ACTA BIOLOGIAE EXPERIMENTALIS

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PREOPTIC AREA OF THE DOG

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The preoptic area constitutes a part of the telencephalon but due to
its location within the brain and its connections it is usually included
in the hypothalamic region. This attitude has been supported by the phy-
logenetic work by R o s e (1942). According to B l e i e r (1961) the
preoptic area is considered a part of the rostral hypothalamus within the
anterior hypothalamic region. B l e i e r (1961) maintains that the anterior
hypothalamic region extends orally from the lateral septal nuclei, Broca's
diagonal band and the nucleus accumbens to the caudal area of the tuber
cinereum. The preoptic area is usually divided into two parts, the medial
and the lateral (C r a i g i e 1925, R i o c h 1929, 1931, G u r d j i a n 1927,
H u m p h r e y 1936, Y o u n g 1936, A d r i a n o v and M e r i n g 1959,
S c h a l t e n b r a n d and B a i l e y 1959, R a n s o n and C l a r k 1959,
B l e i e r 1961, W e s t w o o d 1962).

The present observations show that the dorsal chiasmatic nucleus,
described by B l e i e r in the cat (1961), also lies in the preoptic area
in the dog. This nucleus is known as the nucleus suprachiasmaticus an-
terior and was found by L o o in the opossum (1931) and by H u m p h r e y
in the bat (1936).

MATERIAL AND METHODS

The material consisted of five dog's brains fixed in formalin and alcohol.
After embedding either in paraffin or celloidin, the brains were cut into sections
20—45 microns thick along the basic planes: frontal, sagittal and horizontal. The
sections were stained according to Nissl, Weigert-Wolters and Klüver techniques.

RESULTS

Topography of the preoptic area

The preoptic area extends anteriorly as far as the vertical plane leading through the posterior part of the septum (just in front of the anterior commissure). This part of the septum is mainly occupied by the nucleus of Broca's diagonal band. Dorsad, the preoptic area extends to the plane lying horizontally through the ventral part of the anterior commissure, while laterally it reaches towards the amygdaloid area. Posteriorly, the

Fig. 1. Transverse section through the oral part of the area praeoptica and the nucleus chiasmaticus dorsalis of the dog. Klüver stain.

preoptic area extends towards the anterior hypothalamus, with which it enters into close connection. On its ventral border, the preoptic area is considered a plane leading horizontally through the dorsal part of the optic chiasm (Fig. 6). In frontal sections of the preoptic area, it is ventromedial in relation to the nucleus of Broca's diagonal band. Anterior to the oral parts of the preoptic area, relatively large blood vessels run in the vascular sheath and the subchoroid spaces, which inter alia, belong to the preoptic area. This area is narrow in its oral parts. As the nucleus of Broca's diagonal band diverges laterally and posteriorly, the preoptic area broadens out laterad and dorsad, and in its centre is seen, bordered by it, the lumen of the recessus supraopticus

(Fig. 1). In the oral-ventral parts of the preoptic area, squeezed in between the two optic nerves, is seen the dorsal chiasmatic nucleus (Fig. 1). In the oral parts of the preoptic area are also visible fairly numerous blood vessels, taking a parasagittal course (rather in the central part of the preoptic area), and relatively numerous small blood vessels fanning out perpendicular to the sagittal plane (these appear rather on the periphery of the preoptic area). In the more caudal parts of the preoptic

Fig. 2. Transverse section through the area praeoptica of the dog. In the floor of the recessus supraopticus the nucleus chiasmaticus dorsalis is visible. Klüver stain.

area, there are usually found only numerous blood vessels running perpendicular to the sagittal plane, rather densely arranged fan-wise, and a few vessels running parasagittally, grouped mainly in the region of the base of the recessus supraopticus. The lumen of the recessus supraopticus is separated from the preoptic area by a very distinct layer of ependymal cells. These relations are maintained along almost the whole length of the recessus supraopticus, which in its caudal part passes into the main corpus of the third ventricle.

The preoptic area is basically divided into the area praeoptica medialis and the area praeoptica lateralis (Figs. 2, 3, 4 and 5).

The part of the area praeoptica medialis adjacent to the recessus supraopticus is differentiated in the form of a comparatively narrow layer, termed the periventricular system (Figs. 2 and 3). This system consists of a layer of rather delicate fibres, taking a pale blue stain by the Weigert-Wolters method, with rather wavy contours, lying almost parallel to the walls of the recessus supraopticus. The layer of fibres is separated from the lumen of the recessus supraopticus by a layer of
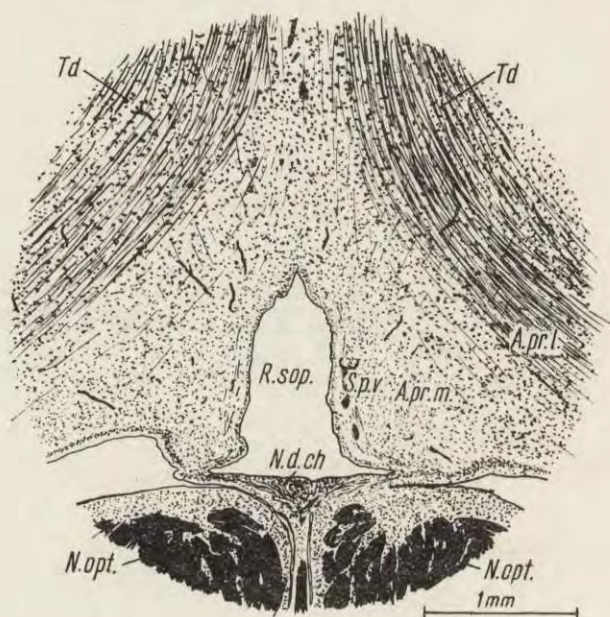
Fig. 3. Transverse section through the area praeoptica and the nucleus chiasmaticus dorsalis of the dog. Periventricular system is also visible. Klüver stain.

ependymal and nerve cells. In principle, the nerve cells are grouped between the fibres of the periventricular system. This system is discussed together with the area praeoptica medialis, since it constitutes a part of that area. Posteriorly, the periventricular system passes fairly smoothly into the periventricular system of the anterior hypothalamus. Dorsally and caudally, it also preserves continuity with the periventricular system of both the hypothalamus and thalamus. Lateral to the system described, there lies part of the area praeoptica medialis proper, so that there is no distinct line of demarcation between them.

