominata has no sharp boundaries. The cells which fill it are large and triangular or polygonal in shape and resemble those of the adjacent parts of the hypothalamus, lateral preoptic area, diagonal band of Broca and the amygdaloid complex. The cells, situated nearer the surface of the brain do not differ at all from those situated within the substantia innominata. They condense slightly near the ventral surface but do not form a compact layer which could be identified with the cortex.

The division of the substantia innominata, suggested in the present paper, is based on the myeloarchitectonics of this area. The cytoarchitectonics of the substantia innominata is comparatively homogenous. In fact, the myeloarchitectonic areas, distinguished here, also do not differ considerably: the fiber systems, met within one part, occur also in other parts, although in different quantities.

All fibers, coming out of the amygdaloid complex and running anteriorly, pass the substantia innominata. Much attention has been paid to these fibers. Smith (1930) investigated them up to a region which he determined as the "medial forebrain bundle" and the "diagonal band". The tract, described by Humphrey (1936) as "tractus tuberculo-amygdaloideus" and which connects the olfactory tubercle with the amygdala lateralis nucleus also belongs to this system. Fibers deriving from the amygdaloid complex and running anteriorly are determined by Gastaut and Lammers (1961) as amygdalo-septohypothalamic connections. "Ventral amygdalo-hypothalamic tract and amygdalo-septal tract", as opposed to the stria terminalis, are distinguished by Klingler and Gloor (1960). Fox (1943) describes a tract which leaves the amygdala and runs anteriorly as the "longitudinal association bundle". In the cat, this bundle passes — in the form of a compact bunch — below the internal capsule and disperses in the interstitial nucleus of the stria terminalis. Two tracts, near earch other, are distinguished by Valverde (1963) in an area, situated anteriorly to the amygdaloid complex. He calls them the "longitudinal association bundle" and the "ventral amygdalofugal pathway".

In the dog, the system of fibers, coming out of the amygdaloid complex and running anteriorly, may be divided into a few components. They originate in different parts of the amygdaloid complex and reach different regions of the brain. A component, corresponding to the tuberculo-amygdaloid tract, described by Humphrey (1936), comes out of amygdaloid

lateral nucleus and of the lateral parts of the basal nucleus and reaches the olfactory tubercle. The medial and cortical nuclei of the amygdaloid complex do not send fibers towards the olfactory tubercle but, like the nucleus of the lateral olfactory tract, join the lateral olfactory tract. The central nucleus of the amygdala seems not to have direct connections with the olfactory parts of the brain.

A band of fibers which come from the anterior parts of the basal and central nuclei of the amygdaloid complex, and from the hippocampal gyrus (Miodoński 1965) is another component of a system, originating in the amygdaloid complex and running anteriorly. These fibers are directed anteromediodorsally and they penetrate the ventrocaudal parts of the globus pallidus. They reach the area which directly adjoins the medial boundary of the globus pallidus. A part of them, however, terminates on the way. The longitudinal association bundle, described by Fox (1943) must have been running among these fibers. Ranson et al. (1941) describe fibers, coming from the amygdaloid complex and passing through the ventral parts of the globus pallidus. It is likely that they correspond to the system, described above.

Fibers coming from the lateral and basal nuclei of the amygdaloid complex join the medial forebrain bundle. They come out of the anterior parts of both nuclei, running antero-medially and, afterwards, together with the medial forebrain bundle fibers, posteriorly. They make up a connection between the amygdaloid complex and hypothalamus, some of them probably running towards the lower sections of the cerebrum (Craigie 1928, Kappers et al. 1936, Gloor 1955, Gastaut and Lammers 1961).

A system of fine fibers which anteromedially penetrate the gaps between the medial forebrain bundle fibers is sent forth anteriorly by the medial nucleus of the amygdaloid complex. They constitute the fourth component of the system of fibers coming out of the amygdaloid complex and, running anteriorly, they reach anterior parts of the hypothalamus and the preoptic area.

The lateral and putaminal nuclei of the amygdaloid complex (Maksymowicz 1963, Miodoński 1965), as well as the lateral parts of the amygdaloid basal nucleus join the posterior part of the anterior commissure. This corresponds to the connections, described by Humphrey (1936) in the bat.

The diagonal band of Broca is considered by many authors one of the major tracts, connected with the amygdaloid complex (Kappers et al. 1936, Johnson 1957 a,b, Klingler and Gloor 1960, Gastaut and Lammers 1961). Little attention is, however, paid to its division within the amygdaloid complex. According to my obser-

vations, most fibers of the diagonal band of Broca terminate in the substantia innominata. Some of them run towards the prepyriform cortex, some other—towards the nucleus lentiformis and the olfactory tubercle. Only very few fibers, running to the prepyriform cortex could be believed to be related to the lateral amygdaloid nucleus.

The lateral branch of the medial forebrain bundle passes the substantia innominata. Among its fibers, the following components are distinguished by Young (1936), the tuberculo-hypothalamic tract, striohypothalamic tract, septo- and cortico-hypothalamic tracts. Zyo et al. (1963) find among the medial forebrain bundle fibers such ones which terminate in the preamygdaloid cortex. Lohman's (1963) observations, concerning the medial forebrain bundle are in full conformity with those of other authors.

Within the medial forebrain bundle in the dog, similar components may be distinguished to those described in the literature. A part, coming out of the caudomedial parts of the anterior olfactory nucleus (Lohman 1963) constitutes the most anterior portion of the medial forebrain bundle. Somewhat more posteriorly, this component is joined by fibers, coming from the olfactory tubercle. However, many fibers join the medial forebrain bundle within the substantia innominata. These are fibers, coming from the prepyriform and pyriform cortex and lower parts of the claustrum which make up the lateral cortico-hypothalamic tract, as well as those from the amygdaloid complex and from the nucleus lentiformis. Fibers, connecting the amygdaloid complex with the medial forebrain bundle come from the basal and lateral amygdaloid nuclei. They run medio-orally and, after joining the medial forebrain bundle delfect posteriorly. With our material, it was difficult to determine the place where these fibers terminate. A part of them may terminate in the lateral nucleus of the hypothalamus, others may run towards lower part of the cerebrum (Craigie 1928, Kappers et al. 1936, Gloor 1955, Gastaut and Lammers 1961).

The pedunculus inferior of the thalamus makes up a system of fibers which, run lateroventrally from the anterior parts of the thalamus. After reaching the laterodorsal boundary of the substantia innominata, they disperse all over its range.

Among other fibers, pedunculus inferior of the thalamus consists of those, coming from the mediodorsal nucleus of the thalamus (Droogleever-Fortuyn et al. 1959, Valverde 1963, Gastaut and Lammers 1961), as well as those, coming from nucleus parataenialis and from the thalamic stria medullaris (Droogleever-Fortuyn et al. 1959). Fibers from the stria medullaris terminate in the olfactory tubercle (tractus olfacto-habenularis), in the substan-

tia innominata (Mitchell 1963), in the pyriform cortex and in amygdala (the lateral cortico-habenular tract, Laursen 1955). Fibers from the mediodorsal nucleus of the thalamus disperse over the entire substantia innominata (Rioch 1931), reaching the anterior temporal neocortex and the amygdala (Droogleever-Fortuyn et al. 1959, Klingler and Gloor 1960, Gastaut and Lammers 1961, Valverde 1963). A part of fibers, coming from the inferior peduncle of the thalamus joins the ansa lenticularis, forming together with it, a band, determined as the ansa peduncularis (Klingler and Gloor 1960) which reaches ventral parts of the putamen.

Stria terminalis pars ad striam medullarem is the only component of the stria terminalis which does not join the amygdaloid complex (Miodoński 1965, 1966). It detaches from the stria medullaris of the thalamus on the anterior surface of the thalamus and joins the stria terminalis (Smith 1930, Mitchell 1963, Miodoński 1966). After encircling the internal capsule, the stria medullaris component of the stria terminalis passes by the amygdaloid complex and, through the substantia innominata, reaches the olfactory tubercle (Smith 1930, Miodoński 1966). A part of fibers from the stria terminalis pars ad striam medullarem join the lateral olfactory tract (Fig. 7).

An area, situated below the putamen and the globus pallidus, has in the present paper been called the area sublenticularis of the substantia innominata. The descriptions of this area may be met with in the literature. It is called either the nucleus ansae peduncularis of Maynert (Kappers et al. 1936), or the nucleus basalis Maynerti (Kodama 1929), or the ganglion basale of Maynert (Laursen 1955), or, sometimes, the nucleus subputaminalis (Kappers et al. 1936). Many fibers, running anterolaterally penetrate the gaps between the cells of this nucleus. These are fibers that come from the ansa lenticularis and from the inferior peduncle of the thalamus which together form the ansa peduncularis (Klingler and Gloor 1960). They reach the ventral parts of the putamen and the globus pallidus. Some of them, however, pass to the remaining parts of the substantia innominata and, according to Valverde (1963), reach the amygdala. The area sublenticularis is dorsally penetrated by fibers from the putamen, from the globus pallidus, as well as from the lamina medullaris externa. We were unable to determine the further trace of these fibers. However, they might reach the anterior part of the amygdala, in particular the anterior parts of the central nucleus of the amygdaloid complex.

Fibers, coming from the dorsal parts of the external capsule are distributed over the whole of the substantia innominata. They run primarily toward the prepyriform and pyriform cortex as well as towards

the anterior parts of the amygdaloid complex. Valverde (1963) describes fibers, connecting the anterior parts of the amygdala, via the substantia innominata (the anterior amygdaloid area), with the external capsule. He also describes other fibers which connect the amygdaloid complex with the claustrum. Among them, there are such fibers, running towards the area which — in the present paper — have been included in the substantia innominata. Our observations indicate that fibers, coming from the claustrum do pass through the substantia innominata. They run medially and, in the area principalis, intermingle with the fibers of the medial forebrain bundle.

SUMMARY

In substantia innominata, an area which fills the space between the anterior portions of the amygdaloid complex and the posterior boundary of the olfactory tubercle, four regions have been distinguished, different from each other in their myeloarchitectonics. The area lateralis, occupying the lateral part of the substantia innominata, is crossed by many fiber systems which run from the basal and lateral nuclei of the amygdaloid complex, from the prepyriform and pyriform cortex, from the external capsule and from the claustrum. These fibers reach the olfactory tubercle, the medial forebrain bundle and the posterior parts of the anterior commissure.

Within the area principalis, the predominant fibers are those, coming from the medial forebrain bundle and, through the area lateralis, reaching the anterior portions of the amygdaloid basal and lateral nuclei, the pyriform and prepyriform cortices and the claustrum, as well as the olfactory tubercle and mediocaudal parts of the anterior olfactory nucleus. A system of fibers coming from the basal and central nuclei of the amygdala, as well as from the hippocampal gyrus and which, via the ventrocaudal parts of the globus pallidus, reaches the region adjacent to its medial boundary, passes the area principalis. In addition, in this area, a system of fine fibers occurs, connecting the medial nucleus of the amygdaloid complex with the anterior portions of the hypothalamus and the preoptic area. These are fibers, coming from the stria medullaris component of the stria terminalis, running to the olfactory tubercle and to the lateral olfactory tract. The fibers of the inferior thalamic peduncle from the dorsolateral parts of the area principalis disperse over the entire substantia innominata. Coming from the stria medullaris thalami and from the mediodorsal and parataenial nuclei of the thalamus, these fibers reach the olfactory tubercle, the pyriform cortex, the anterior portions of the amygdaloid complex and the ventral parts of the putamen.

In relation to the area principalis, the area sublenticularis takes a dorsal position. It makes up part of the substantia innominata, directly contacting the globus pallidus and the putamen. It contains three types of fibers, (1) those coming from the ansa lenticularis and the inferior thalamic peduncle, (2) those from the diagonal band of Broca, from the putamen and from the globus pallidus and (3) those from the amygdaloid complex.

The area diagonalis ventralis constitutes the lower part of the diagonal band of Broca. It occupies an anteromedial position in relation to other portions of the substantia innominata. Fibers, seen in this region, run to the prepyriform and pyriform cortex, as well as, in part, to the putamen and amygdala. The main bulk of these fibers terminates, however, within the substantia innominata.

ABBREVIATIONS

AD,	area dorsalis hypothalami	LE,	lamina medullaris externa
AH,	nucleus anterior hypothalami	LT,	area lateralis
AL,	ansa lenticularis	MA,	nucleus medialis amygdalae
APL,	area praeoptica lateralis	MFB,	medial forebrain bundle
APM,	area praeoptica medialis	MI,	massa intercalata
BA,	nucleus basalis amygdalae	MST,	stria terminalis pars ad striam medullarem
CA,	commissura anterior		
CL,	claustrum	NCA,	nucleus corticalis amygdalae
CP.	caudato-putamen	PC,	area principalis
CPP,	cortex praepyriformis	PTI,	pedunculus thalami inferior
CPYR,	cortex pyriformis	PUT,	putamen
CST,	stria terminalis pars commissuralis	SL,	area sublenticularis
CTA,	nucleus centralis amygdalae	SM,	stria medullaris thalami
DB,	diagonal band of Broca	SO,	nucleus supraopticus
DV,	area diagonalis ventralis	SST,	stria terminalis pars supracommissuralis
EP,	nucleus entopeduncularis		
EX,	capsula externa	ST,	stria terminalis
GP,	globus pallidus	TO,	tractus opticus
HL,	nucleus lateralis hypothalami	TOL,	tractus olfactorius lateralis
IST,	nucleus interstitialis striae terminalis	TOLA,	nucleus tractus olfactorii lateralis
LA,	nucleus lateralis amygdalae	TUB,	tuberculum olfactorium
LB,	longitudinal association bundle	VM,	nucleus ventro-medialis hypothalami

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THE EFFECTS OF PIPRADROL, AMYLOBARBITONE, DRIVE AND EXTINCTION ON THE RELATION BETWEEN S^D INTENSITY AND OPERANT RESPONSE RATE[1]

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In an earlier paper (Gray 1965a), the positive relation between CS intensity and CR magnitude described by Pavlov as the "law of strength" (Pavlov 1927, Gray 1964a) and by Hull (1949) as "stimulus intensity dynamism" was demonstrated in an operant conditioning situation in which response rate on a variable interval (VI) schedule of positive reinforcement was the response measure and the intensity of a discriminative stimulus (S^D — white noise over the range 70–100 db. — was the stimulus variable. The work reported in the present paper uses the same situation to examine the effects on this relationship of variation in drive level and of a stimulant (pipradrol hydrochloride[3]) and a depressant (sodium amylobarbitone) drug.

The experiments were designed with two different theories in mind.

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[3] α-(-Piperidyl) benzhydrol hydrochloride ("Meratran"), kindly supplied by Merrell National (Laboratories) Ltd.

According to Pavlovian theory (Pavlov 1927, Gray 1964a), the law of strength holds only up to a limiting value of stimulus intensity, described as the "threshold of transmarginal or protective inhibition". This threshold itself depends on a number of variables. Among these are drugs and drive level. Briefly, it can be predicted from Pavlovian theory that the law of strength will suffer increasing distortions as (1) drive is increased and (2) the subject is exposed to increasing doses of a stimulant drug (Gray 1964a; Teplov 1964). Listed in order of increasing severity, the distortions of the law of strength which may be predicted are: (1) a decrease in the slope of the curve depicting the law of strength, owing to the fact that response magnitude at higher CS intensities approaches an asymptote; (2) the appearance of a non-monotonic relation between CS intensity and CR magnitude, such that highest response strength is reached at less than maximum CS intensity; and (3) a complete breakdown in the law of strength, response strength being equal at all CS intensities or even showing a negative relation to CS intensity (Gray 1964a, 1964b).

The second theoretical context for the experiments is provided by the hypothesis (Perkins 1953, Logan 1954) that stimulus intensity dynamism is due to generalisation of inhibition from the zero-intensity unreinforced stimulus (S^{Δ}) — usually included in experimental designs which have succeeded in demonstrating the phenomenon — to low intensities of the positive stimulus. On the whole, the available evidence supports this hypothesis (Gray 1965b). A related hypothesis has been proposed by the writer to account for the observation that there is a *negative* relation between S^{D} intensity and response rate during a subsequent presentation of S^{Δ} (Gray 1965a). This relationship was attributed to generalisation of *excitation* from low intensities of the reinforced stimulus to the zero-intensity unreinforced stimulus — a process acting in the same manner as, but in the opposite direction to, the generalisation of inhibition postulated by Perkins (1953) and Logan (1954).

If both these hypotheses are correct, certain consequences follow. Presumably, the extents to which, in the one case, inhibition, and, in the other, excitation generalise will be be related both to one another and to the subject's success in discriminating between positive and negative stimuli (since generalisation of either kind represents a failure of discrimination). In the first place, then, we may predict that the magnitude of the intensity dynamism effect will correlate positively with the degree to which the negative relation between S^{D} intensity and subsequent S^{Δ} response rate appears. Secondly, if discrimination is either perfect or completely absent, there will be, respectively, no generalisation or complete generalisation and, in either case, the relations between S^{D} intensity

and both S^D and S^Δ response rates must disappear; it follows that, between these two extremes, the two intensity functions must become more marked as discrimination improves from zero up to some maximum and then less marked again as discrimination approaches perfection.

The experiment investigates these various predictions by obtaining from rats curves relating response rate during both S^D and S^Δ to S^D intensity under four drug conditions (no drug, placebo, pipradrol and amylobarbitone) and at two levels of drive. Of the two drugs used, pipradrol was chosen because it belongs to the class of so-called "central nervous system stimulants" and, as we have seen, it is to this class that the predictions of Pavlovian theory apply. Amylobarbitone was included as an extra control, to determine whether any effects produced by pipradrol are confined to stimulant drugs or may also be produced by a drug of the "depressant" type. The effects of the two drugs on mean response rates, on the discrimination between S^D and S^Δ, and on other general features of the subjects' responding in the experimental situation have been described elsewhere (G r a y 1964c).

At the end of the main experiment, data were obtained on the effects of S^D intensity on response rate during experimental extinction, using only the no-drug condition. The interest of these data arises from the fact that a number of workers have reported that stimulus intensity may affect response magnitude during the learning or performance of a reinforced response, but cease to do so during extinction (see Gray 1965b for review). This finding could be of importance in accounting for the failure of some studies of stimulus intensity dynamism to find evidence for the phenomenon, since response magnitude has often been measured only in extinction (G r a y 1965b).

METHOD

Subjects. Ss were four adult male rats (r 32, 36, 41 and 80) belonging to the twenty-first generation (S_{21}) of the Maudsley Non-reactive strain (B r o a d h u r s t 1960)-designated MNR by J a y (1963)-and one hooded male (H 20) from a strain maintained at Birkbeck College, London. All Ss were experimentally naive. At the start of the experiment the Maudsley Ss were 161–167 days old; the hooded S was younger-93 days.

Apparatus. The apparatus consisted of three identical Skinner boxes, 8 in. high by 8 in. wide by 12 in. deep, each containing a single lever and a dipper mechanism which dispensed approximately 0.1 c.c. sweetened condensed milk diluted with water as the reinforcer, associated electronic equipment (housed in another room) for programming various schedules of reinforcement in these boxes, and a sound generation system (more

fully described by Gray 1965a) for producing and controlling the intensity of white noise delivered to pairs of eight-inch loud-speakers attached to the side of each box. Each Skinner box was contained within a larger box made of "Celotex". The lever was activated by a force of 12–14 gm. through a 0.125 in. excursion. A 1.2 w. bulb 3 in. above the food-trough was wired in parallel with the solenoid which operated the dipper mechanism and lit up for approximately 0.5 sec. whenever reinforcement was delivered. The intensities of noise used as discriminative stimuli were 70, 80, 85, 90 and 100 db.$\pm$1 db. (re. 0.0002 dynes/cm^2), as measured by a Dawe sound-level meter, type 1400D, roughly where the rat's head would be while responding on the lever. Ambient noise level in the experimental room was the order of 60–65 db.

Procedure. Preliminary Training. Ss were first accustomed to a twenty-two-hour food deprivation schedule. This was followed by three days of habituation during which they were placed in the conditioning boxes and exposed to the five noise intensities, in random order. No reinforcement was available at this time. Training on the barpressing response was then begun and feeding reduced to 1 hour a day. After six days all Ss were performing successfully on VI 30 sec. (Ferster and Skinner 1957). No noise was presented during this stage of the experiment. Training on the discrimination between noise and silence followed and continued for six days. By the end of this time all Ss were performing successfully on the schedule which was maintained for the rest of the experiment — alternating periods of noise plus reinforcement on VI 30 sec. and periods of silence with no reinforcement. Throughout discrimination training, noise intensity was allotted to period in a random order, all intensities occurring equally often.

Design of the Main Experiment. Ss were fed for 1 hr. a day. Each S was tested twice daily, once before and once after feeding. Each of these sessions lasted 55 mins. The first or "high drive" session began 22 hr. after the end of the previous day's feed; the second or "low drive" session began 1$^1/_2$ hr. after the end of feeding on that day. Injections were made $^1/_2$ hr. before each session; the same drug treatment was always given for the two sessions on the same day. Each session was considered to be made up of two half-sessions, each consisting of ten 2$^3/_4$-min. periods of alternating noise and silence. A session always began with a period of noise 15 sec. after S was placed in the conditioning box and ended with a period of silence. During noise (S^D), reinforcement was available on VI 30 sec.; during silence (S^Δ), no reinforcement was delivered. A 5$\times$5 Latin Square was used to randomise the allocation of noise-intensities to periods within a half-session, with days as the other aspect of the Square. Separate Latin Squares were randomly chosen for the four half-sessions mak-

ing up a day's testing, but the same Squares were used for all Ss and for all drug conditions. There were five days of testing (one per column of the Latin Square) under each of the four drug conditions: no drug, placebo, pipradrol and amylobarbitone. Drugs were randomly allocated to successive days within certain restrictions. These were: (a) that the two control conditions always alternated with the two experimental conditions and (b) that each condition occurred once in each successive block of four days. A separate drug condition order was chosen for each S.

Pipradrol was administered in a dose of 5 mg/kg to r 32, r 36, r 80 and H 20, and in a dose of 10 mg/kg to r 41. Amylobarbitone was given in a dose of 15 mg/kg to all Ss; at the end of the experiment, r 41 was tested for a further five days under 30 mg/kg amylobarbitone. Drugs were injected subcutaneously in physiological saline, which also served as the placebo in a dose of 4 c.c./kg. Testing lasted 20 days (25 for r 41).

Extinction. At the end of the experiment, each S was tested for a further five days under conditions of extinction. Apart from the omission of the reinforcer, the only other changes from the main experiment were that injections ceased, testing was reduced to one 55-min. session per day at 22-hr. hunger drive, and the method used to allocate intensities to noise-periods within each half-session was altered so that the data could either be combined across Ss into separate Latin Squares for each of the five test days or combined across days into a separate Square for each S. This change in the method of allocating intensities to periods was instituted so as to make it possible to evaluate interactions between Intensities and Days; these may well be of importance during extinction. The new method involved systematic permutation of a single column of a Latin Square, chosen at random, over both days and animals. On a given day, the order of intensities to which S was exposed was repeated twice, once in each half-session.

RESULTS

Fig. 1 presents mean response rates as a function of reinforcement, drug condition and S^D intensity for each S. The drug effects on mean response rates and on the discrimination between S^D and S^Δ, evident in this Figure, are dealt with elsewhere (G r a y 1964c); the present paper is confined to the effects of S^D intensity, either alone or in interaction with the other factors investigated.

The Effect of S^D Intensity on S^D and Subsequent S^Δ Response Rates. It can be seen from Fig. 1 that previous findings (G r a y 1965a) of a positive relation between S^D intensity and response rate during S^D and of a negative relation between S^D intensity and response rate during the

following period of S^{Δ} have been confirmed. Analyses of variance were carried out on the data from each S; these were done separately for S^{D} and S^{Δ} responses, so that there were two analyses corresponding to each

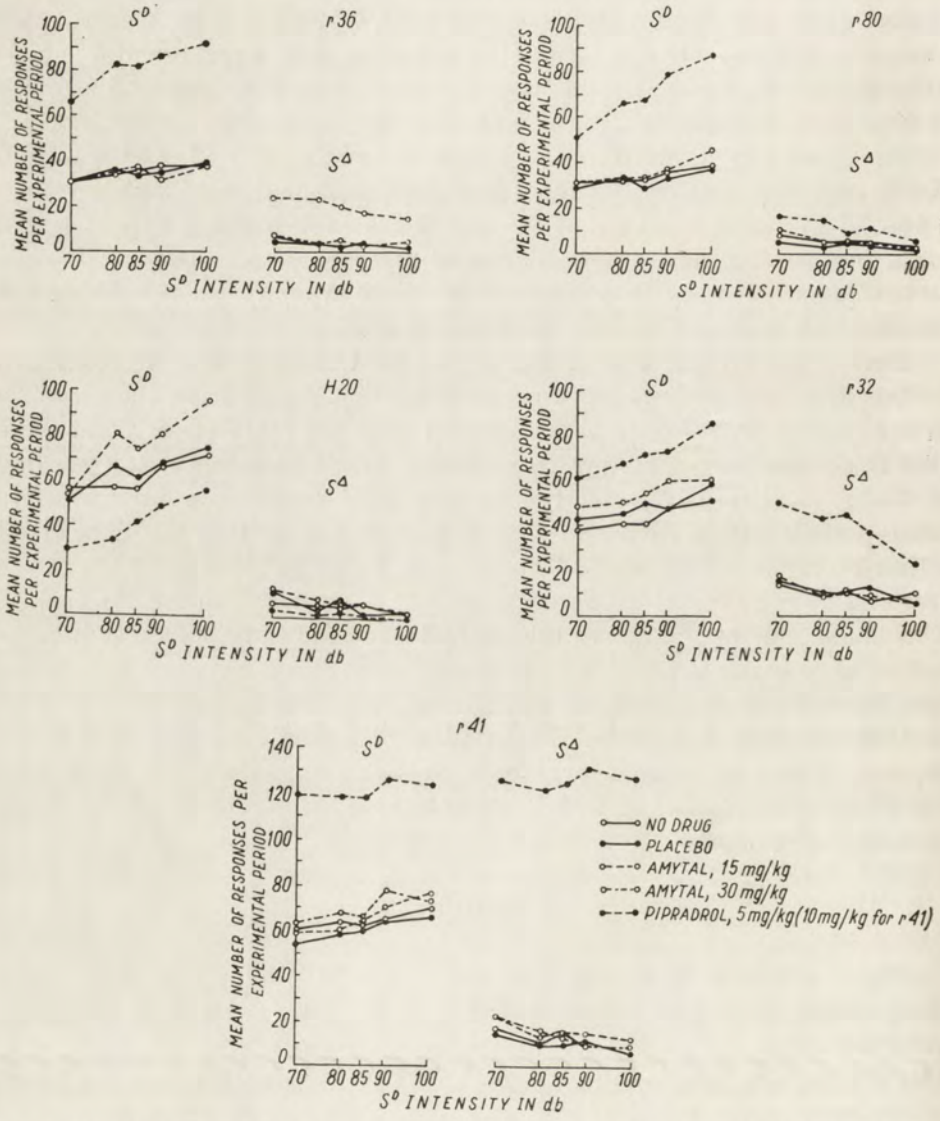

Fig. 1. The effects of S^{D} intensity on S^{D} response rate (left-hand graphs) and on subsequent S^{Δ} response rate (right-hand graphs) as a function of drug condition in five rats. Each point gives the mean number of responses in a 2¾-min. experimental period, either during presentation of the noise-intensity shown on the abscissa (S^{D} graphs) or after presentation of that noise-intensity (S^{Δ} graphs), and is based on twenty readings

of the five parts of Fig. 1. These 10 analyses of variance (henceforth termed the "Level I" analyses) gave highly consistent results. In each case, the main Intensity effect and linear regression of response rate on S^D intensity were highly significant ($p < .001$) and departures from linearity were non-significant; and in each case the regression line for S^D responding on S^D intensity had a positive slope and the regression line for S^Δ responding on preceding S^D intensity had a negative slope.

Drug Effects on the Relation between S^D Intensity and S^D Response Rate. In order to examine the data for drug effects of the kind predicted by Pavlovian theory, separate analyses of variance were carried out for each set of data represented by a single curve in Fig. 1, i.e. for each drug condition each S, S^D and S^Δ data again being treated separately. We shall refer to these 42 analyses of variance as the "Level II" analyses.

In the 21 Level II S^D analyses of variance, the term for Intensities was significant in all but three cases. However, in two of these cases (H 20,

Table I

Coefficients of linear regression (bS^D) of response rate during S^D on stimulus intensity: drug effects

Animal	No drug	Placebo	Amytal		Pipradrol	
			15 mg/kg	30 mg/kg	5 mg/kg	10 mg/kg
r 36	0.256	0.252	0.170		0.775*	
r 80	0.222	0.258	0.423		1.208**	
H 20	0.563	0.718	1.314**		0.999**	
r 32	0.452	0.482	0.448		0,760*	
r 41	0.304	0.442	0.633	0.421		0.213

Mean and standard deviation of No Drug and Placebo coefficients: 0.390±0.162. Entries in the Table are values for b in equations of the form $y = a + bx$, where y = no. of responses in a 2¾—min. period of S^D and x = S^D intensity in db. Entries marked with one asterisk differ from the mean of the control conditions at the five per cent level of significance; those marked with two asterisks differ from the mean of the control conditions at the one per cent level.

departure from linearity in the relationship between S^D intensity and S^D response rate. In each case the level of significance was only $p = .05$. pipradrol 5 mg/kg, and r 41, no drug) when the Intensities term was broken down into components due to linear regression and to departures from linearity, the linear component proved to be significant ($p < .05$). Thus, the only case in which no significant variation could be attributed to S^D intensity was that of r 41 under 10 mg/kg pipradrol (Fig. 1). Turning to effects less severe than the total abolition of the law of strength, we find in the Level II analyses of variance only three cases of significant

Inspection of the relevant curves in Fig. 1 (r 36 in the amylobarbitone condition; r 80 in the no drug and amylobarbitone conditions) reveals little of interest. There was no evidence that pipradrol alters the shape of the law-of-strength curve. However, consideration of the *slope* of the law-of-strength curve as a function of drug condition proved to be of more interest. Table 1 presents the coefficients of linear regression of S^D response rate on S^D intensity, which we shall refer to as "bS^D" for short. It can be seen from this Table and from Fig. 1. that pipradrol in the 5 mg/kg dose had a marked effect on the slope of the law-of-strength curve; however, this effect was the opposite of the one predicted by Pavlovian theory, bS^D increasing in every case. To establish the statistical reliability of these changes, the mean and standard deviation of the distribu-

Table II

Coefficients of linear regression (bS^D) of response rate during S^Δ on preceding S^D intensity: drug effects

Animal	No drug	Placebo	Amytal		Pipradrol	
			15 mg/kg	30 mg/kg	5 mg/kg	10 mg/kg
r 36	.110	.082	.109		.331	
r 80	.124	.068	.195		.325	
H 20	.138	.233	.315		.120	
r 32	.143	.272	.344		.573**	
r 41	.196	.205	.257	.459*		+.140**

Mean and standard deviation of No Drug and Placebo coefficients: −0.190±0.109. Entries in the Table are values for b in equations of the form y = a + bx, where y = no. of responses in a 2¾ — min. period of S^Δ and x = preceding S^D intensity in db. Entries marked with one asterisk differ from the mean of the control conditions at the five per cent level of significance; those marked with two asterisks differ from this mean at the one per cent level. All entries are of negative sign except the single value preceded by a plus sign.

tion of bS^D in the ten control conditions (no drug and placebo for each S) were calculated. Values which fall beyond 1.96 SDs ($p < .05$) from the mean are marked with a single asterisk in Table I, and those falling beyond 2.58 SDs ($p < .01$) are marked with two. It will be seen that the 5 mg/kg pipradrol bS^D is in every case significantly higher than the control mean. The only evidence of an effect of amylobarbitone on bS^D was in the case of H 20, which displayed an increase in slope under this drug.

Drug Effects on the Relation between S^D Intensity and Subsequent S^Δ Response Rate. The Level II analyses of variance of the S^Δ data showed significant linear regression of S^Δ response rate on preceding S^D intensity in all but four cases. It seems possible that three of these four exceptions

(r 32, no drug; r 36, placebo; r 80 placebo) were more apparent than real: in each of these cases, the F (1,48) values for linear regression were not altogether negligible (2.02, 3.96 and 2.75 respectively) and the linear regression line had a negative slope. In contrast, r 41 after 10 mg/kg pipradrol (Fig. 1) displays an F of only 0.36 and a *positive* slope (+0.14). It seems, then, that, like the positive relation between S^D intensity and S^D response rate, the negative relation between S^D intensity and subsequent S^Δ response rate was completely destroyed only by the dose of 10 mg/kg pipradrol given to r 41.

Turning to less complete drug-induced changes in the relationship between S^D intensity and S^Δ response rate, we find that departures from linearity were significant in only one of the Level II analyses of variance, and that was in a no drug condition (r 36, Fig. 1). Once again, the coefficients of linear regression (in this case, of S^Δ response rate on preceding S^D intensity, or "bS^Δ") proved to be of greater interest. It will be seen from Table 2 that 5 mg/kg pipradrol increased the negative slope of three of the four relevant curves presented in Fig. 1. In the 10 mg/kg dose (r 41), this drug substituted a positive slope for the usual negative one. The effects of amylobarbitone tended to be in the direction of an increase in negative slope. Table II shows the significance levels attaching to these various changes, calculated in the same way as for the bS^D data.

The Effect of Drive on the Relationships between S^D Intensity and S^D and S^Δ Response Rates. The analysis of variance of the S^D data revealed two significant interactions between Drive and Intensity. In both cases the interaction is of the form predicted by Pavlovian theory, but the level of significance is low. The Level II analysis for r 41 in the placebo condition gave an F(4,48) of 2.75, $p < .05$; in the low drive condition, peak response rate occurred as usual at 100 db., but in the high drive condition

Table III

Coefficients of linear regression (bS^D) of S^D response rate on S^D intensity in high and low drive conditions

Animal	No drug		Placebo		Pipradol				Amytal			
					5 mg/kg		10 mg/kg		15 mg/kg		30 mg/kg	
	High drive	Low drive	High drive	Low drive	High drive	Low drive	High drive	Low drive	High drive	Low drive	High drive	Low drive
r. 36	.298	.214	.125	.380	.562	.988			.023	.317		
r 80	.224	.220	.158	.359	1.140	1.277			.413	.434		
H 20	.242	.885	.864	.572	.634	1.365			.909	1.719		
r 32	.343	.562	.320	.645	.412	1.108			.411	.485		
r. 41	.233	.376	.361	.524			.050	.376	.718	.548	.386	.457

a non-monotonic relation appeared, with peak responding at 90 db. The Level I analysis for r 32 gave an F (4.192) of 2.61, $p < .05$; again, change between 90 and 100 db. was important in accounting for this interaction — in the low drive condition there was a marked increase in response rate when S^D intensity was increased to 100 db., while in the high drive condition there was no difference between rates at these two intensities.

Both significant interactions between S^D intensity and drive involved a higher slope of linear regression of S^D response rate on stimulus intensity in the low drive condition, as predicted by Pavlovian theory. To see whether this effect was a general one, slope coefficients were calculated separately for each drive level for all drug conditions for each S. Table III presents the results of these calculations. It will be seen that bS^D is greater in the low drive condition in seventeen out of twenty-one cases; chi-square for these proportions is 6.81, $p < .01$ with 1 df. Mean bS^D was +0.658 in the low drive condition and +0.420 in the high drive condition; the difference between these means is significant at the .05 level ($t = 2.16$, $df = 20$).

There were no significant interactions between Drive and Intensity in the analyses of S^Δ data, nor was bS^D affected by drive.

Interrelations between bS^D bS^Δ and Ease of Discrimination. We turn now to an evaluation of the results from the point of view of the Perkins-Logan hypothesis and the related hypothesis suggested by the writer, according to both of which the magnitude of the effects of S^D intensity on both S^D and S^Δ response rates depends on S's success in discriminating S^D from S^Δ. As measures of the extent which the S^D and S^Δ response rates depend on S^D intensity we shall use the slope coefficients, bS^D and bS^Δ, already introduced. As a measure of ease of discrimination we shall use the ratio of mean response rate during S^D to mean response rate during S^Δ (Dinsmoor 1951), which will be called the "discrimination ratio".