The a r e a   p r a e o p t i c a   m e d i a l i s (Figs. 2, 3, 4 and 5) is fused laterally with the area praeoptica lateralis, and medially with the peri-

ventricular system of the preoptic area. Dorsally, it is bordered by the anterior filiform nucleus, and, caudally, at the level of the chiasma opticum it comes into contact with the area of the anterior hypothalamus. In the region of the area praeoptica medialis at least three systems of fibres may be distinguished. The first two are composed of comparatively delicate fibres, crossing one another. The first of these systems is composed of fibres taking a course similar to that of the fibres in Broca's
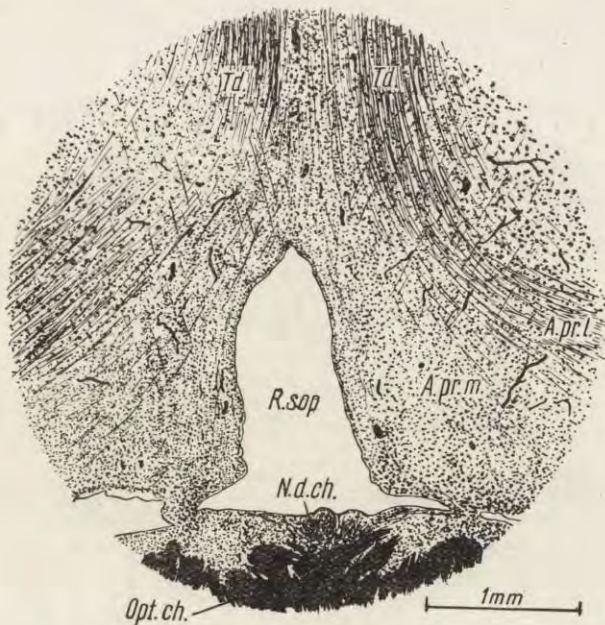
Fig. 4. Transverse section through the area praeoptica and caudal part of the nucleus chiasmaticus dorsalis of the dog. Klüver stain.

diagonal band. The fibres of system I are arranged more or less parallel to those in the diagonal band, and run from the caudal, dorsal and medial aspects ventrally and laterally. The fibres of system I are delicate, with comparatively sharp simple contours, staining blue by Weigert's method, and loosely scattered (Fig. 5-S_1). System II is composed of fibres somewhat more delicate than those in system I. The fibres in system II take a stronger blue stain, have fairly sharp contours, and are also loosely scattered. They run from the caudal, dorsal and lateral aspects towards the nose, ventrally and medially. This system of fibres becomes lost in the central and medial parts of the area praeoptica medialis, while laterally it runs on further through the region of the area praeoptica lateralis into the

region of the nucleus of Broca's diagonal band, and also to the nucleus lateralis septi (Fig. 5-S_2). System III is composed of fibres about one and a half times thicker than those in the other two systems. It stains dark blue by Weigert's method, and takes a slightly wavy course. This system extends from the central parts of the area praeoptica medialis upwards towards the nuclei of the stria terminalis and also towards the thalamus. These fibres have somewhat the shape of a fan, with the axes running almost vertically, extending from the caudal and dorsal aspects forwards and towards the nose (Fig. 5-S_3).
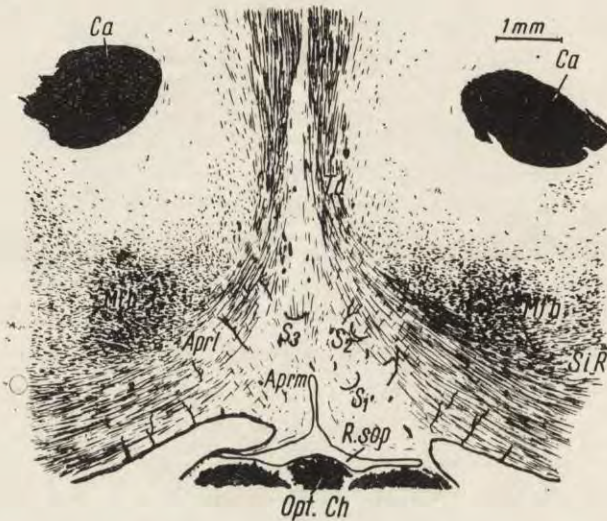
Fig. 5. Transverse section through the caudal part of the area praeoptica of the dog. Weigert stain.

In the region of the area praeoptica medialis, the first two systems form a fairly dense network in the meshes of which cellular elements lie scattered. The third system becomes lost in the central parts of the area praeoptica medialis. Medially, the fibres of the third system run almost parallel to the fibres of the similar system on the opposite side, coming into contact with each other in the central-sagittal plane.

The cells appearing in the region of the area praeoptica medialis are scattered rather densely in the peripheral parts of this area, but more scantily in its central parts. They are cells of moderate size, roundish or oval in shape, with protoplasm staining fairly well, and showing more or less distinctly marked granules in their interior.

The area praeoptica lateralis (Figs. 3, 4, 5) passes medially into the area praeoptica medialis without any clear demarcation.

Laterally it borders the capsula interna, dorsally the ventral parts of the thalamus, and, ventrally, the region of Reichert's substantia innominata. Through the region of the area praeoptica lateralis, there run fibres from the medial forebrain bundle. In the same area are found fibres from the caudal section of the nucleus of Broca's diagonal band reaching the amygdaloid complex. The fibres of the caudal section of the nucleus of Broca's diagonal band run ventrally and laterally. In its dorsal part they become mixed with the fibres from the medial forebrain bundle. The fibres from the nucleus of Broca's diagonal band are thick, take a fairly marked blue stain by Weigert's method, have rather simple contours, and run rather densely together. The fibres of the medial forebrain bundle are about twice as delicate, stain dark blue, and have sharp smooth contours. They are gathered into rather thick bundles, lying ventrally from the anterior branch of the anterior commissure. They take a course similar to that of the fibres of the nucleus tractus diagonalis, but are more sharply inclined in relation to the sagittal plane.

The cells appearing in the region of the area praeoptica lateralis are distributed chiefly among the fibres belonging to the medial forebrain bundle, in this way forming its bed nucleus (Rioch, 1929, 1930). They are of moderate size, and triangular or roundish in shape. Both the cells and their nuclei stain weakly. Large cells are also visible in the region where the area praeoptica lateralis touches Reichert's substantia innominata. These are polygonal in shape and stain fairly well, with nuclei and nucleoli taking a distinct stain.

The nucleus chiasmaticus dorsalis (Figs. 1, 2, 3 and 4) or dorsal chiasmatic nucleus, lies on the rostrodorsal surface of the chiasma opticum in the medial line. The dorsal chiasmatic nucleus extends more or less from the anterior end of the recessus supraopticus to the anterior margin of the decussation of the optic nerves. Dorsally and dorsolaterally, the dorsal chiasmatic nucleus lies adjacent to the lumen of the recessus supraopticus, demarcated only by a layer of ependymal cells.

In the oral section of the dorsal chiasmatic nucleus its components, i.e. fibres and cells, are distributed very loosely. Here the fibres are quite loosely scattered among the cells. In the lateral parts of the nucleus, the fibres are slightly denser (Fig. 2). The cells appearing in the oral part of the dorsal chiasmatic nucleus are grouped chiefly in the central and ventral parts, and are thinly scattered in the other parts of the nucleus.