To consider first the relation between bS^D and bS^Δ, a correlation was run between these statistics (with the negative sign of bS^Δ ignored) for corresponding pairs of curves in Fig. 1 (with the exception of the two curves obtained from r 41 under 10 mg/kg pipradrol, since neither bS^D nor bS^Δ was significantly different from zero in this case). This correlation proved to be positive and significant ($r = +0.455$, $p < .05$, 18 df).

The interrelations between bS^D, bS^Δ and the discrimination ratio are presented in Figs. 2 and 3 in the form of two scattergrams. Drug effects on the discrimination ratio are dealt with in detail in another paper (Gray 1964c). In the present context it is important to note that the 10 mg/kg dose of pipradrol, which, as we have seen, abolished the effects

of S^D intensity on both S^D and S^Δ response rates in r 41, also abolished the discrimination between S^D and S^Δ in this rat (crosses in Figs. 2 and 3). The attempt to evaluate the association between the discrimination ratio and the two slope coefficients at values of the former which are greater than unity is hampered by the fact, evident in Figs. 2 and 3, that the points for H 20 in these scattergrams diverge markedly from the pattern created by the points for the other Ss. This divergence is perhaps due to the fact that this rat belonged to a different strain from the others studied; a number of other ways in which its behaviour differed from

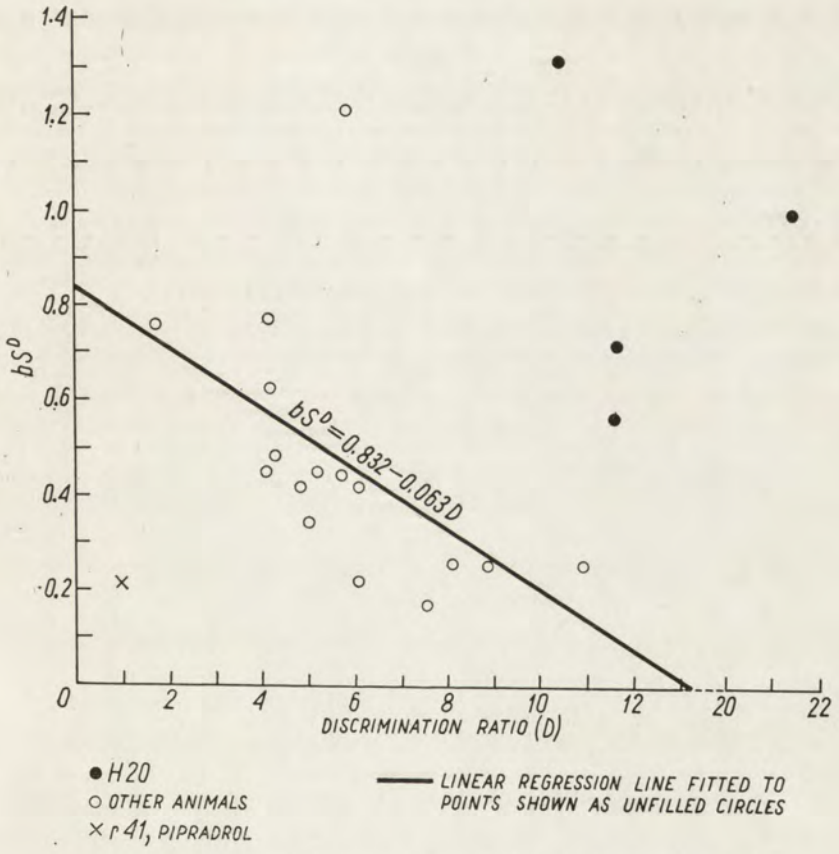

Fig. 2. The relaton between bS^D and the discrimination ratio

that of the other rats are noted elsewhere (G r a y 1964c). If the data due to H 20 are omitted, significant correlations between the discrimination ratio and the two slope coefficients are obtained: $r = -0.520$, $p < .05$ (with 14 df) for bS^D with the discrimination ratio; $r = -0.751$, $p < .01$, for bS^Δ (negative sign ignored) with the discrimination ratio.

Since considerable doubt must attach to correlations based in this way on selected data, a second method was adopted to assess the reality of the association between the discrimination ratio and the two slope coefficients. Baselines were formed by taking the means of the two values of bS^D, bS^Δ and the discrimination ratio recorded in the no drug and placebo conditions for each S. It was found that pipradrol and amylobarbitone caused bS^D and the discrimination ratio to move in opposite directions from these baselines in eight out of ten cases, while bS^Δ and the discrimination ratio moved in opposite directions in nine out of ten cases. Combining these proportions, we have change in opposite directions in seventeen out of twenty cases, for which chi-square is 9.80, $p < .01$, with 1 df.

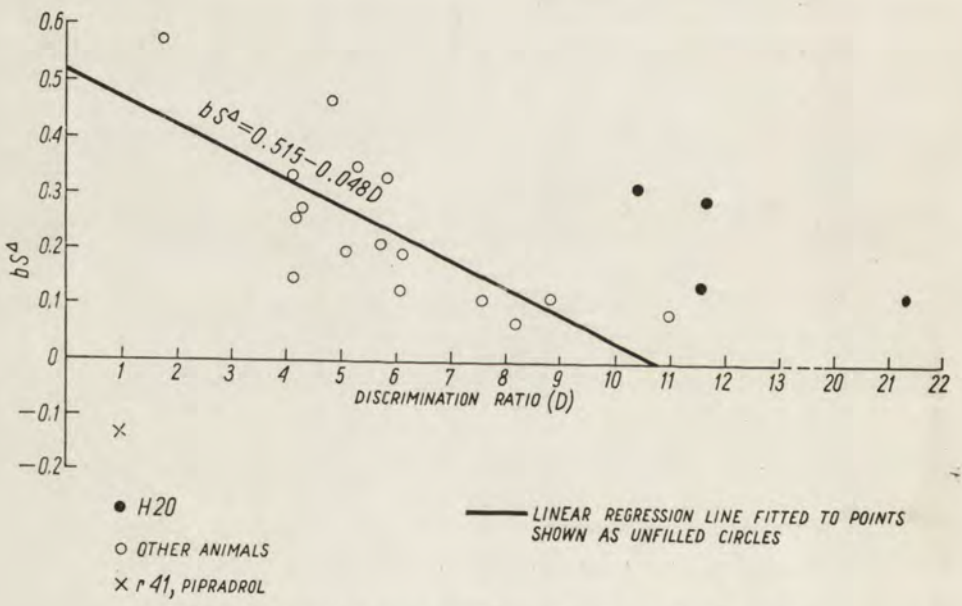

Fig. 3. The relation between bS^Δ an the discrimination ratio

Extinction. The progress of extinction is shown for each S in Fig. 4. By the fifth day, rates in S^D and S^Δ have drawn much closer in all Ss, but rate during noise still exceeds rate during silence in every case. Analysis of variance and associated t tests suggested that in no case did the significant difference between S^D and S^Δ response rates disappear before the third day of extinction at the earliest. However, the existence of significant inhomogeneities of variance in the extinction data makes it impossible to place too much reliance on these and subsequent statistics.

Fig. 5 shows response rate during noise as a function of noise intensity in each S and on each day of extinction. The regular relation between these variables which appeared in the main experiment (Fig. 1) is clearly absent from these curves. They show only one consistent feature: particularly high response rates occur at 100 db. in H 20, r 41 and r 32, in the mean curve for the group, and to some extent on all five days of testing. These impressions were, in the main, confirmed by the statistical analysis of the data. The Intensities effect for the group (tested against the Animals x Intensities interaction) was significant at the 1 per cent level, $F\ (4, 16) = 5.05$; t tests showed that this was due (a) to the fact that rate at 100 db. was higher than at any other intensity ($p < .001$) and (b) to the fact that rate at 90 db. was lower than at any other intensity ($p < .001$). The fact that two Ss — r 36 and r 80 — did not show an elevated response rate at 100 db. was reflected in a significant

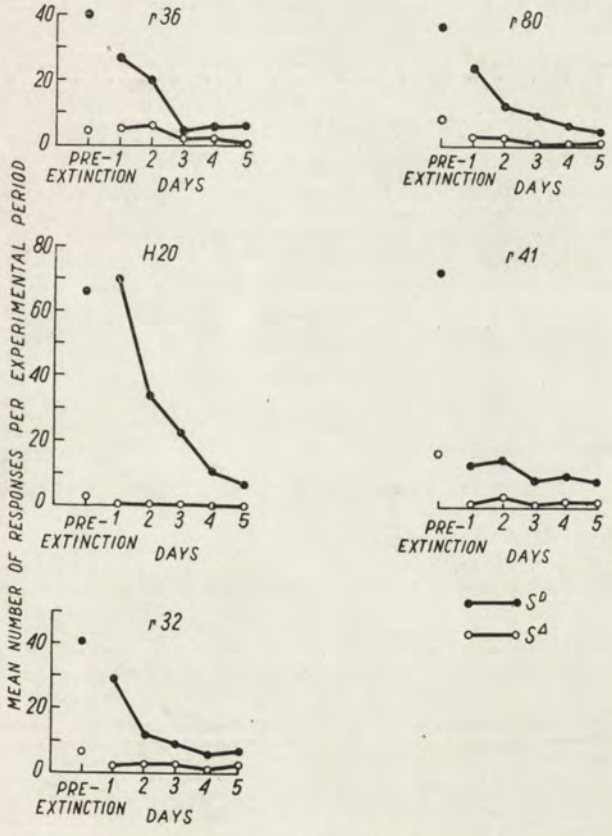

Fig. 4. Change in response during noise (S^D) and silence (S^Δ) over days of extinction. The pre-extinction points represent response rates during the last comparable session (i.e. high drive, no drug) of reinforced responding

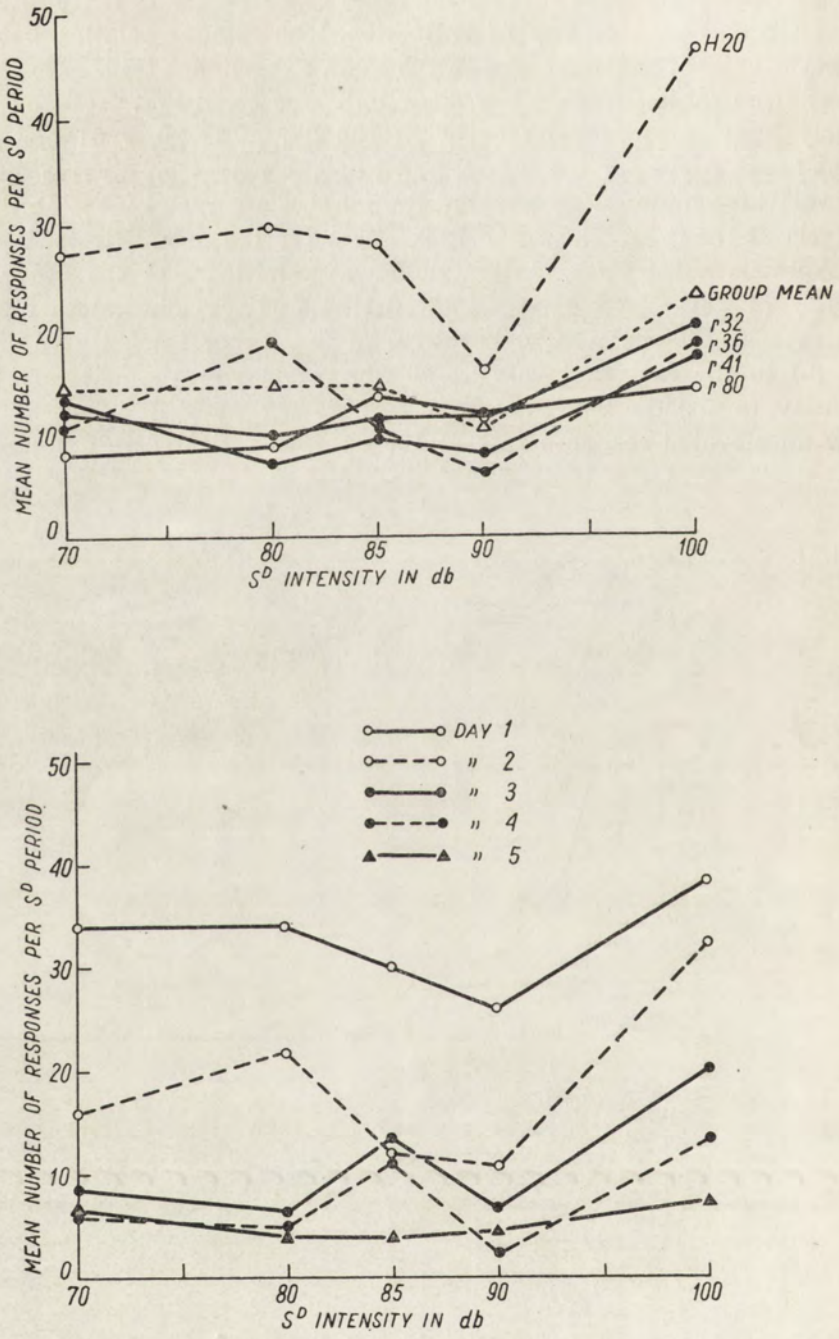

Fig. 5. Response rates in noise during extinction as a function of noise intensity for five subjects (upper graph) and on five test days (lower graph)

Animals x Intensities interaction, $F(16, 120) = 1.83$, $p < .05$. The interaction between Days and Intensities was not significant, $F = 0.93$.

Examination of the scores recorded during periods of silence revealed no relation between S^Δ response rate and the intensity of the preceding period of noise.

DISCUSSION

The results of the experiment confirm previous findings (Gray 1965a) of a positive relation between S^D intensity and S^D response rate and a negative relation between S^D intensity and response rate during the next period of S^Δ. The earlier indications that these relationships are usually linear when S^D intensity is expressed in db. are also confirmed. In addition, a certain amount of empirical support has been obtained for both the Pavlovian and the generalisation of inhibition analyses of the effects of CS intensity.

As far as Pavlovian theory (Pavlov 1927, Gray 1964a) is concerned, the experiment has confirmed the predicted effect of drive on the law of strength: as suggested by an earlier experiment (Gray 1965a) increased drive reliably decreased the slope of the law-of-strength curve; in addition, there were two significant interactions between Drive and Intensity, and both took the predicted form — under high drive, peak or asymptotic response rate tended to occur at a lower S^D intensity. The drug effects were more ambiguous for Pavlovian theory: the abolition of the law of strength in the one rat given the 10 mg/kg dose of pipradrol is in agreement with prediction; the *increase* in the slope of the law-of-strength curve produced by the 5 mg/kg dose of this drug, on the other hand, is the direct converse of the predicted effect. The question naturally arises whether the abolition of the law of strength which occurred in r 41 only was due to the dose of pipradrol used or to this animal's individual characteristics (which, in the context of Pavlovian theory, are expected to be important — Gray 1964a). Some unpublished data obtained by the writer (Gray 1964b) from the four rats tested in the present experiment under 5 mg/kg pipradrol throw some light on this question. These rats were tested at 10 mg/kg pipradrol under the same conditions as in the present experiment. However, it was found (Gray 1964c) that this dose had extremely disruptive effects on their responding, so that it was not possible to obtain more than three days' data (i.e. three columns of the Latin Square) for each animal. Analysis of these incomplete data suggested that the law of strength was unaffected by the 10 mg/kg dose of pipradrol in two Ss (r 32 and H 20) but abolished in the other two (r 80 and r 36). Thus it appears that whether

or not pipradrol abolishes the law of strength depends both on the dose and on the individual subject.

Turning to the Perkins-Logan generalisation of inhibition account of stimulus intensity dynamism and the related hypothesis advanced by the present writer to account for the negative relation between S^D intensity and subsequent S^Δ response rate, we find that, as predicted, there is a close connection between the extent of the two effects, as shown by the significant correlation between the slope coefficients, bS^D and bS^Δ. As for relations between bS^D and bS^Δ, on the one hand, and the discrimination ratio on the other, the data appear to make the following conclusions reasonable. Complete failure of discrimination (as was produced in r 41 by 10 mg/kg pipradrol) is accompanied by values of bS^D and bS^Δ which do not differ significantly from zero. There is then an initial rapid rise in the slopes of the intensity functions as the discrimination ratio increases from unity to 1.7 (Figs. 2 and 3) at the most for these Ss, followed by a much slower fall as the discrimination ratio continues to increase. The regression lines shown in Figs. 2 and 3 suggest that bS^D becomes zero again when the S^D response rate exceeds the S^Δ response rate by a factor of about 13 and that bS^Δ falls to zero when the discrimination ratio is about 11 — values which are encouragingly close to one another. All in all, then, the observed relations between bS^D, bS^Δ and the discrimination ratio take forms which are consistent with the two generalisation hypotheses. It should also be noted that the disappearance of the stimulus intensity effect when discrimination between S^D and S^Δ breaks down is in agreement with the finding (Perkins 1953, Gray 1965a) that stimulus intensity dynamism is only obtained in an operant conditioning situation when the intensity of a *discriminative* stimulus is varied.

The data obtained during extinction tend to confirm earlier reports that stimulus intensity dynamism, even though it may be present during reinforced responding, disappears during extinction (see Gray 1965b, for review). The regular relation between S^D intensity and both S^D and S^Δ response rates was severely disrupted during extinction, though a trace of this relation may have remained in the elevated response rate during 100 db. observed in three of the five Ss. The high rate during 100 db. may have been an artefact of the particular Latin Square column which was permuted to determine allocation of intensities to periods during extinction: though chosen at random, this column had the unfortunate property (not noticed till the experiment was under way) that each intensity was followed by the next lowest intensity, with the exception of 70 db., which was always followed by 100 db. Even so, two Ss failed to show high rates at 100 db., and in no case was there a positive as-

sociation between S^D intensity and S^D response rate over the range 70–90 db. It is noteworthy that the disruption of the regular relationships observed during reinforced responding occurred on the very first day of extinction, at a time when the difference between response rates during noise and silence was still quite marked. On the generalisation of inhibition hypothesis, this is puzzling: if the discrimination between the previously positive nad negative stimuli can still produce different rates of response to these stimuli, why should it not also continue to produce stimulus intensity dynamism? It is more in harmony with the two generalisation hypotheses that the intimate relation between the effects of S^D intensity on S^D and S^Δ response rates, which we have seen to be present in the data on reinforced responding, also appears in the extinction data: the disturbance in stimulus intensity dynamism was accompanied by the total disappearance of the relation between S^D intensity and subsequent S^Δ response rate.

SUMMARY

The effects of drugs (pipradrol hydrochloride and sodium amylobarbitone), drive and extinction on the relationships between S^D intensity and the S^D and S^Δ response rates were investigated in an operant conditioning situation in which rats received milk reinforcement on a VI schedule for barpressing responses performed in the presence of the S^D (white noise from 70 to 100 db.) and no reinforcement during presentation of the S^Δ (silence). Previous findings of a positive relation between S^D intensity and S^D response rate and of a negative relation between S^D intensity and following S^Δ response rate were confirmed. Pipradrol in a 10 mg/kg dose usually abolished both these relations; in a 5 mg/kg dose, on the other hand, it increased the slopes of the curves depicting these effects. An increase in drive decreased the slope of the curve describing the effect of S^D intensity on S^D response rate. The slopes of the two curves were significantly correlated with one another, and both were related to the degree to which the subject discriminates between S^D and S^Δ. Extinction severely disrupted the relation between S^D intensity and S^D response rate and abolished the relation between S^D intensity and S^Δ response rate.

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INSTRUMENTAL CONDITIONED REFLEXES AFTER PYRAMIDOTOMY IN DOGS[1]

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In our previous experiments on cats (Górska et al. 1966a, b), it has been found that sectioning the pyramidal tract affects differently two groups of instrumental reflexes. The manipulatory instrumental CRs such as placing the forelimb on a platform, pressing or pushing a button, were relatively well preserved after pyramidotomy. These results were in agreement with the findings obtained with respect to similar movements both in cats (Laursen 1966) and monkeys (Bucy and Keplinger 1961, Lawrence and Kuypers 1965). On the other hand, the instrumental CRs derived from unconditioned reactions like scratching, cleaning or rubbing of the skin appeared to be much more dependent on the integrity of the pyramidal system, since they were in cats almost completely abolished after pyramidotomy.

In the present paper the effects of sectioning the medullary pyramids on the instrumental CRs were investigated in dogs. This problem, except for a few preliminary reports (Gambarian et al. 1964, Górska 1966), was so far not analyzed. Dogs as compared with cats seem to present several advantages in studying instrumental CRs. Their movements are more isolated and can be easily conditioned to sporadic stimuli. Moreover, the same instrumental CR may be established in dogs using different methods of preliminary training and different reinforcements, and these factors have been suggested to play an important role in the

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CR performance after ablations of sensorimotor cortex (Samoilov 1962, Ioffe 1962). Three different instrumental CRs were used in this study, and both their retention after uni- and bilateral pyramidotomy and their acquisition after the latter operation were investigated. The instrumental CRs were in various animals trained in a different manner and associated with different reinforcements. It will be shown that, on a whole, the instrumental CRs in dogs were less affected after pyramidotomy than it was found in cats.

MATERIAL AND METHODS

Sixteen adult mongrel dogs, eight with a unilateral and eight with a bilateral pyramidotomy, were used[2]. The animals were trained, either pre- or postoperatively, to perform a definite conditioned motor response to the sound of an acoustic stimulus (buzzer or tone). The experiments were carried out in a regular soundproof conditioned reflex chamber, with a dog being placed on a stand. Ten to 15 trials were given in each session, with 1–1,5 min. of intertrial intervals. In those dogs in which a second CR was trained after the operation both the experimental situation and the CS were changed (Wyrwicka 1958).

The instrumental CRs were either alimentary or avoidance. In alimentary CRs, the food (bread and meat, soaked with broth) was given in a foodtray situated in front of the animal. The bowls in the foodtray were automatically rotated and the food was offered immediately after the animal had performed the required movement. In avoidance CRs, the negative reinforcement consisted of an electrical stimulation (50 p.c.s.) of the skin, through attached electrodes. It was applied whenever the animal did not perform the required movement within 5–7 sec. of the CS exposure.

The following instrumental CRs were studied, each of them in a separate group of animals: 1) The instrumental placing CR (group 1, dogs Nos. 1 to 7). The instrumental response consisted in animal's lifting the right forelimb and placing it on a platform (foodtray) situated in front of the dog (Fig. 1A). Five animals were trained preoperatively and then subjected to a unilateral (Nos. 1, 2 and 3) or a bilateral (Nos. 4 and 5) pyramidotomy. In two dogs (Nos. 6 and 7) a bilateral pyramidotomy had been first performed and then a postoperative conditioning was carried out. In all the dogs, except No. 3, the instrumental CRs were established using the method of reinforcing by food the passive movements (Konorski and Miller 1933). In the dog No. 3, an avoidance CR was established by utilizing adventitious movements which, at the beginning of training, were provoked by electrical stimulation of the animal's right flank (the left forelimb at the beginning of training was fastened to the floor). After some time the dog learned to perform the required movement in response to the CS, thus avoiding the noxious stimulation. 2) The instrumental rubbing CR (group 2, dogs Nos. 4, 8, 9, 10, 11 and 15). It consisted in the animal's lifting the left forelimb and approaching it to the cheek as in order to rub it (Fig. 1B). Four dogs received a preoperative training and then underwent a unilateral (Nos. 8 and 9) or a bilateral (Nos. 10 and 11) pyramidotomy. In the other two dogs (Nos. 4 and 15) with a bilateral

[2] The data obtained in the bilaterally operated animals were partly included in a previous publication (Górska 1966).

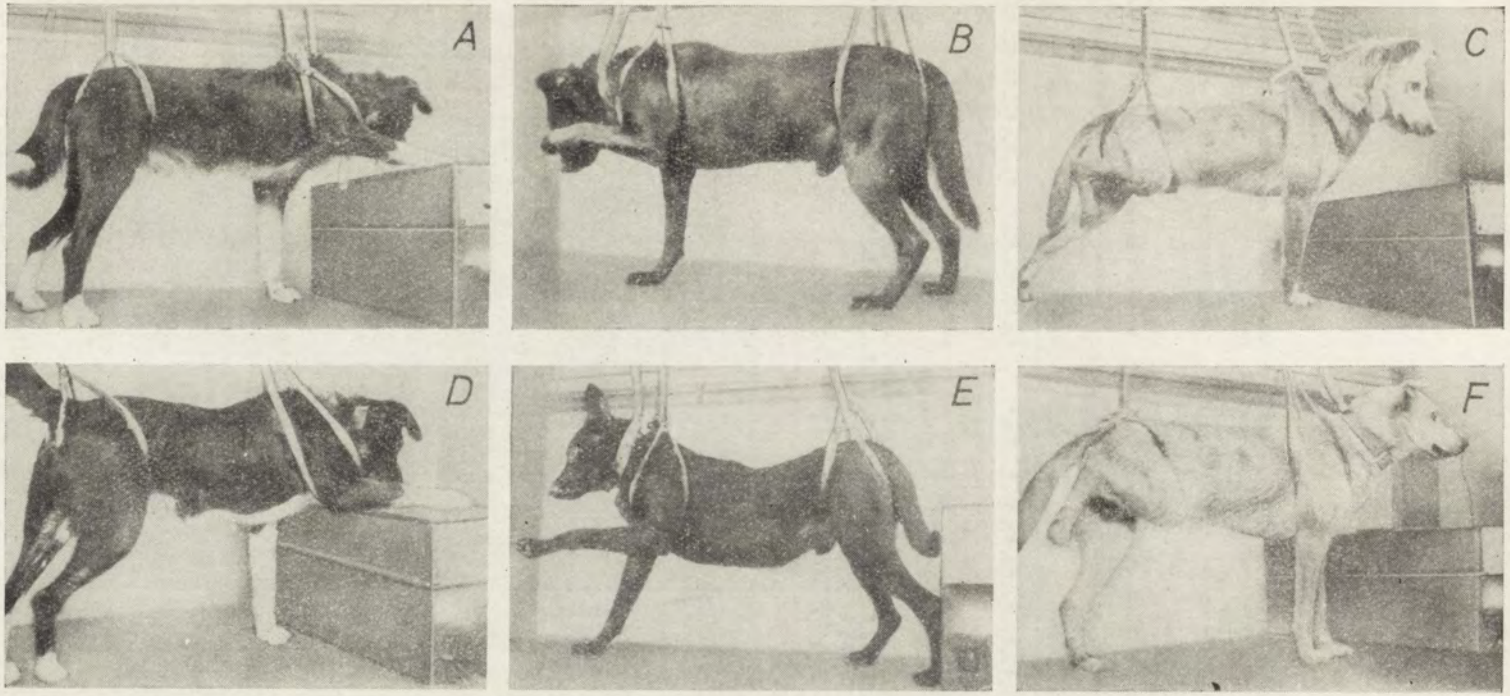

Fig. 1. Examples of the placing (A, D), rubbing (B, E) and flexion (C, F) instrumental CRs. The photographs in the upper and lower row show the movements in normal and bilaterally pyramidotomized animals respectively. In E, a movement performed with electrodes attached to the foot is shown

pyramidotomy a postoperative conditioning was carried out. In all the animals an avoidance procedure has been used. The CS was followed by an electrical stimulation of the left cheek producing the unconditioned rubbing movements by the left forelimb. When the rubbing-like movements appeared in response to the CS, the US was not presented. 3) The instrumental flexion CR of the right hindlimb (Fig. 1C) (group 3, dogs Nos. 10 to 16). Five dogs were conditioned before operation and then subjected to a unilateral (Nos. 12, 13 and 14) or a bilateral (Nos. 15 and 16) pyramidotomy. The remaining two animals (Nos. 10 and 11) received training only after a bilateral pyramidotomy. In dogs Nos. 12 and 13, an alimentary CR has been established reinforcing by food the unconditioned flexion movements, which were provoked at the beginning of training by the electrical stimulation of the right hindfoot. After some time the animals learnt to lift the limb in response to the CS in order to get food (Konorski and Miller 1933). In the dogs Nos. 10, 11, 15 and 16, the required movements at the beginning of training were also provoked by the electrical stimulation of the trained limb, but the avoidance procedure was used, so that the animals learnt to

Table I

Experimental procedure used in different subjects

Instrumental CR	Dog No.	Pyramidotomy	Training	Type of CR	Method of shaping of the CR	Position of the electrodes
Placing the right forelimb on a platform (group 1)	1	unilat.	pre-op.	alim.	passive mov.	—
	2	unilat.	pre-op.	alim.	passive mov.	—
	3	unilat.	pre-op.	avoid.	adventitious mov.	flank
	4	bilat.	pre-op.	alim.	passive mov.	—
	5	bilat.	pre-op.	alim.	passive mov.	—
	6	bilat.	post-op.	alim.	passive mov.	—
	7	bilat.	post-op.	alim.	passive mov.	—
Rubbing the cheek with the left forelimb (group 2)	8	unilat.	pre-op.	avoid.	rubbing UR	cheek
	9	unilat.	pre-op.	avoid.	rubbing UR	cheek
	10	bilat.	pre-op.	avoid.	rubbing UR	cheek
	11	bilat.	pre-op.	avoid.	rubbing UR	cheek
	4	bilat.	post-op.	avoid.	rubbing UR	cheek
	15	bilat.	post-op.	avoid.	rubbing UR	cheek
Flexion of the right hindlimb (group 3)	12	unilat.	pre-op.	alim.	flexion UR	foot
	13	unilat.	pre-op.	alim.	flexion UR	foot
	14	unilat.	pre-op.	avoid.	passive mov.	flank
	15	bilat.	pre-op.	avoid.	flexion UR	foot
	16	bilat.	pre-op.	avoid.	flexion UR	foot
	10	bilat.	post-op.	avoid.	flexion UR	foot
	11	bilat.	post-op.	avoid.	flexion UR	foot

In dogs Nos. 4, 10, 11 and 15 two instrumental CRs, one trained before and the second after the operation, were investigated.

perform the response in order to avoid the painful stimulation of the limb. In dog No. 14, an avoidance reflex was established using the method of passive movements (Konorski and Miller 1933). In this case the painful stimulation was applied to the right flank, and the CS was followed either by the electric shock or by the passive flexion of the right hindlimb. When the animal started to flex the hindlimb actively in response to the CS, the US was not presented.

The instrumental CRs investigated in each dog and the methods used in the preliminary training are shown in Table I.

All the normal animals, independent of the kind of the CR elaborated and the methods of ist training, reached the level of 95–100% of the CR performance after 50–150 trials. The training was then continued for additional 250–300 trials in order to assure a stable response. In total, 350–400 trials were given preoperatively in each animal. In all the dogs in which an avoidance CR has been established, in the last period before operation the instrumental CRs were tested in two conditions. In some trials, the electrodes originally used for applying the electrical stimulation were simply attached to the skin, i.e. to the flank, cheek or foot (see Table I), while in other trials they were removed. In each experimental

Table II

Histological verification of the lesions

Pyramidotomy	Dog No.	Degeneration of the pyramids		Degeneration of the medial lemniscus	
		Left side	Right side	Left side	Right side
Unilateral	1	total	—	1/3	—
	2	total	—	1/3	—
	3	total	—	—	—
	8	—	total	—	—
	9	—	total	—	—
	12	total	—	—	—
	13	total	—	1/4	—
	14	total	—	—	—
Bilateral	4	total	total	—	—
	5	total	total	—	2/3
	6	total	total	1/5	—
	7	total	5/6	1/2	1/3
	10	total	total	—	—
	11	total	total	1/3	1/3
	15	total	total	1/3	1/10
	16	total	19/20	—	1/10

session in half of the trials the electrodes were present and in half of them they were taken off. Sessions beginning either with or without electrodes were given in an alternating order. In each dog at least 50 trials without electrodes were applied.

The postoperative testing of the CRs started one week after the operation and lasted 2–5 months. These animals, in which the instrumental CRs were preserved, were tested 2–3 times a week, with a similar number of trials (10–15) per session as before operation. In those, in which the CRs were strongly impaired or abolished, the experiments were performed only once a week, with a reduced (4–6) number of trials. If after 6 weeks the instrumental responses did not spontaneously reappear, the retraining was given, using the same procedure as that during preoperative training.

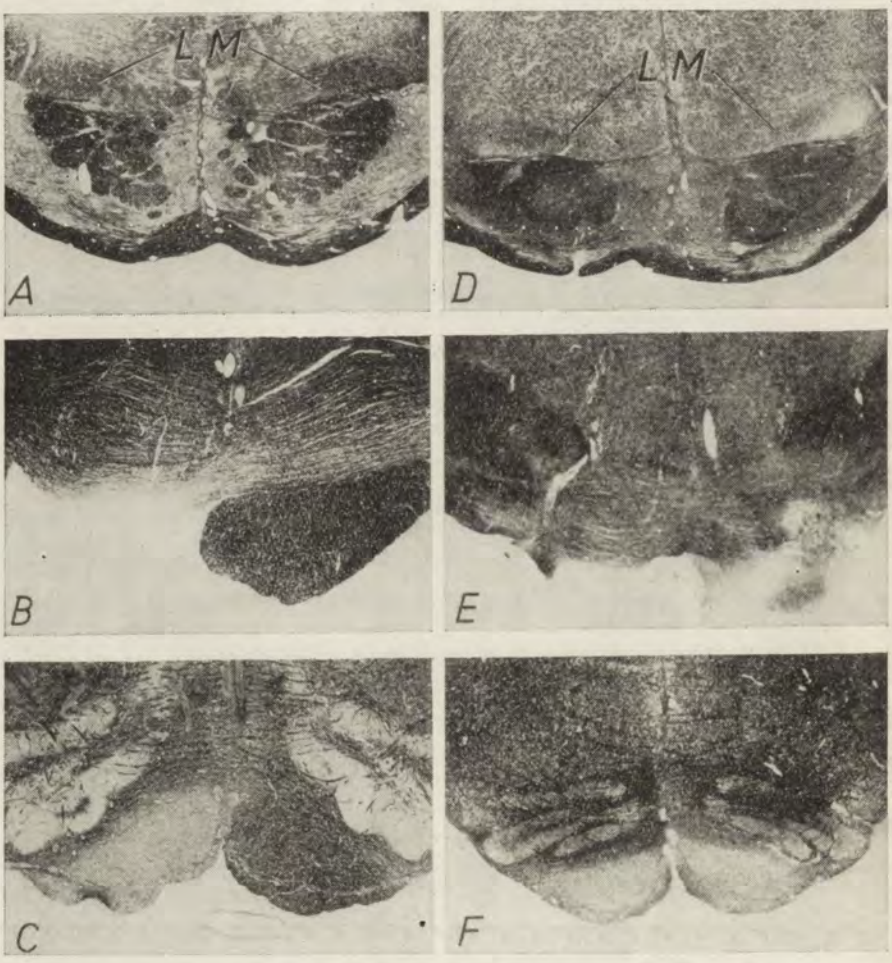

Fig. 2. Photographs of transverse sections of the pons and medulla in 2 dogs (Nos. 9 and 15) after a unilateral (A—C) and a bilateral (D—F) pyramidotomy. B and E show the maximal depth of the lesions, while the resulting degeneration of the pyramids and of the medial lemniscus are presented in C, F and A, D respectively. Note that in A the medial lemniscus on the lesioned side seems to be unchanged, while in D about 1/10 and 1/3 of the surface occupied by the medial fillet, on the left and right side respectively, are degenerated

Similarly as before operation, the dogs with the avoidance CRs were tested postoperatively in two conditions, i.e. with and without electrodes attached to the respective part of the body. Trials with and without electrodes on the foot were also applied after the operation in dogs Nos. 12 and 13 with an alimentary flexion CR of the hindlimb. The testing procedure and the amount of trials applied in these two conditions were in all the dogs analogous to that used preoperatively.

In all experiments, the latencies and the amplitudes of instrumental movements were checked. The latencies were measured with an accuracy of 0.1 sec. by means of an electric clock which was switched on and off together with the CS. The differences between the median latencies were tested with the two tailed Kolmogorov-Smirnov test (Siegel 1956). The movements were classified from the point of view of their amplitude into three categories: high, medium and small movements. In order to test the change in the amplitude of movements, the percentages of trials with movements of different categories were counted and they were examined by the Chi-square test for two independent samples (Siegel 1956).