In the caudal section (Figs. 3, 4 and 5) of the dorsal chiasmatic nucleus, both fibres and cells appear in greater concentration. The cells

of the caudal section are chiefly grouped in the central and dorsal parts of the nucleus, and are somewhat more thinly scattered in the lateral parts. On the dorsal surface of the caudal section of the dorsal chiasmatic nucleus, the centrodorsal grouping of the cells forms a bowl-shaped eminence protruding into the lumen of the recessus supraopticus. In this way the posterior part of the dorsal chiasmatic nucleus assumes a rather characteristic shape. The nerve fibres appearing in the posterior section of the nucleus are grouped much more densely at the sides of the centro-dorsal group of cells. They appear more densely in the ventrodorsal parts of the nucleus. The central parts of the dorsal chiasmatic nucleus are characterized by the fibres loosely scattered between the cells grouped here.

The anterior parts of the dorsal chiasmatic nucleus in shape recall a prism whose apex is directed ventrally. The arms of this prism are concave on account of the cylindrical shape of the optic nerves. In the caudal portion, a transversal section of the dorsal chiasmatic nucleus is rather like a cave in shape, with the base rather markedly extended laterally, the "sharp edge" also directed ventrally, and the convex bed rising into the lumen of the recessus supraopticus. In the ventral portions of the dorsal chiasmatic nucleus a few small blood vessels run perpendicular to the cross-section.

Myeloarchitectonics

In the rostral portion in the region of the dorsal chiasmatic nucleus is found a comparatively small number of fibres (they appear more plentifully in the caudal part of the nucleus), which are usually delicate, rather markedly twisted in spirals, and run from the caudal dorsal and lateral aspects towards the nose, ventrally and medially. These fibres exhibit a fan-like arrangement and join up with the fibres of the periventricular system. In the centre of the dorsal chiasmatic nucleus are also found fibres taking an almost completely parasagittal course. In the ventral and ventrolateral parts are found delicate fibres, staining dark blue by Weigert's method, with distinct sharp smooth contours, running tangentially to the ventral margin of the dorsal chiasmatic nucleus. They extend towards the ventrocentral part of the nucleus, where they mingle with similar fibres from the opposite side. In the caudal parts, just before the decussation of the optic nerves, the dorsal chiasmatic nucleus is markedly drawn in a lateral direction, so that it enters the vicinity of the area praeoptica medialis. The fibres appearing

in the posterior portion of the nucleus exhibit the same morphological characters as those in the rostral portion. The fibres in the caudal parts of the dorsal chiasmatic nucleus are arranged concentrically on both sides of the small centrodorsal area, with their axes inclining more and more laterally from the sagittal plane. In this way, the fibres in the lateral parts of the dorsal chiasmatic nucleus come into contact with those of the chiasma opticum, and still further laterally with those of the area praeoptica medialis. Some fibres running tangentially to the
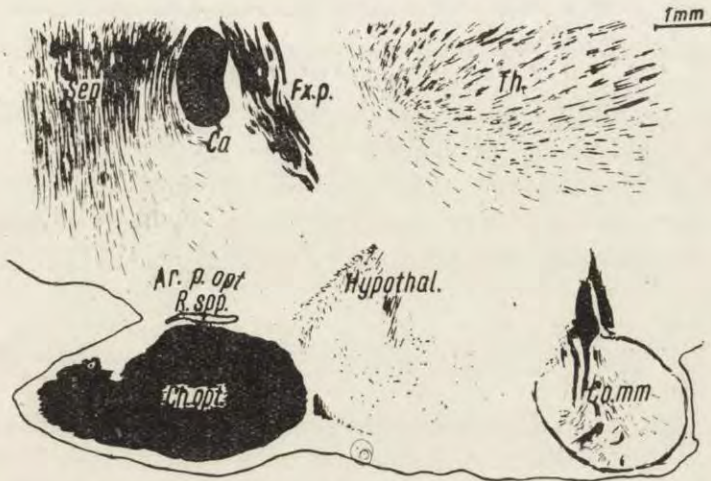
Fig. 6. Sagittal section through the brain of the dog, showing situation of the area praeoptica. Weigert stain.

ventral surface of the dorsal chiasmatic nucleus, and reaching from the dorso-lateral aspect of the thalamus and cauda towards the centre nasally and ventrally are also found.

In frontal sections passing through the beginning of the chiasma opticum, the arrangement of fibres described as characteristic of the dorsal chiasmatic nucleus is not found, but only a layer of ependymal cells and bundles of fibres of the decussation of the optic nerves, rising high dorsally.

In Nissl preparations, among the cells found in the region of the dorsal chiasmatic nucleus, there may, in principle, be distinguished larger cells, in their morphological characters approaching the large cells appearing in the region of the nucleus of Broca's diagonal band, and small cells, round or elongated in spindle-shape, staining weakly with no distinct granules in their interior. The cells in the dorsal chiasmatic

nucleus are distributed among the fibres, but are concentrated rather in the central part of the nucleus, sending out laterally a narrow and not very distinct band of cells in the direction of the preoptic area.

SUMMARY

From microscopic observations it has been established that the preoptic area is composed of two parts, the area praeoptica medialis and the area praeoptica lateralis (Figs. 2, 3, 4 and 5). It has also been found that in the dog the dorsal chiasmatic nucleus lies within the preoptic area (Figs. 1, 2, 3 and 4).

The area praeoptica medialis (Figs. 2, 3 and 5) is, on the medial aspect, (i.e. the side of the lumen) separated from the recessus supraopticus by a layer of ependymal cells and the periventricular system. This system (Figs. 2 and 3) is composed of a layer of delicate fibres with undulating contours, running almost parallel to the walls of the recessus supraopticus. Between the fibres of the periventricular system are scattered nerve cells. Posteriorly, it passes into the periventricular system of the anterior hypothalamus.

Three systems of fibres may also be distinguished in the region of the area praeoptica medialis.

System I is composed of delicate fibres with sharp simple contours, staining blue by Weigert's method, loosely distributed. They are arranged more or less parallel to the fibres of Broca's band, and run from the cauda dorsalis and the medial aspect towards the nose ventrally and laterally (Fig. 5-S_1).

System II is composed of more delicate fibres than system I. The fibres in system II stain a stronger blue by Weigert's method, have rather sharp smooth outlines, and are loosely scattered. They run from the caudal aspect of the dorsum and the lateral aspect towards the nose ventrally and medially (Fig. 5-S_2).

System III is composed of fibres about 1.5 times as thick as those in systems I and II. They stain dark blue by Weigert's method, and take a slightly undulating course. They fan out, running from the cauda dorsalis forwards and ventrally (Fig. 5-S_3).

The fibres of systems I and II cross one another, forming further on, in the area praeoptica medialis, a dense network, with nerve cells lying in the meshes.

The area praeoptica lateralis (Figs. 4 and 5). The fibres from the medial forebrain bundle run through this region, as do the fibres of the caudal section of Broca's band. The fibres of the medial

forebrain bundle are much more delicate than those of Broca's band, take a dark blue stain, have sharp smooth contours, and are gathered into fairly thick bundles, rather sharply inclined in relation to the sagittal plane. The fibres of the nucleus of Broca's band are thick, stain blue, and have simple outlines, are fairly dense and run orally and ventrally.