The pyramidotomy was done in aseptic conditions under Nembutal anesthesia (35 mg/kg). The ventral approach as first described by Starlinger (1895, 1897) was used. The basioccipital bone was removed between the bullae thympani and the pyramids were sectioned at the level of the trapezoid body. In the dogs bilaterally operated, both pyramids were transected on one stage. As it was described by Starlinger (1895, 1897), Maffre (1955), and Gambarian et al. (1964) the animals on the next day after the pyramidotomy were able to eat and walk. The neurological symptoms observed in our animals will be described in another paper.

The histological control of the lesions was done on serial transverse sections of the mesencephalon and medulla, fixed in formalin, embedded in paraffin and stained with the Klüver-Barrera and Nissl methods. Both the extent of the lesion as well as the descending and ascending degenerations were studied. The results obtained are presented in Table II. As seen from this Table in almost all the dogs the pyramids were completely sectioned. Only in two bilaterally operated dogs (Nos. 7 and 16) a small amount (1/6 and 1/20) of fibres was spared in one of the pyramids (in both dogs ipsilateral to the trained limb).

In nine of the animals, the pyramidotomy was followed by a partial degeneration of the medial lemniscus on one or both sides. In the majority of dogs, the impairment of the medial lemniscus ranged from 1/5–1/3 and only in two cases a more severe impairment (up to 1/2 and 2/3) of the ipsilateral to the trained limb (dog No. 5) or contralateral (dog No. 7) medial fillet was found. The degeneration of the lemniscal fibres was present in all the dogs in which more than 1/5–1/4 of the ventral layers of the trapezoid body were destroyed and it was roughly proportional to the depth of the lesion (Fig. 2).

RESULTS

1. The instrumental placing CR. The instrumental CR of placing the forelimb on a platform was totally preserved after pyramidotomy. In all the uni- and bilaterally pyramidotomized animals, irrespective of whether an alimentary or avoidance CR has been preoperatively established, the instrumental movements were present from the very beginning of the postoperative examination and during the whole period of testing

(150 trials) they appeared in 94–99% of the trials (Table III). The amplitude of movements was unchanged (Fig. 1B), their latencies were, however, slightly increased as compared with the preoperative values (Table III). The increase of the median latencies of movements ranged from 0.1–0.6 sec. and was approximately the same after uni- and bilateral pyramidotomy. In all the dogs but one (No. 3) the latencies of movements in the last 50 trials of the postoperative testing (2 months after the operation) were still statistically significantly increased ($p < 0.5$) as compared with the preoperative values.

Table III

Effects of pyramidotomy on the instrumental placing CR

Pyramidotomy	Dog:	Before operation (last 150 trials)	After operation (150 trials)	P
Unilateral	No. 3	1.9 sec.	2.5 sec.	$<.001$
	(avoid.)	100 %	99 %	—
	No. 1	1.3 sec.	1.8 sec.	$<.001$
	(alim.)	100 %	98 %	—
	No. 2	0.9 sec.	1.2 sec.	$<.001$
	(alim.)	100 %	94 %	—
Bilateral	No. 4	1.0 sec.	1.1 sec.	$<.001$
	(alim.)	100 %	99 %	—
	No. 5	1.0 sec.	1.5 sec.	$<.001$
	(alim.)	100 %	96 %	—

For each subject the median latency and the percent of trials in which the CR occurred are given.
avoid., avoidance CR; alim., alimentary CR.

In dog No. 3 with an avoidance CR, attaching or removing the electrodes off the flank, i.e. the place where the noxious stimulation was originally applied (see method), did not change the CR performance. No statistically significant differences between the latencies of movements performed in these two testing conditions were observed either pre- or postoperatively.

In all the operated animals the reaction of taking the limb off the platform was slightly impaired. While before pyramidotomy the dogs placed the limb back on the stand as soon the CS was discontinued or the food had been eaten, after pyramidotomy they always kept their limb on a platform during the whole time of eating and removed it only when they turned away from the foodtray. The limb dropped down in a passive-like manner.

In dogs trained after bilateral pyramidotomy (Nos. 6 and 7), the rate of acquisition of the instrumental placing reflex was similar as in normal animals. Both dogs reached the criterion of 100% of performances after 50 and 100 trials, as compared with the values of 50–150 trials in intact animals. However, the latencies of the instrumental movements were in these dogs slightly longer than in normal animals. They were similar to the values obtained by the operated dogs, which had been trained before operation.

2. *The instrumental rubbing CR.* The instrumental rubbing CR was more impaired after pyramidotomy than the placing CR. The degree of its impairment appeared partly to depend on the testing procedure, i.e. whether the instrumental movements were performed with or without electrodes attached to the animal's cheek (see method).

During the first 5 postoperative sessions the instrumental movements were tested only once a week and only with the electrodes attached to the cheek. No electric current was, however, applied when the movements were absent. In such conditions, in unilaterally operated dogs the instrumental movements appeared in the first or second experimental session, they were, however, irregular and of much longer latencies and lower amplitudes than before operation. During the next 2–3 sessions the number of trials in which the movements occurred gradually decreased, until they eventually disappeared. In the bilaterally pyramidotomized dogs the instrumental movements were totally absent during the first 5 sessions. In the presence of the CS, the animals either stood motionless or performed only irregular and extremely small movements which did not resemble the learned responses.

In both uni- and bilaterally pyramidotomized dogs the instrumental responses could be, however, easily reestablished by retraining. Beginning from the 6th experimental session the electric current was applied whenever the instrumental movements were absent. After a few (5–10) applications of the electrical stimulation to the cheek, the instrumental movements reappeared in all the dogs, and during the next 150–200 trials they were performed in almost 100% of the trials.

After the retraining the instrumental movements were tested with and without electrodes attached to the cheek. The latencies and amplitudes of the movements performed in the last preoperative period and after retraining, without and with electrodes on the cheek are compared in Table IV. As seen from this Table after the retraining, both the movements performed with and without electrodes, were of smaller amplitude and/or of longer latencies than before operation. Instead of movements of high amplitude, i.e. up to the cheek, the operated animals in the ma-

jority of the trials performed movements of moderate amplitude (cf. Fig. 1B and C) which in most of the dogs had also longer latencies than before operation. However, while before the operation attaching and removing the electrodes off the cheek did not evoke any statistically significant changes in the CR performance, after the operation attaching the electrodes to the cheek significantly facilitated the instrumental rubbing movements. The movements executed with electrodes on the cheek were

Table IV

Effects of pyramidotomy on the instrumental rubbing CR of the forelimb performed without and with electrodes attached to the cheek

Pyramidotomy	Dog:	Parameters of movements	Before operation			After operation		
			Without electr.	With electr.	P	Without electr.	With electr.	P
Unilateral	No. 8	Mdn. latency	2.8	2.5	n.s.	8.9	5.5	< .001
		Amplitude in %						
		small	—	—		44	21	
		medium	10	—	n.s.	52	66	< .02
		high	90	100		4	13	
	No. 9	Mdn. latency	3.0	2.6	n.s.	4.2	3.1	< .025
		Amplitude in %						
		small	—	—		4	—	
		medium	4	2	n.s.	43	24	< .001
		high	96	98		53	76	
Bilateral	No. 10	Mdn. latency	1.5	1.1	n.s.	4.3	2.6	< .001
		Amplitude in %						
		small	—	—		11	4	
		medium	12	8	n.s.	83	69	< .01
		high	88	92		6	27	
	No. 11	Mdn. latency	5.8	5.1	n.s.	5.6	4.0	< .001
		Amplitude in %						
		small	—	—		5	12	
		medium	15	8	n.s.	84	63	< .02
		high	85	92		11	25	

For each subject the medium latency (in sec.) of movements and the percent of trials with movements of different amplitude are given. n.s., not significant.

of shorter latencies and higher amplitudes, than those performed without electrodes, and these differences were in all the dogs statistically significant.

It is also worth noticing that the instrumental rubbing CR was not more impaired after a bilateral pyramidotomy than after a unilateral operation, except for the first few postoperative session (before retraining). As seen from Table IV after the retraining, the changes in the latencies and amplitudes of movements were similar in both these groups of animals.

In bilaterally pyramidotomized dogs trained after the operation (Nos. 4 and 15) the instrumental rubbing CR was established with a similar rate as in normal animals i.e. both dogs reached the level of 95% of performances after 50 trials. The instrumental movements were, however, either of longer latencies or of lower amplitudes than in normal animals. These changes were similar to those observed in the operated dogs which had been trained before operation.

3. The instrumental flexion CR. The postoperative impairment of the instrumental flexion CR of the hindlimb appeared to vary greatly depending on whether the instrumental movements were tested with or without interdigital electrodes attached to the trained limb (see method).

In all the uni- and bilaterally pyramidotomized dogs, irrespective of the method used in the preoperative training, the instrumental movements tested without electrodes attached to the trained limb almost completely disappeared. To the sound of the CS the dogs performed only very small, multiple threading movements of all the four limbs. This behaviour did not change till the end of the postoperative period (3–5 months) and neither the lack of the alimentary reinforcement (dogs Nos. 12 and 13) nor the prolongation of the CS in case of avoidance CRs (dogs Nos. 14, 15 and 16) resulted in reappearance of isolated movement of the trained limb even of small amplitude (Table V).

In contrast, when the CRs were tested with the interdigital electrodes attached to the trained limb, the instrumental movements were present both in the unilaterally and in the bilaterally pyramidotomized dogs. In the latter animals testing with electrodes started from the first postoperative session. In such conditions the learned movements spontaneously reappeared on the 2nd or 3rd postoperative session (2–3 weeks after the operation). During further experiments (100–150 trials), they were performed regularly, in 92–96% of the trials, without need of any retraining (dog No. 16) or with an only very short retraining (dog No. 15). The instrumental movements had only slightly longer latencies and lower amplitudes than the movements performed before operation. The animals' postoperative performance was in this condition even better

Table V

Effects of pyramidotomy on the instrumental flexion CR of the hindlimb performed without and with electrodes on the foot

Pyramidotomy	Dog:	Parameters of movements	Before operation			After operation	
			Without electr.	With electr.	P	Without electr.	With electr.
Unilateral	No. 12 (alim.)	Mdn. latency	2.8	not investigated		x	3.2
		Amplitude in %					
		very small	—			100	33
		small	—			—	33
		medium	30			—	18
		high	70				16
	No. 13 (alim.)	Mdn. latency	1.4	not investigated		x	1.8
		Amplitude in %					
		very small	—			100	17
		small	—			—	33
		medium	10			—	15
		high	90			—	35
	No. 14 (avoid.)	Mdn. latency	1.2	1.1	n.s.	x	1.5
		Amplitude in %					
		very small	—	—		100	—
		small	—	—		—	75
		medium	8	—	n.s.	—	18
		high	92	100		—	7
Bilateral	No. 15 (avoid.)	Mdn. latency	2.9	1.0	< .001	x	2.0
		Amplitude in %					
		very small	—	—		100	8
		small	9	—		—	18
		medium	57	4	< .001	—	11
		high	34	96		—	63
	No. 16 (avoid.)	Mdn. latency	1.0	0.9	n.s.	x	1.1
		Amplitude in %					
		very small	—	—		100	4
		small	—	—		—	17
		medium	69	14	< .001	—	19
		high	31	86		—	60

Denotations as in Table IV.

In dog No. 14, the postoperative data refer to the period after the retraining. The latencies of the very small, threading movements performed by the operated dogs without electrodes, were not considered.

than that tested before operation but without electrodes on the foot (Table V).

Similar results were obtained in two of the three unilaterally operated animals in which an alimentary CR has been established before operation by reinforcing by food the unconditioned flexion movements (Nos. 12 and 13). In these animals the effects of attaching the electrodes on the foot were tested only after 3 months after the operation (in the preceding period only trials without electrodes were given). In both dogs the instrumental movements reappeared without any retraining as soon as the electrodes had been attached to the foot and during further experiments (100 trials with electrodes) they were performed in 68–87% of the trials. However, they were of lower amplitude and less regular than the movements performed with electrodes by the bilaterally operated dogs (cf. Table V). It is possible that this difference was due to a partial extinction of the CR since in these animals during the first 3 months after the operation only trials without electrodes on the foot were applied. It should be stressed, however, that both the uni- and bilaterally operated dogs performed the instrumental movements only as long as the electrodes were attached to the foot and taking them off in the same experimental session resulted in instantaneous disappearance of the isolated flexions and reappearance of the multiple threading movements. This effect was consistently observed till the end of postoperative period.

Slightly different results were obtained in the third unilaterally operated dog (No. 14) in which an avoidance CR had been preoperatively established using the technique of passive movements. In this dog, attaching the electrodes to the foot did not spontaneously restore the instrumental response. Moreover, the movements could not be reestablished either by systematic application of the electrical stimulation to the animals right flank, i.e. where it was originally given, or by using the method of passive movements. The only procedure which proved to be successful was to evoke the unconditioned flexion by the electrical stimulation of the foot and to establish the instrumental reflex on that basis. The instrumental movements which appeared after such training had relatively short latencies but their amplitudes were much decreased as compared with the preoperative period (Table V). Similarly to the remaining dogs the instrumental movements were executed only as long as the electrodes were on the foot, and after taking them off only very small threading movements appeared in response to the CS.

As far as the acquisition of the instrumental flexion CR after bilateral pyramidotomy is concerned, in both dogs trained after the operation (Nos. 11 and 12) the avoidance movements of the hindlimb appeared with

a similar rate as in intact animals, in which the same training procedure has been used (cf. Table I Nos. 15 and 16). However, the CR performance was in these dogs much poorer than in the bilaterally pyramidotomized animals which had been trained before operation. Although during the whole period of training the electrodes were attached to the foot, the instrumental movements were of relatively long latencies (4–6 sec.) and lower amplitudes. One of the dogs performed isolated flexion but of very small amplitude. In the second, the movements were of higher amplitude, but unisolated. They appeared during a strong general defensive reaction and were always accompanied by lifting of the ipsilateral forelimb. In both dogs the character of responses did not change during the whole period of training (300–400 trials) and did not improve by applying the electrical current to the trained limbs.

DISCUSSION

Our results are in agreement with the findings of other authors (Bucy 1957, Bucy and Keplinger 1961, Gambarian et al. 1964, Lawrence and Kuypers 1965, Górska et al. 1966a, Laursen 1966) showing that the pyramidal system is not indispensable for performing voluntary movements. None of the instrumental CRs studied in this work was after bilateral pyramidotomy abolished. The CR of placing the forelimb on a platform was totally preserved. The other two CRs, the rubbing movements of the forelimb and the flexion movements of the hindlimb were more impaired, althought they could be also regularly performed either after a short retraining (rubbing CR) or some changes in the testing procedure (flexion CR). All these reflexes could be also established in naive bilaterally pyramidotomized dogs with a similar rate as in normal animals. The constant effect of pyramidotomy was an increase in the latencies of the instrumental responses and/or a decrease of their amplitudes.

In the case of instrumental CRs derived from some unconditioned motor reactions, the effects of pyramidotomy could be partly compensated by merely attaching the electrodes to the skin area, from which these unconditioned reflexes were originally evoked. Attaching the electrodes to the cheek shortened the latencies and enhanced the amplitudes of the retrained instrumental rubbing movements as compared with movements executed without electrodes. Attaching electrodes to the foot resulted in the reappearance of the instrumental flexion movements of the hindlimb, which were almost completely absent in pyramidotomized animals, when tested without the electrodes. The same procedure in normal animals evoked either no or only much smaller effects on the

CR performance. Similar facilitatory effects of attaching the electrodes were observed in our previous experiments in dogs with sensori-motor ablations (Górska 1963).

The problem arises whether the positive effects of attaching the electrodes was due to the stimulation of the specific reflexogenic areas or rather to the increase of the fear drive, since the presence of the electrodes could also signal the possibility of getting the painful stimulation. The following facts seem to support the first assumption. First, attaching the electrodes produced a similar effects both in alimentary and avoidance CRs. In the group of dogs with the flexion CR there were animals with alimentary or avoidance CRs and in all of them attaching the electrodes to the foot caused the reappearance of the instrumental movements. Secondly, in avoidance CRs, established by other methods than provoking the respective unconditioned movements (dog No. 3 with the placing CR, and dog No. 14 with the flexion CR), attaching the electrodes to the place where the electric current was originally applied and even applying the electrical stimulation did not facilitate the trained movement. It seems therefore that the facilitatory effects produced by attaching the electrodes were mainly due to a subthreshold stimulation of the receptive field of the unconditioned reflex from which the instrumental CR was derived. This suggests that the instrumental CRs utilize the reflex arcs of the reactions from which they originally derived, as already postulated (Górska et al. 1966b) and that one of the main factor of deterioration of the instrumental CRs after pyramidotomy is the removal of facilitatory influences exerted on these reflex arcs (Lundberg and Voorhoeve 1962, Lundberg 1964).

The next point to be commented upon concerns the differences between the effects of pyramidotomy on various instrumental CRs. Each of the CRs investigated in this study was affected to a different degree after pyramidotomy. These differences were not due to the length of the preoperative training, since the rate of acquisition of the CRs and the amount of trials applied during the training was in various groups of dogs the same. They were neither due to differences in the extent of lesions, since in all the dogs the pyramids were completely or nearly completely sectioned and in each experimental group there were animals in which the lesion was limited to the pyramids as well those in which the medial lemniscus was partly damaged (cf. Table I and II). Contrary to the results obtained after cortical lesions (Samoilov 1962, Ioffe 1962), the postoperative impairment of the CRs did not depend in our experiments on the kind of reinforcement used and the methods of the preliminary training. In groups of animals with the placing and flexion CRs there were dogs with either alimentary or

avoidance CRs, in which also different methods of preliminary training were used, and the postoperative changes in these animals were similar to those observed in other dogs of the same group but differently trained.

Although the possible sources of differences between the effects of pyramidotomy on various instrumental CRs require further experimental analysis, our results suggest that they might be partly due to differences between the anatomo-physiological structure of the movements of the fore- and hind extremities. The instrumental flexion CR of the hindlimb was more impaired after pyramidotomy than both the CRs of the forelimb, since the instrumental movements almost completely disappeared when tested without electrodes on the foot. Contrary to the results obtained by Gambarian et al. (1964), in our experiments also the acquisition of this CR after bilateral pyramidotomy was impaired, and much poorer than in the case of the remaining two CRs. Taking into account that the number of corticospinal fibres descending to the lumbar enlargement are by far less numerous than those ending in the cervical enlargement (Lassek 1946, Brookhart and Morris 1948, Morin and Poursines 1948, Maffre 1955, Mossakowski and Górska, unpublished data) one should expect just an opposite effect. Therefore, the greater impairment of the instrumental movements of the hindlimb after pyramidotomy probably reflects the fact, that other non-pyramidal descending pathways of supraspinal origin also innervate to a smaller extent the lumbar than the cervical enlargement (Torvik and Brodal 1957, Nyberg-Hansen 1964). This would correspond to the fact that in quadrupedes the movements of the hindlimbs, are less differentiated than those of the forelimbs, as they are mainly used in postural and locomotor activities.