The anterior chiasmatic nucleus (Figs. 1, 2, 3 and 4) lies on the rostrodorsal aspect of the chiasma opticum. In its anterior section the dorsal chiasmatic nucleus is represented by a very small number of fibres and cells. In the caudal section, it is composed of a relatively large number of cells, which form a bowl-shaped eminence protruding into the lumen of the recessus supraopticus, and fibres running between the cells and also in the ventrolateral parts.

In the region of the dorsal chiasmatic nucleus the fibres are delicate, take a deep blue tint by Weigert's method, are markedly undulating but have also sharp smooth contours. They run from the cauda dorsally and laterally towards the nose ventrally and medially. The further course is parasagittal, and there are also fibres running tangentially to the ventral margin of the dorsal chiasmatic nucleus.

ABBREVIATIONS

Apr.	— area praeoptica	S_1	— system I
Aprl.	— area praeoptica lateralis	S_2	— system II
Aprm.	— area praeoptica medialis	S_3	— system III
Ca.	— commissura anterior	S. pv.	— periventricular system
M. f. b.	— medial forebrain bundle	SiR.	— Reichert's substantia innomi-
N. opt.	— nervus opticus		nata
Opt. ch.	— chiasma opticum	Td.	— Broca's diagonal band
R. sop.	— recessus supraopticus		

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FASCICULUS MAMMILLARIS PRINCEPS AND ITS BRANCHES IN THE DOG

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The aim of this work was to carry out a myeloarchitectonic analysis of the bundle connecting the mammillary body with the thalamic nuclei and the branch of this bundle running to the mesencephalon in the dog.

MATERIAL AND METHOD

Four continuous series of microscopic sections of the dog brain were used for this study, that is, a sagittal series stained by Klüver's method and frontal, horizontal, and sagittal sections stained by the Weigert-Wolters method. The study was based for the most part on the sagittal and horizontal sections. The Weigert sections were used for observation of nerve fibres, while the Klüver ones were applied to obtain more information about the localization of the terminations of nerves.

RESULTS

Mammillary bodies and their connexions

The mammillary bodies of the dog are a single protuberance situated medially on the ventral side of the brain. The diameter of the protuberance approximates to 2 to 3 mm.

The shape of the mammillary body of the dog is, roughly speaking, globular. The whole consists of two symmetrical parts. In either half there is a big nucleus, filling its greater part. This is the medial nucleus or, according to the old nomenclature (Koelliker 1896) the ganglion
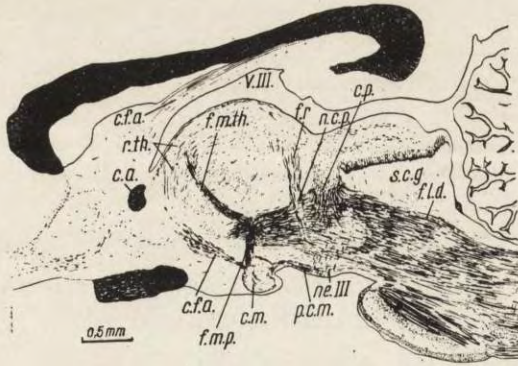
Fig. 1

Fig. 2

Fig. 3

Fig. 4

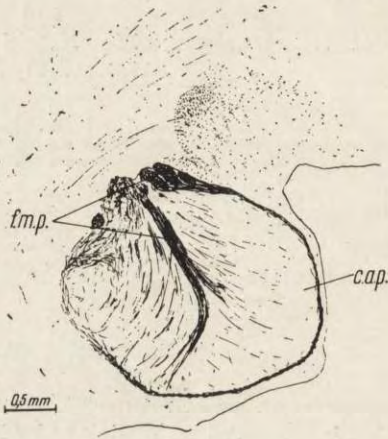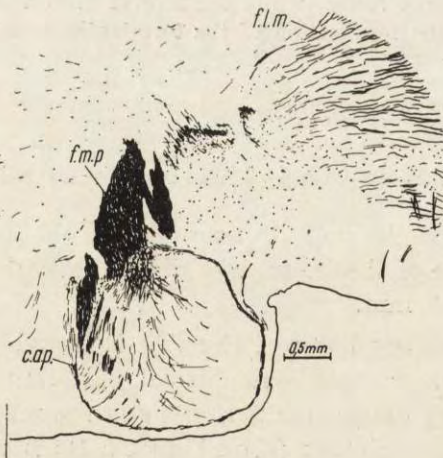mediale. R a m o n y C a j a l 1904 called it "nucleo interno". Another, considerably smaller, nucleus is situated in the lateroventral portion of the mammillary body. This is the lateral nucleus, formerly called the ganglion laterale (K o e l l i k e r 1896) and "nucleo mamilar externo" (R a m o n y C a j a l 1904). The halves of the mammillary body are approximately intermediate between kidney-shaped and oval (Fig. 9). The

convex sides of the halves face each other, the concave ones are turned outwards. Moreover, a caudal concavity can be noticed in either half in the sagittal sections (Fig. 1 — p.c.m.), where the peduncles of the mammillary body leave this formation. The lateral concavities have been formed as a result of the bulging of the dorsolateral and ventrolateral portions of the mammillary body by two branches of the anterior column of the fornix, i.e., the dorsal and the ventral columns of the fornix, which both tend towards the mammillary body. The halves of the mammillary body are connected by the commissure of the mammillary body (Figs. 7,9 — c.c.m.), the first mention of which was made by K o e l l i k e r (1896).

The surface of the mammillary body is covered by a capsule (Figs. 2—6, 9, 10 — cap.) composed of capsular fibres of the mammillary body. It consists mostly of compactly arranged fibres, partly crossing each other, partly interweaving. The fibres run round along the surface of the capsule, which they compose. Some of them run away from the internal surface of the capsule as soon as they reach the most ventral places and, somewhat higher, from both the internal and the external surface. They join together to form bundles of fibres originating or terminating in the mammillary body (Figs. 2—4).

The compactness of the capsule loosens in the dorsofrontal portion, where the fibres become less dense expanding the capsule. Here, they are arranged irregularly, in all directions, making up a meshwork and not a solid fibrous sheath. Within the mammillary body there is a fine meshwork formed by the fascicles of several fibres running together or by single fibres. Some fibres and fine fascicles of fibres, which combine in larger ones, pass through the meshes. Then, tending towards the mammillary body, they increase in size receiving other fibres and fascicles. The fascicles directly entering or coming out of the mammillary body form the anterior and posterior columns of the fornix, the peduncle of the mammillary body, and the main mammillary bundle (Figs. 1, 4, 5, 10 — c.f.m., c.f.d., c.f.v., p.c.m., f.m.p.).

Column of the fornix

According to K o e l l i k e r (1896) the column of the fornix of the rabbit bifurcates at the right angle at its entrance into the mammillary body giving rise to the ventral and the dorsal column of the fornix, whereas in the dog it splits at an acute angle. The dorsal portion passes with its most dorsal fibres into the dorsal wall of the mammillary body, its other part terminating in the medial nucleus of this body. On the other hand, the most ventral fibres of the ventral column of the fornix

pass into the frontal wall of the mammillary body bordering on the medial and anterior nuclei and partly into the lateral wall adjoining the medial and lateral nuclei. Most fibres of the column of the fornix, however, run to the medial nucleus and terminate in it, or pass on to constitute the posterior portion of the column of the fornix. The fibres of the column that enter the medial nucleus anteriorly are slightly brownish, while those leaving it posteriorly are void of this coloration. Part of the fibres composing the further, caudal portion of the column of the fornix, probably take rise in the medial nucleus. At the exit of the anterior column of the fornix from the mammillary body the compactness of the dorsofrontal portion of the capsule is disturbed. This disturbance is due also to the exit of the main mammillary bundle, which is shifted more frontally (Figs. 2—4 — c.m.).

Peduncle of the mammillary body

The fibres of the peduncle of the mammillary body run off the external surface of the capsule at its caudal depression at the same level as the caudally running fibres of the column of the fornix, but more medially. There is no clear distinction between the fibres of these two bands at the exit. Hence, it is difficult to determine which fibres belong to the peduncles of the mammillary body and which ones to the column of the fornix. In the lateroventral portion of the capsule the fibres come to the outside for a short distance, probably to the grey matter, which is present just out of the capsule.

Main mammillary bundle

In this work most attention was given to the main mammillary bundle and its branches.

The fibres of the main mammillary bundle concur to form this bundle while still within the mammillary body (Figs. 2, 3, 5, 6), which however is not true of all of them, as a part of the fibres join the main bundle only outside the mammillary body. This refers particularly to the fibres emerging from the capsule and the dorsal portions of the medial nucleus.

Within the mammillary body the main mammillary bundle is not uniform but consists of smaller fascicles running to the common exit located in the dorsal portion of the mammillary body. These fascicles are the narrowest and most numerous in the ventral portion of the mammillary body, from where they pierce upwards through the meshwork formed by fine fibres, mostly single or joined a few together. Superiorly,

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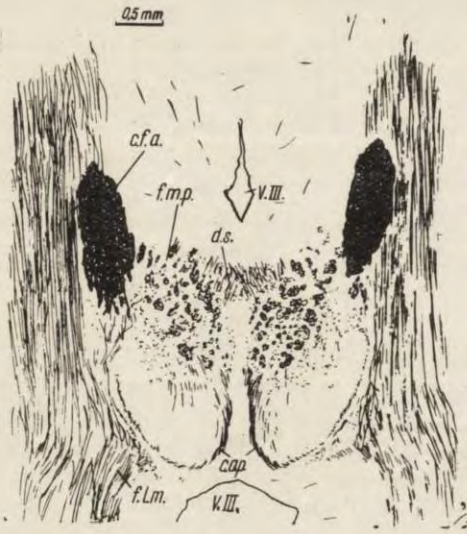
Fig. 5

Fig. 6

these fascicles combine in larger ones or run side by side to form a whole
in the dorsal portion of the mammillary body. The majority of the fibres
uniting in fascicles within the mammillary body come from its fibrous
capsule. Many fibres disappear in the area of the medial and lateral

Fig. 7

nuclei of the mammillary body. In the most dorsal portion of the mam-
millary body the fibres of this bundle cross and intertwine with the
fibres of the capsule.

After leaving the capsule the main mammillary bundle, which in the
dog consists of more or less parallel fibres, runs dorsad (K o e l l i k e r
1896). Next, it splits into two branches, the mammillothalamic bundle

Fig. 8

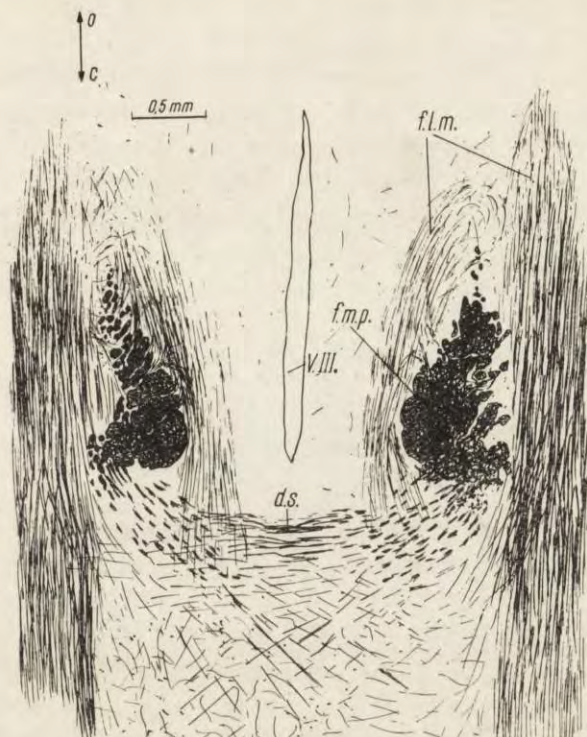and the mammillotegmental. The latter turns to the back of the brain and, according to Koelliker (1896), reaches the ganglion tegmenti profundum. The mammillothalamic bundle extends orodorsally, reaches the thalamus and then (within the thalamus) arches to the dorsal nucleus of this region.

The main mammillary bundle runs unbranching dorsally for a short distance of 1 mm and next arches dorsocaudally. Koelliker uses the term „main mammillary bundle" for the section from the mammillary body to the ramification into the mammillothalamic and mammillotegmental bundles. He localized the ramification at one point of the bundle. As a matter of fact, in the dog the fibres branch off at many places along its 1.10 mm long section, and for this reason in the present paper the name is applied for the portion of the bundle from its origin, still within the mammillary body, up to the place where the last fibre branches away from the common trunk of the bundle to the mammillothalamic bundle (Fig. 4 — f.m.p.).

The main mammillary bundle is about 0.6 mm thick at the exit and about 1.10 mm at the first ramifications, but it is less compact there. After the departure of all the collaterals of the mammillothalamic bundle there are only single fibres left, which merge in the medial longitudinal bundle. The portion of the main mammillary bundle within the mammillary body is nearly as long as the distance between the ventral and the dorsal wall of the fibrous capsule (about 2.3 mm). The bundle increases in thickness gradually, still within the mammillary body, as it passes dorsally, because it receives fibres all along its length. A compa-
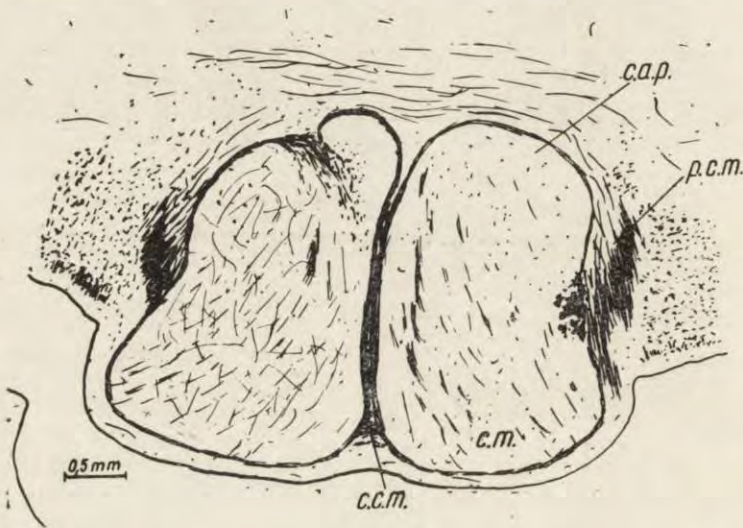