The smaller impairment of the instrumental placing CR as compared with the rubbing CR, support our previous findings (Górska et al. 1966a, b) showing that voluntary movements belonging to the category of manipulatory CRs are less dependent on the pyramidal system than other instrumental movements. However, since in dogs the placing CR was preserved both after alimentary and avoidance procedure, these differences could not be attributed to the probably alimentary character of the manipulatory movements. It seems, therefore, that the visual stimuli may play a decisive role in the performance of the manipulatory CRs. This is in good agreement with the fact that other visually guided motor responses, as for example the visual placing, are also less affected after pyramidotomy than other forms of placing reactions based on somatosensory input (Marshall 1934, Maffre 1955, Górska, unpublished data).

Our results in dogs did not confirm our previous findings in cats

(Górska et al. 1966b) showing that the instrumental CRs derived from the unconditioned reflexes are almost completely abolished after pyramidotomy. Both the rubbing and the flexion CRs could be regularly performed by pyramidotomized dogs. This shows that in cats, the profound deterioration of the instrumental scratching, cleaning and rubbing CRs after pyramidotomy was due to some other factors, and could not be related to the origin of the CRs itself. As suggested by our results, one of the possible factor which might additionally enhance the postoperative impairment is the posture of the animal. For example, in the case of the rubbing CR, the operated cats when waiting for food, offered through a hole at the level of the floor, stood all the time with a head bent down and this posture seemed to interfere with the performance of the instrumental rubbing movements. Similar antagonism between the reaction of lowering the head and of lifting a forelimb was observed in dogs with sensori-motor ablations (Ioffe 1962). Since in the rubbing CR in dogs the experimental situation did not involve such postural antagonism, the deterioration of this CR after pyramidotomy was much less pronounced than in cats.

Another difference between the results obtained in dogs as compared with cats, concerns the effects of uni- and bilateral pyramidotomy on instrumental CRs. In the present experiments the impairment of the CRs after both these lesions was in general the same. However, in cats some differences were found, especially in the case of the CRs which involved preparatory postural elements of the whole body (as for example in the scratch and cleaning CRs). This is consistent with the observations of Bucy and Keplinger (1961) who reported that in monkeys the generalized movements of the whole body were more affected after a bilateral section of the pyramidal tract as compared with a unilateral section, while they did not observe such differences in case of isolated movements of one extremity.

SUMMARY

The effects of unilateral and bilateral section of the medullary pyramids on the instrumental CRs of placing the forelimb on a platform, rubbing of the cheek with a forepaw, and flexion of the hindlimb were studied in dogs. Each instrumental CR was differently affected after pyramidotomy; however, none of them was irreversibly abolished. The placing CR was totally preserved, the rubbing CR could be easily reestablished by retraining and the flexion reflex could be restored by merely attaching the electrodes to the trained limb. All the CRs could be also established in naive bilaterally pyramidotomized animals with a similar

rate as in normals. The constant effect of pyramidotomy was on increase in the latencies of the instrumental movements and/or a decrease in their amplitudes. The impairment of the CRs after uni- and bilateral pyramidotomy was in general similar.

In the case of the instrumental CRs derived from some unconditioned motor reflexes, the effects of pyramidotomy could be partly compensated by a subthreshold stimulation of the receptive field of a corresponding unconditioned reflex. Attaching the electrodes to the cheek facilitated the appearance of the retrained instrumental rubbing movements after pyramidotomy, i.e., shortened their latencies and increased their amplitudes, as compared with movements performed without electrodes. Attaching the electrodes to the foot restored the instrumental flexion movements, which almost completely disappeared after pyramidotomy, when tested without electrodes. In normal animals the same procedure had either no or only small effects on the CR performance. These results suggest that the pyramidal system plays a facilitatory function in the performance of instrumental CRs, which could be partly substituted by an adequate peripheral stimulation.

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SOME PROPERTIES OF THE ACUTE MIDPONTINE PRETRIGEMINAL CAT [1]

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The properties of the midpontine pretrigeminal cat, with special regard to the ocular and EEG responses to visual stimuli, were studied by several authors (Batini, Moruzzi et al. 1959, Affanni, Marchiafava and Żernicki 1962a, b, Elul and Marchiafava 1964, Żernicki and Dreher 1965). In particular, it was found that the activity of the isolated cerebrum of this preparation is in many respects normal (cf. Żernicki 1964). The aim of the present investigation was the further analysis of some of the properties of the midpontine pretrigeminal cat. The spontaneous EEG activity, the responses to olfactory stimuli and the variability of responsiveness to visual and olfactory stimuli were studied in detail. Moreover, the properties of the midpontine pretrigeminal cat were compared with those of the cats with rostropontine and prepontine transection.

MATERIAL AND METHODS

The experiments were carried out on 79 midpontine pretrigeminal cats, 10 rostropontine cats and 10 prepontine cats. The brain stem transection was done in tracheotomized animals under ether anaesthesia. The plane of transection was oriented 60° from the horizontal plane. The transection was done with a spatula; for the

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rostropontine and prepontine transections, a Z-shaped spatula was used, which could cut the brain stem just behind the tentorium. In the midpontine cats, the transection was performed at the level or immediately in front of the trigeminal rootlets (Fig. 1). In the rostropontine cats, the cut passed dorsally through the caudal poles of the inferior colliculi or just behind them, and ventrally 1–5.5 mm behind the midbrain. Finally, in the prepontine cats, the transection passed dorsally through the middle of inferior colliculi and ventrally through the border between midbrain and pons. Immediately after the transection the ether narcosis was dis-

Fig. 1. Drawings of horizontal sections of the brain stem in front of the midpontine (A), rostropontine (B) and prepontine (C) transections in the typical preparations C.I.: colliculus inferior; C.P.: commissura posterior; C.S.: colliculus superior; F.L.M.: fasciculus longitudinalis medialis; H.: habenula; I.P.: nucleus interpeduncularis; P.: pons; P.C.: pedunculus cerebri; R.P.O.: n. reticularis pontis oralis; T.T.C.: tractus tegmentalis centralis

continued. In order to counteract an edema of the brain and to allow the introduction of the Z-shaped spatula, the anterior part of the cerebellum was removed by suction; in the rostropontine and prepontine preparations the removal was done before the transection and in the midpontine preparations immediately after the transection. The nictitating membranes and the upper eyelids were partially removed in order to permit better observation of the eyeballs.

Following surgery the animal remained in the stereotaxic apparatus (designed for a wide visual field) and was placed in a small, optically isolated chamber. The preparations were observed there from 4 to 12 hr. On the white screen of the chamber, 120 mm in front of the animal's eyes, two black X-shaped figures were located. One of the figures was situated on the horizontal plane passing through the nodal points of the eyes of the preparation (horizontal figure X) and the other 25° above this level (upper figure X). The angular diameter of the figure X was 12°. As a visual stimulus the rotation of one of the figures X at a rate of 1 cycle/sec for about 3 sec was used. Before location of the animal in the chamber, vertical movement of the piece of the cotton wool in front of the eyes was used as the stimulus.

As olfactory stimuli, the odors of valerian, butyric acid, amyl acetate, xylene, collidine, picoline and piperidine were used. The odor was introduced into both nostrils of the cat, using a modified blast injection method: for about three seconds, 400 ml of the air was blown in three strokes by a pump; the air passed through a 100 ml bottle containing 20 ml of the odorous liquid. With this technique the odors produced stronger response than when introduced into the nostrils by suction through post-nasal cannula (Adrian 1942).

The EEG activity was recorded bipolarly from the sensori-motor, visual and occasionally temporal cortical areas. The electrodes were placed on the dura matter; the interelectrode distance was 10 mm. The ocular behaviour was filmed. For the valuation of the angular size of the eye movements the technique described elsewhere was used (Żernicki and Dreher 1965).

The nursing care of the preparation was limited to maintaining the body temperature between 37° and 39°C, sporadic injection of 5% glucose and protecting the eyes from drying. In order to determine the level and extent of transection the brains were fixed in 10% formalin and serial sections stained with Klüver technique were examined. In the statistical analysis, the Mann-Whitney U test was used (Siegel 1956).

RESULTS

1. Spontaneous EEG activity in the midpontine pretrigeminal cat. Four elements of the EEG activity could be distinguished: (i) desynchronized activity characterized by the frequency of 35–46 c/sec and amplitude of 20–40 μV, (ii) 11–17 c/sec rhythm with an amplitude 60–140 μV, (iii) 10–13 c/sec rhythm of spindle form having an amplitude of 100–270 μV, and (iv) slow waves periods of 125–300 msec, and amplitude of 40–110 μV. The EEG of a preparation could be either permanently desynchronized, or desynchronized EEG activity was mixed in different proportion with synchronized activities (Fig. 2). The EEG pattern of drowsiness was often present, but never that of the light (synchronized)

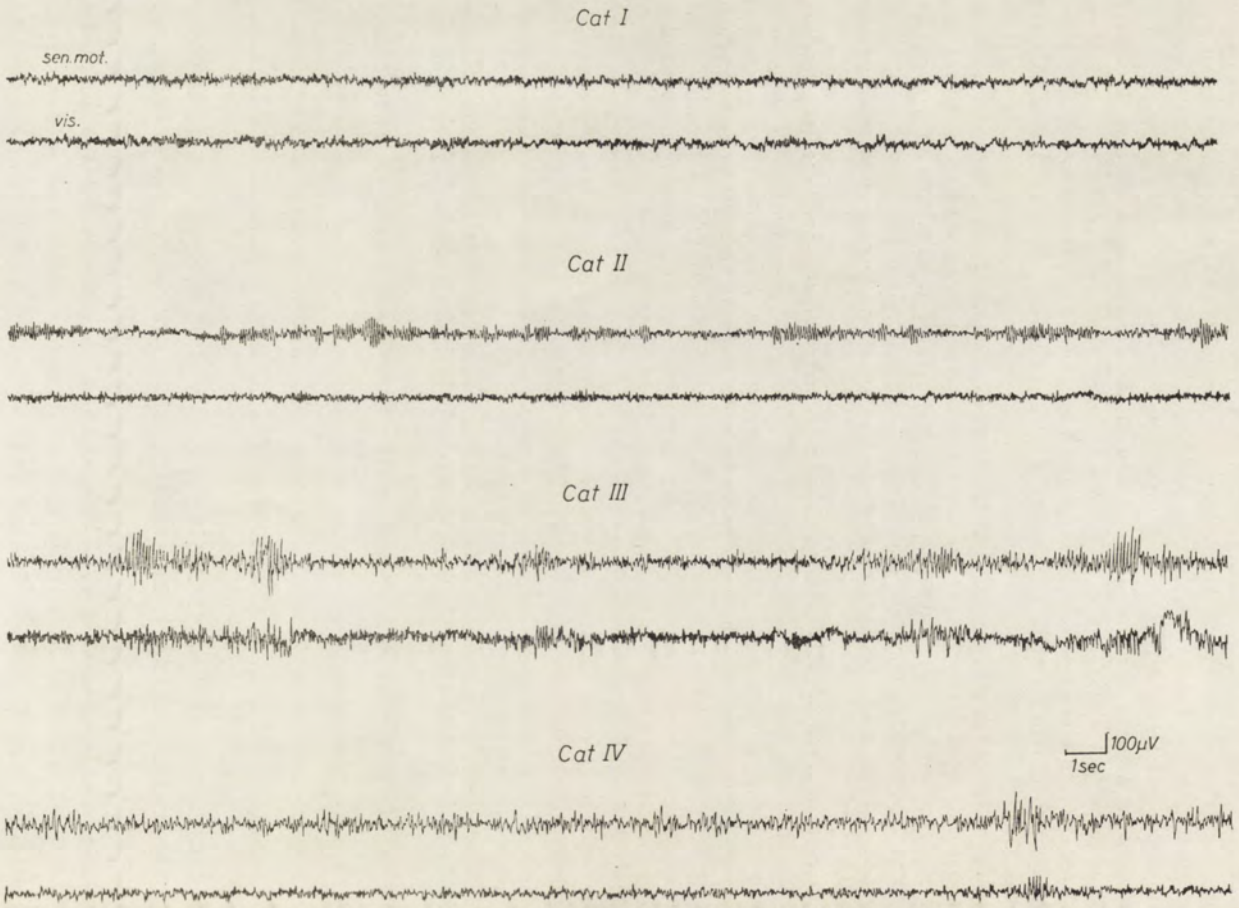

Fig. 2. Typical spontaneous EEG activity in the midpontine pretrigeminal cats

Cat I: EEG activity is permanently desynchronized. Cat II: 11-17 cycle/sec rhythm is dominant in the sensori-motor lead. Cat III: Spindle bursts are present. Cat IV: Irregular waves with periods 125-300 msec are dominant in the sensori-motor lead

sleep (cf. Hess, Koella and Akert 1953). The amount of the desynchronized activity was usually much more abundant in the visual areas than in the sensori-motor ones.

Soon after the transection, in the majority of preparations (46 cats) the EEG activity was permanently desynchronized. However, 2–6 hr later in many of these preparations the synchronized activity also appeared. Except for this change, a given EEG pattern usually remained during the whole period of observation.

The desynchronized EEG activity did not seem to be due to the presence of deep (desynchronized) sleep. Except for periods of coma (cf. Section 3), even weak visual or olfactory stimuli, presented during EEG desynchronization, usually produced clear-cut ocular and EEG responses. Moreover, the latter response never consisted in appearance of the synchronized EEG activity, which occurs in the intact animal when an external stimulus is presented in deep sleep (cf. Jouvet 1961), but an acceleration and increase of the amplitude of the EEG activity could be usually observed (cf. Fig. 3).

2. Responses to olfactory stimuli in the midpontine pretrigeminal cat. In the majority of preparations the olfactory stimuli produced a clear-cut reaction consisting of the EEG arousal, pupillary dilation and vertical movement (or movements) of the eyeballs (Fig. 3). The latency of the EEG arousal and of the pupillary dilation was, on the average, about 1.5 sec and 1 sec respectively. The reaction usually lasted for several seconds. The intensity of the reaction depended considerably on the individual properties of the preparation (cf. Section 4) and the kind of olfactory stimulus. Butyric acid, valerian, collidine and amyl acetate formed the group of "strong stimuli". The responses to xylene, picoline and piperidine were considerably weaker (the latter two stimuli produced respiratory responses in preparations in which the trigeminal roots were not destroyed by the transection). The smallest, but considerable, reaction was evoked by introduction of the room air into the nostrils of the preparation.

The responses to olfactory stimuli were compared with those to the visual ones. Because the visual stimuli used in our study were strong (cf. Żernicki and Dreher 1965), for the comparison only the responses to the "strong" olfactory stimuli were selected. Several differences could be noted: (i) the EEG arousal to olfactory stimuli was similar both in the sensori-motor and visual areas, while that to the visual stimuli was stronger in the visual areas (Fig. 4), (cf. Żernicki and Dreher 1965), (ii) the EEG arousal to olfactory stimuli was less pronounced than to visual stimuli (especially in visual areas), (iii) the olfactory stimuli often interrupted the train of spindle bursts which could disappear for

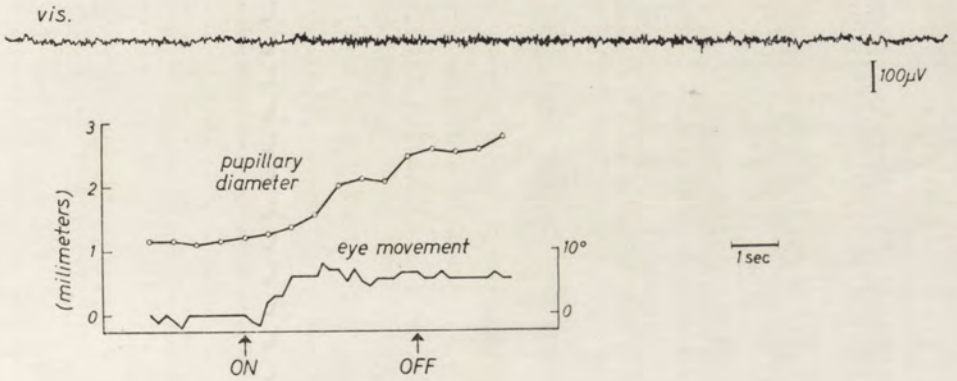

Fig. 3. EEG and ocular response to the strong olfactory stimulus (amyl acetate) in midpontine pretrigeminal cat

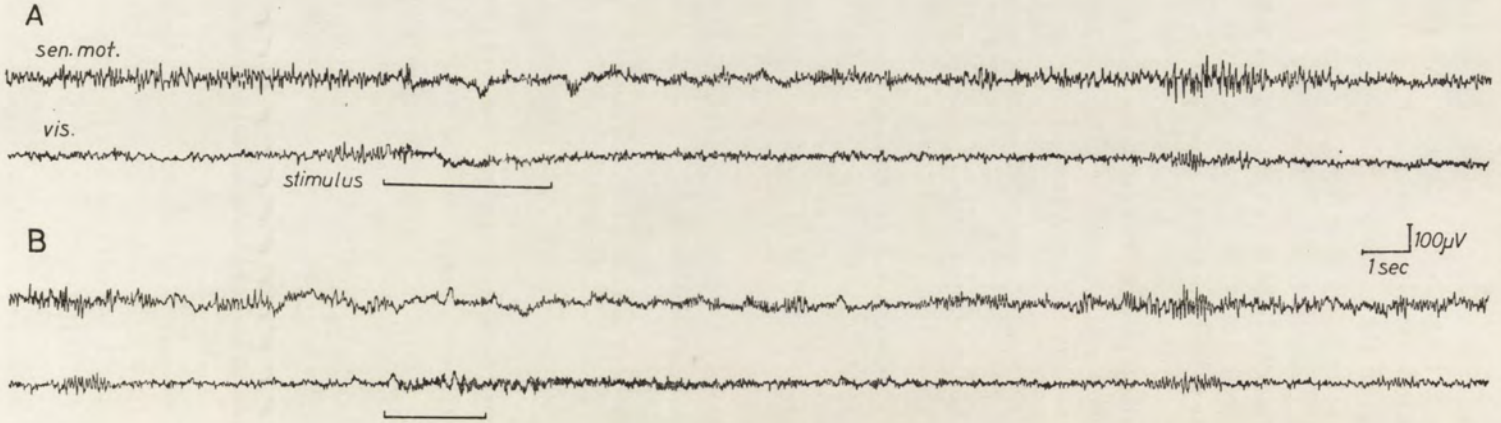

Fig. 4. Comparison of EEG arousal to the strong olfactory (A) and visual (B) stimulus in the midpontine pretrigeminal cat

The olfactory stimulus was the odor of the valerian, and the visual stimulus was the rotation of the horizontal figure X. Note the strong EEG arousal to the visual stimulus in the visual lead

as long as a few minutes, while the visual stimuli interrupted the spindles very rarely and only for a few seconds; occasionally the EEG arousal to an olfactory stimulus consisted only in the cessation of the spindles, while other synchronized EEG activity remained intact, (iv) the spindles evoked by the intravenous admistration of the small doses of nembutal (2.5–4 mg/kg), could be also much easier interrupted by the olfactory than by the visual stimulus, (v) pupillary dilation to the olfactory stimuli was usually weaker than that to the visual stimuli, (vi) the odors produced much weaker eye movements than the upper figure X (the horizontal figure X did not usually evoke eye movements).