Fig. 9

ratively great difference between the thickness of the bundle before its leaving the mammillary body (about 0.3 mm) and that after leaving (about 0.6 mm) corroborates the fact that it is joined by a large number of fibres from the capsule (Figs. 2—4 — f.m.p.). The length of the main mammillary bundle from its emergence from the mammillary body to the place where the mammillothalamic bundle runs off is about 2.1 mm. The length of the mammillothalamic bundle is about 8 mm, its width being 1.1 mm at the beginning, 0.6—0.7 mm in the course, and 1 mm at the end. The scattering of the fibres of the mammillotegmental bundle and their joining the medial longitudinal bundle (Fig 4 — f.m.t.) make the measurement of this bundle impossible.

Above the mammillary bodies I noticed fibres connecting the main mammillary bundles of both sides (Figs. 6, 10 — c.v.). The fibres of which this connexion is composed come from the dorsal portions of these bund-
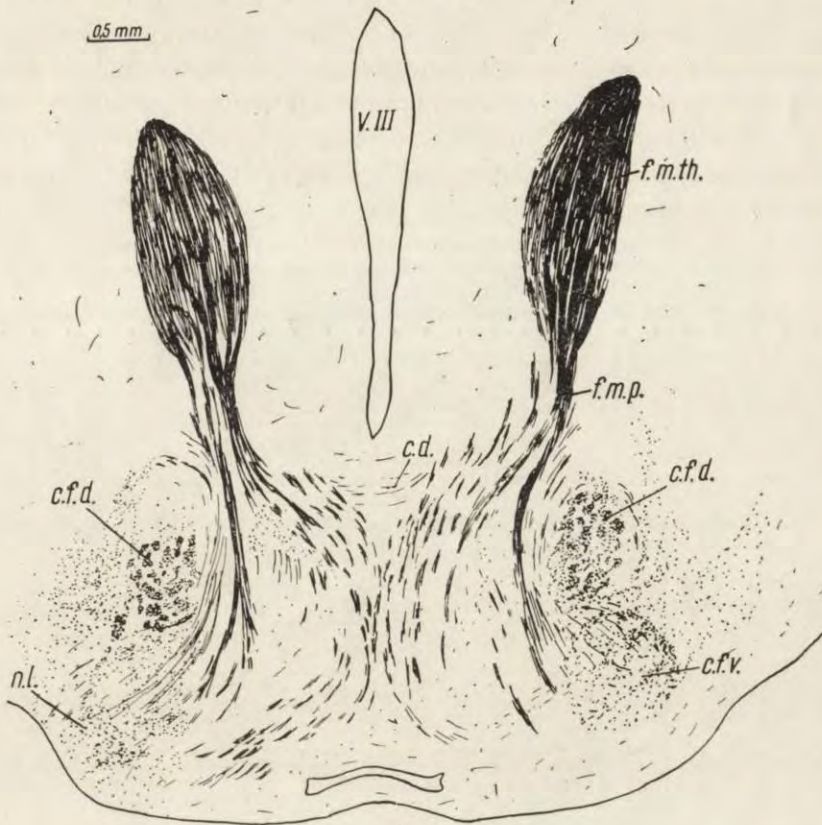
Fig. 10

les (frontal section) and also from their posterior portions (horizontal section). They may come from the thalamus or from the areas which the fibres of the mammillotegmental bundle join. In addition, the connexion receives fibres coming from the medial portion of the mammillary body (Fig. 10). The fibres from the mammillary body join the connexion where it branches away from the main mammillary bundle and above the half of the mammillary body in which they have taken rise. These fibres direct mostly to the bundle coming from the same half as they do, but part of them can possibly pass over to the bundle coming from the opposite half of the mammillary body. Above the foregoing connexion there is another wider connexion between the main mammillary bundles (Fig. 8 — c.d.). The fibres of this connexion enter the main mammillary bundle posteriorly. They have hitherto been reckoned among

the fibres of the fountain of Meynert in accordance with the atlas of Winkler and Potter (1916) and that of Adrianov and Mering (1959). The fibres of the dorsal (wider) connexion form an arch resembling a hanging bridge the ends of which are higher than the middle part.

In the preparations examined by me the fibres connecting both halves of the mammillary body are mingled with those of the lower connexion of the main mammillary bundles (Fig. 10). In Adrianov's atlas of the dog brain the lower connexion is shown in the Nissl sections, but the

Fig. 11

author has not described this fragment. A somewhat similar arrangement will be seen in the Nissl sections in Bleier's atlas of the cat brain (1961). Here, the white matter present between the main mammillary bundles has not been named either, but in the next drawing the white matter above the mammillary body is called the supramammillary fountain. According to Winkler and Potter (1914), who described the cat brain, the fountain of Forel and the fountain of Meynert are situated above the mammillary body, whereas Adrianov and Mering (1959), describing the dog brain, locates both these fountains above the interpeduncular ganglion.

Mammillotegmental bundle and its decussation with the medial longitudinal bundle

The mammillotegmental bundle is the proper prolongation of the main bundle coming from the mammillary body. The mammillothalamic portion having branched off, the mammillotegmental bundle assumes its basic dorsocaudal direction (Figs. 4, 6, 7 — f.m.t.), which is, however, more caudal than dorsal, and next runs only orocaudally.

The fibres of the mammillotegmental bundle turn towards the posterior portion of the brain and mingle with the fibres of the medial longitudinal bundle. The mammillotegmental bundle slants in relation to the horizontal plane in which the medial longitudinal extends. Thus, its branching fibres are hard to perceive. They do not differ in thickness nor show any other characters distinguishing them from the fibres of the medial longitudinal bundle and consequently in the further course the mammillotegmental bundle of the dog constitutes only part of the fibres belonging to the medial longitudinal bundle (Figs. 1, 3-8 — f.l.m.), Besides, observation is made difficult by the fact that part of its fibres probably terminate, after a short course, in the grey matter lying caudally to the mammillary body.

I use the name „medial longitudinal bundle" (fasciculus longitudinalis medialis) after C l a r a (1959) for the bundle wchich according to the older nomenclature was called the fasciculus longitudinalis dorsalis (K o e l l i k e r, 1896) or fasciculus longitudinalis posterior (W i n k l e r and P o t t e r, 1914; R a m o n y C a j a l 1904).