When the same odor was applied repeatedly at 2–3 minute intervals, the reaction produced by it decreased rapidly (Fig. 5). The diminution did not seem to be due to sensory adaptation, because the olfactory receptors are resistant to adaptation (cf. Adrian 1950, Arduini and Moruzzi 1953, Ottoson 1959). The fatigue seemed to be also improbable because the diminution was rapid and had enduring character. Therefore, it may be considered as the result of habituation. Consequently in the midpontine pretrigeminal cat the reaction to the olfactory stimulus appears to be an orientation reflex. There were considerable individual differences in the time-course of habituation. On the average, the reaction disappeared completely within ten trials, i.e., quicker than did the orientation response to a visual stimulus (cf. Żernicki 1964). The spontaneous recovery of the completely habituated reaction was usually difficult (Fig. 5). After an interval of 1–2 hr the recovery was poor and the reaction rehabituated after only a few repetitions of the stimulus. Moreover, the dishabituation of the reaction could be often obtained neither by other odors, nor by visual stimuli.

3. Variability of responsiveness in a midpontine pretrigeminal cat. The variability of responsiveness was tested by visual stimuli, which could be easily applied soon after the operation. After the transection preparations remained in a coma. At this stage visual stimuli did not produce the orientation reflex, which in this preparation consists in pupillary dilation, fixation response and EEG arousal (Affanni et al. 1962a), but only the light reflex, which usually resumed a few minutes after the transection. Stimulation of the mesencephalic reticular formation, which produced a pupillary dilation, EEG arousal and eye movements, could not awake the preparation as shown by the continuing absence of the orientation reflex to visual stimuli. Duration of the post-transectional coma varied considerably. In the majority of preparations (49 cats) wakefulness was resumed within two hours after the transection (in a few cats already about 20 min after transection). In 16 cats

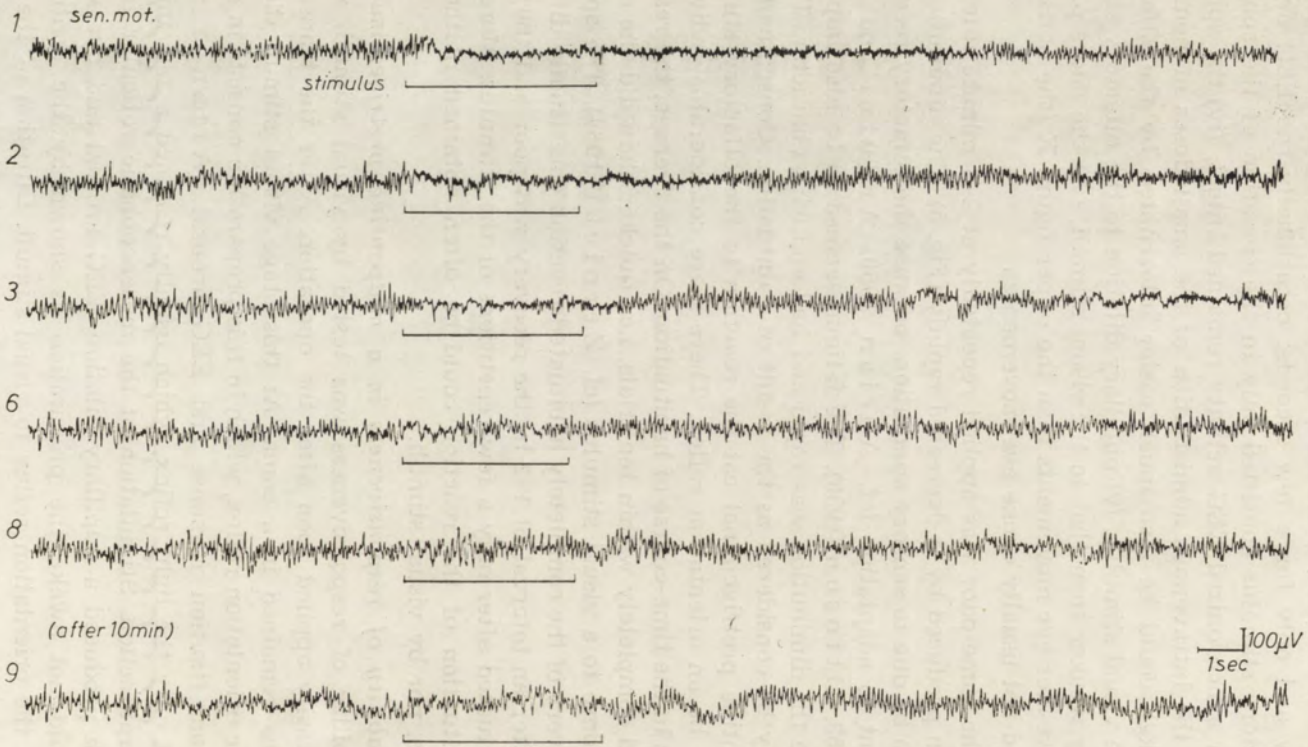

Fig. 5. Habituation of the EEG arousal to the odor of valerian in the midpontine pretrigeminal cat
Note the lack of spontaneous recovery in 9th trial given after 10 min interval

coma lasted between 2 and 3 hr. In 14 cats wakefulness was resumed later or was not resumed at all.

To elucidate the mechanism of the coma, some intact cats were kept under ether narcosis for 15 min, i.e., for the time usually needed for the performance of the brain stem transection. In these animals the orientation reflexes to the visual stimuli were resumed about 20 min after discontinuation of the ether application. Therefore the ether narcosis could be the cause of the coma only in a few cats, in which the latter was very short. The coma was obviously not due to the circulatory collapse because the arterial pressure was then not depressed. As far as the role of the respiratory factor is concerned, considerable anoxia during the coma seemed to be improbable because the rate of respiration was then not lower than in the following state of wakefulness. Strong hyperventilation seemed to be also excluded because the activation of the EEG activity, which may be considered an index of the carbon dioxide content, was on the average even stronger during the coma than in the wakefulness. It seems to be probable, therefore, that the coma was mainly due to the cerebral shock (diaschisis) produced by the brain stem transection (cf. Adametz 1959).

During the following state of wakefulness in some preparations the responsiveness remained unchanged (except for the gradual diminishing of the orientation reflex due to habituation). In some preparations, however, the responsiveness showed some variations. Besides, in a considerable proportion of cats 4–7 hr after the transection a secondary coma developed. Our previous experiments on the chronic midpontine preparations showed that it lasts 1–2 days (Żernicki and Osetowska 1963). This time-course of the secondary coma may suggest that it is due to the development of the local edema of the brain stem. It may be noted that our preliminary observations (obtained in collaboration with Dr. H. Wiśniewski) suggest that the local edema was considerable in our preparations because the fluorescein sodium administered intravenously just before the transection could be found 6 hr later a few milimeters in front of the lesion.

It is worth noting that the changes of responsiveness were not correlated with the less frequent changes of the activation of the spontaneous EEG activity.

4. Individual differences in responsiveness in the midpontine pretrigeminal cat. In the state of wakefulness, which appeared in 68 cats, there were strong individual differences in responsiveness to visual and olfactory stimuli, but the responsiveness to visual stimuli (evaluated by the duration of the EEG arousal) was positively correlated with the responsiveness to the olfactory stimuli ($p < 0.01$). It is convenient to describe

the differences in responsiveness using as a test the visual fixation reflex, the strength of which is positively correlated with the intensity of other components of the reaction to the visual stimulus (Elul and Marchiafava 1964, Żernicki and Dreher 1965). In some preparations (30 cats), the rotation of the upper figure X evoked the "full single fixation reflex", i.e, the reflex consisting in one fixation with an amplitude sufficient to bring the image of the object on the area centralis (cf. Żernicki and Dreher 1965). Some other preparations (26 cats), however, responded to this stimulus with the "abortive single fixation reflex". On the other hand, 12 cats responded with the "serial fixation reflex".

In cats displaying different responsiveness the degree of activation of the spontaneous EEG activity could be similar, and in cats with opposite EEG activity the reflexes of similar strength could be observed (Fig. 6). For the purpose of comparison two groups of cats with extremely different EEG activity were selected: in the first group the spontaneous EEG

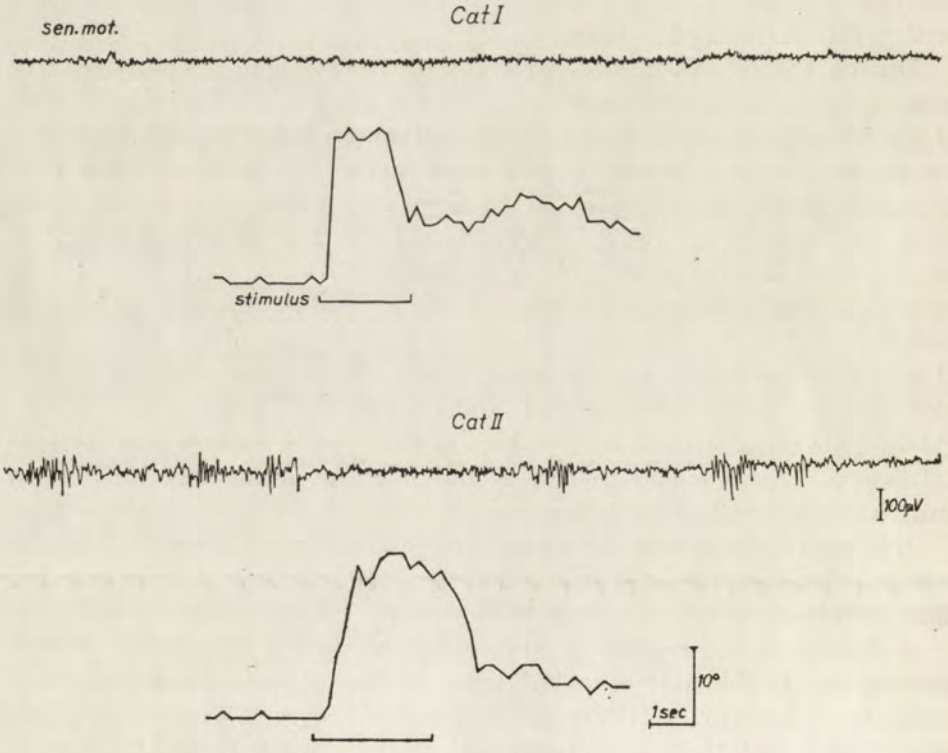

Fig. 6. Similar fixation reflexes to the rotation of the upper figure X in cats whose spontaneous EEG activity differed markedly

activity was permanently desynchronized, and in the second group the synchronized EEG activity prevailed over the synchronized one. The difference in responsiveness between the two groups of the cats was not significant ($p > 0.05$).

5. *Cats with rostropontine transection.* The properties of the rostropontine cats were in general similar to those of the midpontine preparations. EEG activity was permanently desynchronized in two cats, and in eight cats the desynchronized activity was mixed in different proportion with synchronized activity, which showed the same characteristics as that present in the midpontine cat. For the purpose of statistical analysis, depending on the percentage of time during which the synchronized activity was present, the scores from one to four were given for a combined group of rostropontine and midpontine cats. The difference between both types of preparations was not significant ($p > 0.05$). The pupillary diameter was also similar in the rostropontine and midpontine preparations ($p > 0.05$). As far as the responsiveness is concerned, one rostropontine cat reacted to the rotation of the upper figure X with serial fixation reflex, two with full single reflex, five with abortive reflex, and two cats were unresponsive. Again the difference between the rostropontine and midpontine cats was not significant ($p > 0.05$).

6. *Cats with prepontine transection.* Two different types of preparations were obtained. The preparations of the first type (5 cats) seemed to be similar to the midpontine cat. In two preparations the EEG was permanently desynchronized, and in three cats the desynchronized activity was mixed with the synchronized one. The pupils were narrow, but not fully constricted (light reflex was present). Visual and olfactory stimuli produced EEG and ocular reactions in three cats (two preparations showed abortive fixation reflex and one full single reflex).

Another five preparations were of the "low cerveau isolé" type (cf. Moruzzi 1964). The EEG activity was characterized by spindle bursts, which were much more developed than those occurring in the midpontine preparation (cf. Fig. 7). During the interspindle lulls the EEG was desynchronized in three cats, and in two preparations the desynchronized activity was mixed with waves of higher amplitude. Pupils were miotic in all cats. Visual stimuli produced neither EEG nor ocular responses (Fig. 7). Olfactory stimuli also did not produce any ocular reaction, but in three cats they evoked a clear EEG arousal cosisting mainly in the cessation of the spindles; the cessation lasted in different cats from a few seconds to 1.5 min. The intravenous injection of amphetamine (1 mg/kg) produced EEG desynchronization and pupillary dilation in all cats, and in four preparations the appearance of the EEG ocular responses to visual stimuli and of ocular responses to olfactory stimuli.

DISCUSSION

1. "Pretrigeminal preparation" versus low cerveau isolé preparation. In his recent review, Moruzzi (1964) summarized the differences between midpontine pretrigeminal cat and low cerveau isolé cat; the latter was obtained by Bizzi and Spencer (1962) with prepontine (postcollicular) transection, and by Batini, Moruzzi et al. (1959) with rostropontine transection. In short, the midpontine pretrigeminal preparation is awake showing ocular and EEG responses to visual stimuli, while the low cerveau isolé preparation is a sleep, but the spindle bursts present in the EEG activity may be interrupted by the olfactory stimuli.

In the present investigation, the low cerveau isolé preparation could be obtained only by the prepontine transection, and even then only in 50% of cases. The cause of the discrepancy between our results and those of Batini, Moruzzi et al. (1959) may be that the transection obtained with coagulation by the latter authors produced bigger functional lesion than ours produced by a spatula. On the other hand, our results seem to be in agreement with those of Bizzi and Spencer (1962). These authors obtained the cerveau isolé preparation after the prepontine transection which passed the midbrain just behind the exit of the third nerve rootlets, i.e. ventrally the cut was more anterior to ours.

Our preparations obtained by transections at the midpontine and rostropontine levels showed, on the average, similar properties both in terms of EEG activity and responsiveness. These results are in agreement with recent observations of Carli and Zanchetti (1965), that an extensive damage of the rostropontine tegmentum in the cat does not produce any increase of the synchronized sleep pattern. It is tempting to think, therefore, that in the reticular formation of the rostral part of the pons there are deactivating structures as well as activating ones, and that both types of structures remain in some functional equilibrium. From the functional point of view, both the midpontine pretrigeminal preparation and the rostropontine preparation may be simply named "pretrigeminal preparation".

2. The factors influencing the state of the isolated cerebrum of the pretrigeminal preparation. Our pretrigeminal cats showed considerable differences in both responsiveness to visual and olfactory stimuli, and spontaneous EEG activity. Several factors may be considered as responsible for these differences.