According to R ó ż y c k i (1961) and C l a r a (1959) the nerve fibres of which the medial longitudinal bundle is composed take rise in the vestibular nuclei as well as in the formatio reticularis, the interstitial nucleus, and the nucleus of Darkewitsch. In the literature this bundle is described perfunctorily and inexactly. My observations show that its fibres reach a well-vascularized area of the hypothalamus, situated orally to the main mammillary bundle, anteriorly. A part of them terminate there and the other part passes on anteriorly. Before reaching the hypothalamus, that is, caudally to it, the fibres of the medial longitudinal bundle cross the main mammillary and the mammillothalamic bundle. On their way to the hypothalamus most fibres pass through the mammillary bundles, while smaller numbers of them do not pierce through the bundles, but intertwine with their fibres and together with them run either to the thalamus or to the mammillary body. It is the fibres extending from the medial longitudinal bundle to the mammillary body that form the mammillotegmental bundle.

The portion of fibres running just above the mammillary body directly joins the column of the fornix, which emerges from the mammillary body frontodorsally (Figs. 1, 4, 6, — c. f. a., f. l. m.). This junction is visible at the lateral margin of the column of the fornix.

Just above the medial longitudinal bundle is the dorsal longitudinal, also named the bundle of Schütz (C l a r a 1959, C r a i g i e 1925), and according to the older nomenclature the grey longitudinal bundle (K o e l l i k e r 1896). It is composed of fine fibres running in the central grey matter orodorsally. This bundle also reaches the hypothalamus, but more medially than the medial longitudinal.

The medial longitudinal bundle has an interest for me, because it crosses the area of the ganglion tegmenti profundum, which the mammillotegmental bundle reaches according to K o e l l i k e r (1896).

The connexion between the medial longitudinal bundle and the mammillotegmental is best visible in the horizontal sections. It will be seen from them that part of fine fascicles of fibres belonging to the medial longitudinal bundle terminate or take rise in the main mammillary (Figs. 6-9 — f. l. m., f. m. p.). The fibres of the main mammillary bundle do not run compactly, but there are clear spaces between them. These gaps separate the fascicles, the number of which is varying and which keep connexions between each other. More dorsally, these portions of fibres fuse into a whole to divide again — now as the mammillothalamic bundle — into two, three, or more bundles. The medial longitudinal bundle, approaching the main mammillary caudally, splits intto branches (Figs. 7,8 — f. l. m., f. m. p.). The greater part of its fibres run on the lateral side of the main mammillary bundle, fewer ones on its medial side. The portion of the medial longitudinal bundle running on the medial side extends as far as the anterior part of the main mammillary bundle and there it loses its regularity. The fibres scatter between the main mammillary bundle and the column of the fornix and re-join the lateral portion of the bundle. The fascicles of the lateral portion, entering or leaving the main mammillary bundle find their way through the gaps between the fibres of this bundle. These gaps are also entered by the fascicles penetrating through the main mammillary bundle from the lateral portion of the medial longitudinal to its medial portion (Figs. 7,8 — f. l. m., f. m. p.). After passing through the main mammillary bundle and joining the medial portion of the medial longitudinal, these fascicles send out fibres frontad and caudad, thus confining the portions of fibres of the main mammillary bundle. The particular fibres coming medially from the mammillary bundle in the frontal and caudal directions behave similary, confining the individual portions of fibres of the main

mammillary bundle (Figs. 7,8 — f. l. m., f. m. p.). The main mammillary bundle receives chiefly the fibres of the medial longitudinal bundle, entering it on the lateral side obliquely, dorsoventrally. Among the fibres running laterally out of the main mammillary bundle to the medial longitudinal there are also fibres directed orally, but their number is small. Caudally, the fibres of the medial longitudinal bundle meet a number of nuclei, of which the major ones are the ganglion tegmenti profundum, the ganglion tegmenti dorsale, the nucleus commissurae posterioris, and the nuclei of nerves III and IV (Fig. 1 — f. l. m.). A part of the fibres of the medial longitudinal bundle terminate or take rise in these nuclei, the others only pass through them or avoid them.

Mammillothalamic bundle

The mammillothalamic bundle has origin at the place where it branches away from the main mammillary bundle and then it runs orodorsally to the thalamus.

According to Rioch (1931) it splits into four bundles in the dog. Still inside the mammillary body he distinguishes the fibres which will compose these separate bundles. During the present study no division of the bundle into four branches was observed all along its course in any preparations of the dog brain. It runs as a single bundle from the very beginning and its course is disturbed only inside the thalamus. These disturbances are caused by the fascicles of fibres passing more or less transversely or diagonally in the thalamus to the mammillothalamic bundle and by the blood vessels. Owing to this fact, the bundle divides into two or more bundles, or rather fine fascicles, according to the circumstances. In the initial course the fascicles may meet again, in the upper portions of the thalamus they keep distinct up to the end. In the same preparation the bundle may sometimes split into two fascicles on one side and into three on the opposite side of the thalamus. In all the sections examined the mammillothalamic bundle was divided into at least two fascicles (Figs. 1, 4 — f. m. th.).

The fibres of the mammillothalamic bundle are parallel and some of them intertwine with each other or with the fibres which join it from the medial longitudinal bundle. The fibres coming to the mammillothalamic bundle from the medial longitudinal are chiefly those lying on the dorsal side of the latter or in its medial portions, though there are also some from the parts situated more ventrally (Figs. 1,4 — f. l. m., f. m. th.). Besides, the fibres from the medial longitudinal bundle join the main mammillary on its caudal side, in front of the final branching of the mammillothalamic bundle (Figs. 1,4 — f. l. m., f. m. p., f. m. th.).

In K o e l l i k e r's opinion (1896) just before sinking into the thal-
amus the mammillothalamic bundle comes across the dorsal longitudinal
bundle, which occupies the width equal to that of the medial longitudinal.
According to my observations the medial longitudinal bundle approaches
close to the thalamus, to the place where the mammillothalamic bundle
enters it (Figs. 1,4 — f. l. m., f. l. d., f. m. th.). On the other hand, the
dorsal longitudinal bundle can be seen distinctly in the more medial
places. Only sigle fibres or small bands of a few fibres, but never in the
form of a compact tract, running from the most lateral and at the same
time dorsal portion of the dorsal longitudinal bundle cross or interweave
with the mammillothalamic bundle and next enter the thalamus together
with its fibres. They enter or leave the mammillothalamic bundle on the
caudal side. The fibres of the mammillothalamic bundle cross those of
the thalamic radiations as early as the dorsal portion of the thalamus,
some of them separating from the bundle and joining these radiations.
The fibres coming from the mammillothalamic bundle join the radiations
of the thalamus on the internal (caudal) side of the arch formed by this
bundle while the connexions between the mammillothalamic bundle and
the thalamic radiations on the external side of the thalamus are very
rare (Fig. 4 — f. m. th., r. th.). The bundle decreases in thickness as it
passes from one nucleus of the thalamus to another.