(i) It was already noticed that the comatic states in the pretrigeminal cat are probably due to the cerebral shock and local edema of the brain stem (cf. Section 3 of Results). The problem arises whether or not these

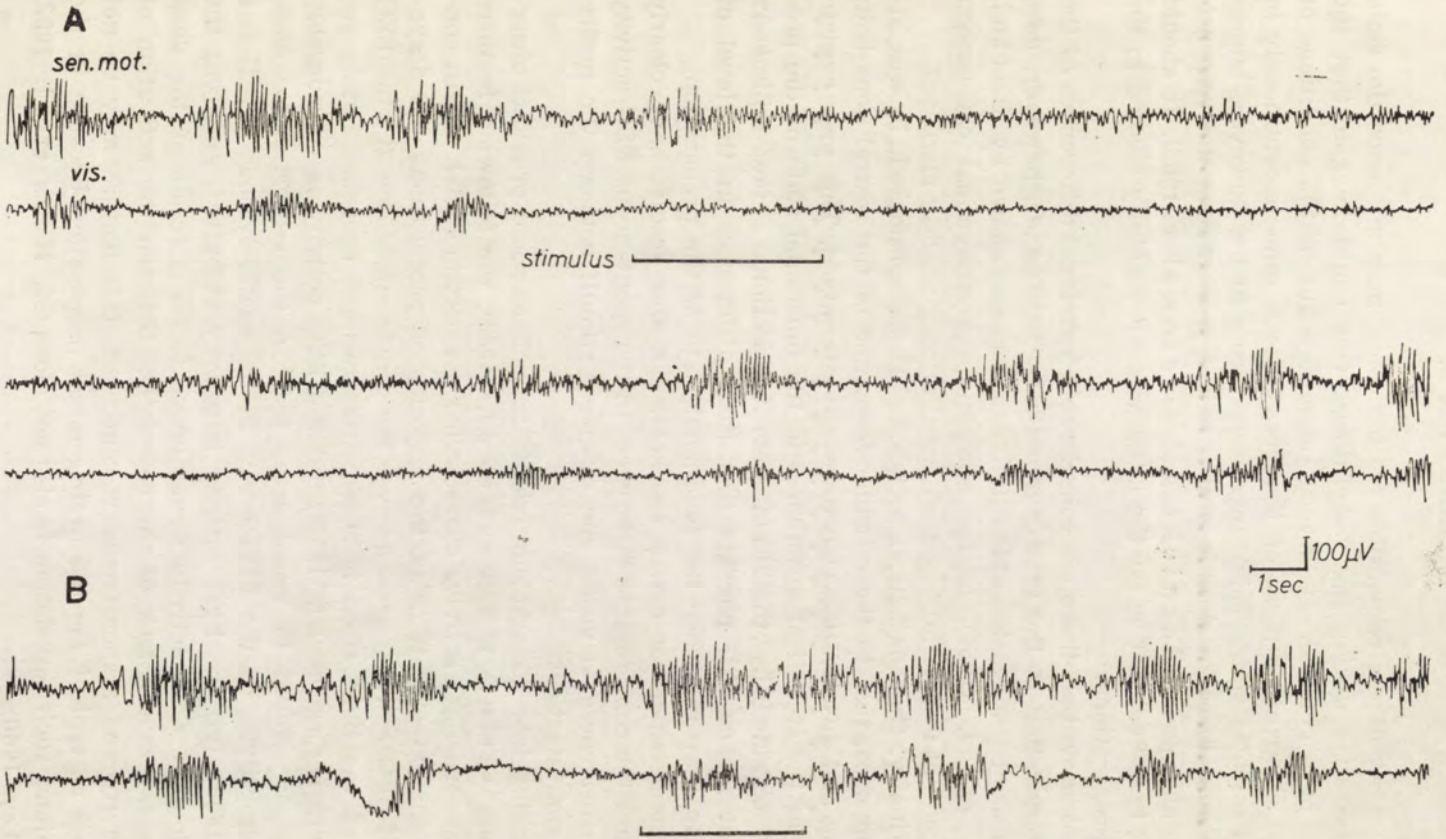

Fig. 7. Comparison of EEG responsiveness to olfactory and visual stimulus in the prepontine cat

A: the interruption of the spindle bursts by the odor of the collidine. B: 1,5 min afterwards no response to the rotation of the upper figure X

factors (or any others responsible for the coma) may influence the state of a preparation during the wakefulness. One could imagine that the "normal" pretrigeminal cat is very responsive but in the conditions of the acute experiment most of the preparations remain continously in the semi-comatic state. This supposition seems to be, however, improbable because in some chronic pretrigeminal preparations the responsiveness is also poor (Żernicki and Osetowska 1963). It should be noted, however, that so far the latter was not carefully studied in the chronic preparations.

(ii) We know that there are considerable individual differences of the rate of respiration in the pretrigeminal cats. This factor, however, does not seem to play a considerable role because as was shown by Batini, Magni et al. (1959), in the midpontine pretrigeminal cat carbon dioxide content in arterial blood is normal or only slightly increased.

(iii) Finally, the anatomical factor should be considered. It was already supposed, that in the reticular formation of the rostral pons both activating and deactivating structures are intermixed. This may explain the lack of the statistical differences in the functional state of the preparations obtained by the brain stem transections a few milimeters apart, but makes still possible that little differences in the level of transection may influence the functional state of the preparation.

3. Pretrigeminal cat versus an intact cat. Our results have clearly pointed out the considerable differences in the spontaneous EEG activity and responsiveness to visual and olfactory stimuli between the pretrigeminal and intact cat.

(a) Taking into account our results as well as some previous observations of Batini, Moruzzi et al. (1959), the following features of spontaneous EEG activity characterize the pretrigeminal cat, in contrast to the intact cat: (i) in the majority of preparations the desynchronized EEG activity prevails over the synchronized one, (ii) the EEG pattern of the light sleep is absent, (iii) the 5–8 cycle/sec bursts are absent (cf. Hess et al. 1953), (iv) the EEG activity is considerably more desynchronized in visual areas than in the sensori-motor ones, (v) the amplitude of the EEG seems to be relatively low (cf. Hess et al. 1953), (vi) the EEG activity is usually stabilized, and (vii) the desynchronized EEG activity seems never to be a result of the deep sleep. As far as the lack of the correlation between the activation of EEG activity and responsivenes is concerned, this feature may be not considered as typical for the pretrigeminal preparation because in the intact animal such correlation is also not close (cf. Hess et al. 1953, Lindsley 1960).

Most of these differences may be easily understood. The striking de-

synchronization of the spontaneous EEG activity in the pretrigeminal cat may be explained by the absence of the deactivating influences of medulla (cf. Moruzzi 1964). The absence of the deep sleep shows that midpontine transection can eliminate the influence of the pontine centre responsible for this stage of sleep (cf. Jouvet 1962, Rossi, Minobe and Candia 1963, Carli and Zanchetti 1965, Hobson 1965). The fact that the EEG activity is more desynchronized in the visual than in the sensori-motor areas may be due to the lack of the proprioceptive impulses. Furthermore, the stabilization of the EEG activity may be due to the isolation of the cerebrum from the interoceptors. On the other hand, it is less understood that in spite of those differences the isolated cerebrum may show normal behavioural and EEG responses to external stimuli.

(b) We know, that in the intact cat, under similar experimental conditions, rotation of the upper figure X evokes a full single fixation reflex (Żernicki and Dreher 1965). Therefore, these pretrigeminal cats, who responded with abortive fixation reflex to this stimulus, may be consideraed as "hyporesponsive". On the other hand, the preparations, who showed serial fixation reflex, would be "hyperresponsive". The possible mechanism of these individual differences was discussed in Section 2.

4. Olfactory stimuli versus visual stimuli. The prominent difference between visual and olfactory stimuli was that the latter interrupted much easier the spindle bursts; this feature of the olfactory stimuli could be easily observed in the low cerveau isolé preparation and nembutilized pretrigeminal preparation. It is tempting to think, therefore, that the olfactory stimuli have the specific property to inhibit directly (with omission of the brain stem reticular formation) the activity of the telencephalic spindle producing structures.

In is worth mentioning that due to their property of producing EEG arousal in the low cerveau isolé cat, the olfactory stimuli were considered stronger than the visual ones (Arduini and Moruzzi 1953). Our results showed, however, that in the pretrigeminal cat, i.e., in the awake preparation, olfactory stimuli produce weaker response that the visual stimuli.

SUMMARY

1. The spontaneous EEG activity as well as the responsiveness to visual and olfactory stimuli were, on the average, similar in the midpontine pretrigeminal and rostropontine cats. This suggests that in the reticular formation there are present both activating the deactivating

structures. Functionally, both midpontine pretrigeminal cat and rostropontine cat may be simply named "pretrigeminal cat".

2. In the spontaneous EEG of the pretrigeminal cat four elements could be distinguished: (i) desynchronized activity, (ii) 11–17 c/sec rhythm, (iii) 10–13 c/sec rhythm of spindle form, and (iv) slow waves with periods of 125–300 msec. The EEG of the preparation could be permanently desynchronized or EEG activity was mixed in different proportion with synchronized activities. The EEG pattern of drowsiness was often present, but never that of light sleep. The desynchronized EEG activity was not a result of deep sleep.

3. In the pretrigeminal cat, olfactory stimuli produced an orientation reflex consisting in EEG arousal, pupillary dilation and small eye movements. Habituation of the reflex was easily obtained.

4. In the pretrigeminal cat, olfactory stimuli evoked smaller orientation reflex than visual stimuli, but olfactory stimuli interrupted much easier the spindle bursts. In the low cerveau isolé cat, visual stimuli did not produce any reaction, while the olfactory stimuli still interrupted the spindles. It is concluded that olfactory stimuli may specifically inhibit the activity of the telencephalic spindle originating structures.

5. Strong individual differences in responsiveness to visual and olfactory stimuli were observed in the pretrigeminal preparations. These differences were not correlated with those in the activation of the EEG activity.

6. In the majority of preparations the comatic states appeared, which were probably a result of the cerebral shock and development of the local edema of the brain stem.

The authors are much indebted to J. Konorski, W. Kozak, G. Moruzzi, L. Stępień, H. Wiśniewski, and K. Zieliński for valuable suggestions during preparation of the paper, and to Mrs. J. Rokicka for skillful technical assistance.

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Book reviews

Elektroentsefalograficzeskie issledowaniia uslovnoreflektornykh reaktsii (Electroencephalographic investigation of conditioned-reflex reactions). By R. S. MNUKHINA. Published by Izdatelstvo Leningradskogo Universiteta, Leningrad 1964, 158 pp., 49 figures.

The electrophysiological approach to brain functioning is becoming more and more important for further development of the research on the higher nervous activity.

The present work provides experimental material on the formation of conditioned reflexes and various sorts of internal inhibition (e.g. extinction, differentiation), with the wide use of modern EEG and electrometric techniques. The interpretation of the findings presented follows the Wedensky's and Ukhtomsky's conceptions.

This book is concise account of basic fundamentals and current views on the parabiosis and dominant. Emphasis is laid on further studying these two neural phenomena to understand better the higher nervous activity.

The following criteria were used to assess the brain functioning: the rate, amplitude and time course of wave discharges, and the polarization level of the cortical surface.

The author has shown that regardless of whether the conditioned reflex is formed, extinguished, or differentiated a diphasic activity occurs in the cortex: the initial desynchronization precedes a phase of slow wave discharges. This suggests that the two basic cortical processes, that is, excitation and inhibition, are essentially the same phenomena. The various forms of internal inhibition are characterized only by varying durations of either of the two successive phases. Thus during differentiation training the high frequency wave form is predominantly obtained, whereas the extinction of a conditioned reflex causes a brief phase of fast activity followed by a long-lasting phase of slow activity. Diphasic sequence of electrical events and other electrical complexes which are recorded from the cortex during training of a conditioned reflex or certain forms of internal inhibition suggests that the diphasic electrical activity is the general reaction of excitable tissues: an increase in lability of response is followed by a decrease of lability.

It is commonly held that an orienting reflex is accompanied by desynchronization of the cortical rhythm. Mnukhina has demonstrated that depending on the initial functional state of the cerebral cortex an orienting reflex may be associated with desynchronization, synchronization, or hypersynchronization of the cortical rhythm, a finding which agrees with Wedensky's observation that the reaction of the substratum is a consequence of the initial physiological state of the substratum.

The author's studies of cortical responses during the formation, extinction and differentiation of classical defensive conditioned reflexes (flexing of the foot elicited by an electric shock administered to the foot) have shown that the potentials evoked in the cortex are marked by a diphasic configuration in a sense that the initial, less pronounced wave activity is followed by distinctive wave discharges which occur with the performance of the conditioned reflex. Mnukhina's assumption has been that the poorly pronounced evoked potentials which occur at the early stage of the conditioned- reflex training correspond to the desynchronization phase, whereas the well-pronounced potentials reflect the phase of slow wave activity. Identical observation was made during the extinction of a conditioned reflex. On the basis of these findings, the conclusion has been drawn that the configuration of evoked potentials during both training and extinction is essentially the same.

Mnukhina found that when a conditioned reflex is formed wave discharges of opposite direction are recorded from the cortex. Evidence has been presented that during the formation of a conditioned reflex to an acoustic stimulus the two phases of the potentials evoked in either cortical acoustic area display opposite deflection. This suggests reciprocal changes in excitability in either acoustic receiving area. A reciprocal phase configuration of wave discharges in homologous sites of the two brain hemispheres has been demonstrated: a mainly negative wave discharge in one hemisphere, and a mainly positive discharge activity in the second hemisphere.

The author presents extensive information on time relations of the cortical responses, thereby giving a quantitative evaluation of the functional lability of the cortex. Furthermore, she reports on the chronaxy and summation interval of the motor cortex (when the cortex is directly stimulated) during the formation, extinction and differentiation of a classical defensive reflex. It must be emphasised that the author's results obtained with the excitometric techniques confirm her own results obtained with the EEG technique. Thus it has been demonstrated that during the formation, extinction and differentiation of conditioned reflexes, there is always a diphasic electrical activity in the cortex: an increase in lability develops into a decrease of lability. These findings are of primary importance for understanding the interrelations between cortical excitation and inhibition.

In order to further analyze the principles and mechanisms of the conditioned--reflex formation, Mnukhina studied the electrical activity of the cortex during the training of a conditioned reflex in intact animals. The author considers the fast acquisition of the conditioned reflex by 2–3 month old puppies a result of great reactivity of the cortex, well-pronounced local potentials and afterpotentials, and summation phenomena, which are the factors that facilitate the transformation of the local potential into an active, propagated potential, thereby speeding up the closure of the temporal connection (that is, the formation of the conditioned reflex).

Of particular interest is the author's finding indicating that the cortex of young dogs and rabbits up to 2 months of age displays an increased poststinuation electrical activity. The lability of the cortex of infant animals is considerably lower than that of grown-up animals (longer-lasting chronaxy and summation interval). Local potential and afterpotentials are well-pronounced in infant animals. However, the afterpotentials of infant animals are of short duration relative to those of adult animals. Therefore, the aftereffects of the stimulation can hardly be retained in infant animals. In adult animals, on the contrary, there is a deep--cut preservation of poststimulation effects associated with a long-lasting retention

and ability to replicate the previously acquired reactions. In the opinion of the author, the difficulty of the training of complex internal inhibition forms in young organisms may be related to the low capacity to retain traces of the preceding stimulation.

Much information has been provided on the closure of the temporal connections. The finding that prior to the occurrence of the first indices of the conditioned-reflex formation opposite driftings of the isoelectrical line level of the electroencephalogram occur led the author to the conclusion that the closure of the temporal connection is associated with the occurrence of the opposite (reciprocal- changes in the excitability of various cortical sites.

In seeking an explanation for the reciprocal changes of excitability in the cortex, Mnukhina has undertaken studies of the cortical polarization induced by anodal and cathodal currents. It has been shown that at a given distance from the polarizing electrodes changes of excitability in opposite direction may be noticed. The fact that the changes retain after the administration of chlorpromazine suggests that they are mediated by transcortical mechanisms. The nature of the opposite changes of excitability has satisfactorily been examined in an investigation of cortical slow wave discharges during the formation of the conditioned reflex. It has been found that at the early stage of the conditioned-reflex training the negative potential is replaced by the positive one. This suggests an increase in the polarity. When the training of the conditioned reflex proceeds the height of the local excitation (the level of depolarization) increases. The performance of the conditioned reflex occurs in association with the opposite shifts in the slow wave activity. These observations seem to favor the author's conclusion about the relationship between the formation of the conditioned reflex and the unspecific diphasic polarizing-depolarizing process.

Unfortunately, the results reported in the last two chapters of the book do not appear to the reviewer to be sufficiently precise. Some chapters (1 and 2) are not easy to read because they are compressed into a very limited space. At the end of the book is an extensively written discussion followed by 4 conclusive remarks. The latter is not so desired as might be a set of conclusions at the end of each chapter. It might be worthwhile emphasizing the use of microelectrode method to prove the validity of the author's main thesis on the polarizing-depolarizing mechanism of the temporal connection closure.

This is a valuable book. It is recommended to those physiologists and psychologists who are conducting research or teach the subject of brain function. It will be also of most interest to neurologists and psychiatrists. The author has performed a very fruitful service in pointing out the usefulness of the concepts of the Wedensky-Ukhtomsky school in research on brain function and higher nervous activity.

N. A. Shustin, Leningrad, USSR

Sex determination. By Guido BACCI. International series of monographs in pure and applied biology. Zoology division. General Editor: G. A. KERKUT. Published by Pergamon Press, Oxford 1965, 307 pp., 3 plates, 5 tables, 87 figures. Price 87s.

This monograph by Dr. Guido Bacci, Professor of Zoology, The University of Turin, makes up a review of earlier and present findings and concepts on the sex determination with an emphasis on evolutionary problems.

The sexual reproduction which has been found in most plants and animals results in a variety of genetic combinations and thus leads to the hereditary variability, constituting the basis of evolutionary processes.

The analysis of these problems and various sexual combinations are discussed in twelve chapters: sexual and asexual reproduction (chapter 1), reproductive cycles (2), sex in lower organism (3), a review of classical findings on gonochorism, gynandromorphism and intersexuality (4 and 5) sex determination, sex polygamety (6), sex phenotype as a function of genotype, and the genetic basis of hermaphroditism (7 and 8), sex differentiating processes in Amphibians and Crustaceans (9), sex determination in parthenogenetic populations (10 and 11) and some evolutionary aspects resulting from the analysis of the sex determination (12).

A review of the present-day trends in research on sex determination is given in an appendix.

The monograph contains references (about 800 items), a brief glossary of the terms used and an index. Clear and easy-to-understand illustrations, presented in the form of photographs, figures, plates and diagrams make up a considerable aid for the reader.

This monograph may be recommended to biology and medicine students with proper understanding of zoology, botany and genetic problems.

The excellent treatment and presentation of the subject material makes this monograph a valuable contribution.

Jerzy Sikora, Warsaw, Poland

XXIV
INTERNATIONAL CONGRESS OF PHYSIOLOGICAL SCIENCES

The XXIV International Congress of Physiological Sciences will be held in Washington, D. C., U.S.A., August 25–30, 1968. The Congress is sponsored by the International Union of Physiological Sciences (IUPS).

Preliminary notices will be mailed in January 1967, and final notices in October 1967. Plans are already being made for special symposia and invited speakers. Specific suggestions for symposium topics or special lectures should be submitted as early as possible to the President of the Congress, Professor Wallace O. Fenn, University of Rochester, Medical Center, Rochester, N.Y. 14620, U.S.A.

In selecting topics for symposia it is expected that the program Committee will give preference to subjects of a somewhat controversial nature, but of broad general interest, and not recently covered in an international symposium. For speakers, special consideration should be given to promising young physiologists with active research programs as well as to older men of established reputation.

All inquiries concerning the Congress may be addressed to:

Mrs. Helena B. Lemp
Congress Manager
XXIV International Congress of Physiological Sciences
9650 Rockville Pike
Bethesda, Maryland 20014
U.S.A.

ERRATA

On page 63, Fig. 2 should be turned upside down.

On page 91, lines 16 and 17 of the text should be transferred to the very bottom of the page.

On page 92, substitute ($bS^{\triangle}$) for (bS^{D}) in the title of Table II.

On page 124, substitute 1–1.5 mm for 1–5.5 mm.

Cena zł 30.—

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