The mammillothalamic bundle passes through the following nuclei:
the posterior nucleus of the hypothalamus, the dorsal area of the hypo-
thalamus, and the ventral nucleus of the thalamus. After the division of
the bundle in the ventral nucleus, its medial portion reaches to the
anteromedial nucleus of the thalamus and the lateral portion to the
anteroventral nucleus of the thalamus. In the final sections of both bran-
ches, the fibres disperse not very widely in the form of brushes (Fig. 11 —
f. m. th., n. a. m., n. a. v.). The fibres lying most caudally in the brushes
separate from them and join the thalamic radiations, which run caudad.
At the ends of both branches of the mammillothalamic bundle the fibres
are hard to trace, because their number in the branches decreases and
their coloration is poor.

SUMMARY

The fibres of the main mammillary bundle of the dog take rise in
the medial and the lateral nuclei of the mammillary body, mainly in
its capsule. The fibres and small fascicles of fibres run away from the

internal and, higher, from the external surface of the capsule, pass through the fine meshwork of fibres inside the mammillary body, turn to its dorsal portion and gradually combine into the main mammillary bundle.

On emerging from the mammillary body the main mammillary bundle runs dorsally up to the place of branching, from where the mammillothalamic bundle directs rostrodorsally to the thalamus and the mammillotegmental bundle arches in the dorsocaudal direction, next losing its fibres either in the medial longitudinal bundle or in the contiguous grey matter. Above the mammillary body there are two connexions between the main mammillary bundles. These connexions receive fibres from the dorsal portions of the mammillothalamic bundles. The main mammillary bundle runs between two branches, a broader lateral one and a medial, of the medial longitudinal bundle, which subsequently re-unite in front of the column of the fornix. There are connexions running anterioly and posteriorly between these branches and the main mammillary bundle. The dorsal longitudinal bundle extends dorsally to the medial longitudinal, but approaching the hypothalamus it runs more medially than the latter. Both the bundles cross the mammillothalamic bundle and some of their fibres intertwine with the fibres of this bundle and tend towards the thalamus. Part of fibres of the medial longitudinal bundle join the anterior column of the fornix directly. The dorsal fibres of the medial longitudinal bundle provide connexions between the mammillothalamic bundle and the retroflexed bundle as well as between the retroflexed bundle and the posterior commissure.

The fibres of the mammillothalamic bundle form a single (not always compact) band. In the area of the ventral nucleus of the thalamus they divide into two branches, of which the medial runs to the anteromedial nucleus of the thalamus and the lateral to the anteroventral. In the ventral portion of the thalamus the mammillothalamic bundle sends out small numbers of fibres to the thalamic radiations.

LIST OF FIGURES

ABBREVIATIONS

c. a. — commissura anterior
cap. — capsula corporis mamillaris
c. c. m. — commissura corporis mamillaris
c. d. — commissura dorsalis fasciculi principis
c. f. a. — columna fornicis anterior
c. f. d. — columna fornicis dorsalis
c. f. v. — columna fornicis ventralis
c. m. — corpus mamillare
c. p. — commissura posterior
c. v. — commissura ventralis fasciculi principis
d. s. — decussatio supramamillaris
f. m. p. — fasciculus mamillaris princeps
f. m. t. — fasciculus mamillotegmentalis
f. m. th. — fasciculus mamillothalamicus
f. l. d. — fasciculus longitudinalis dorsalis
f. l. m. — fasciculus longitudinalis medialis
f. r. — fasciculus retroflexus
n. c. p. — nucleus commissurae posterioris
h. — hypothalamus
n. a. d. — nucleus anterior dorsalis thalami
n. a. m. — nucleus anterior medialis thalami
n. a. v. — nucleus anterior ventralis thalami
n. c. p. — nucleus commissurae posterioris
ne III — nervus oculomotorius
n. l. — nucleus lateralis corporis mamillaris
n. m. — nucleus medialis corporis mamillaris
n. v. — nucleus ventralis thalami
p. c. m. — pedunculus corporis mamillaris
r. th. — radiatio thalami
s. c. g. — substantia centralis grisea
s. m. — stria medullaris
th. — thalamus
V. III — ventriculus tertius
v. — arteriola

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BIDIRECTIONAL MOVEMENTS OF AXOPLASM
IN PERIPHERAL NERVE FIBRES

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In neurons grown in tissue culture accelerated cinematographic records reveal an incessant traffic of particles up and down the axons. In neighbouring layers of axoplasm various granules move in opposite directions. Near the axon tips pinocytozed droplets ascend some way along the axon before they become invisible (H u g h e s 1953, N a k a i 1956, G o d i n a 1956, P o m e r a t 1960). This pattern of movements is similar to that observed in elongated cell processes of many other types of cells.

The bidirectional streaming persists for some time (H u g h e s 1953, J a h n and R i n a l d i 1959) in processes cut from cell bodies and even in portions of cytoplasm aspired into a capillary tube (A l l e n 1960). In plant cells, where cytoplasmic movements were studied extensively (cf. K a m i y a 1959), the character of streaming remains unchanged in fragments of cells under a rather wide range of experimental conditions indicating that the pattern of intracellular movements is inherent in the organization of cytoplasm.

Mature nerve fibres *in situ* are rarely accessible to direct investigation by optical means. The existence of movements of axoplasm or of some axoplasmic components in these fibres was suggested by the dependence of the axon on its continuity with the cell body and was often used to interpret this dependence.

The character of axonal movements was first studied by W e i s s

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(1944, 1961). He put forward the concept that the axoplasm moves continually as a whole column in the proximo-distal direction at a rate of about one millimetre a day. W e i s s' theory was based on an analysis of enlargements appearing in fibres above the site of a partial constriction of nerve. These deformations were interpreted as the result of damming up of the incoming axoplasm at the constricted region. Many subsequent findings, in particular the accumulation of neurosecretory granules and of various enzymes above the site of compression or section of the nerve (S c h a r r e r 1954, S n e l l 1957, F r i e d e 1959, H ebb and S i l v e r 1961, L u b i ń s k a et al. 1961, S h u t e and L e w i s 1961)), were consistent with the concept of damming of the proximo-distal flow.

Such pattern of flow would be, however, very different from that observed in other cells and in axons in culture. It will also leave unaccounted for many properties of neurons *in situ* such as, for example, the axon reaction or the initial changes occurring at the proximal end of the peripheral stump described by R a n s o n (1912), as "abortive regeneration". These phenomena suggest the existence of ascending movements of axoplasm in axons *in situ* besides the movements in cellulifugal direction.

This suggestion was recently strengthened by several findings showing that in interrupted nerves various enzymes (G o u l d and H o l t 1960, Z e l e n a and L u b i ń s k a 1962, K r e u t z b e r g 1963) and neuro-secretory granules (C h r i s t 1962), accumulate not only on the proximal but also on the distal side of the lesion. We tried to interpret the accumulation of enzymes below the lesion along the same lines as accumulation above the lesion was interpreted by earlier workers, that is, as a manifestation of the damming up of ascending movements of some axoplasmic layers at the interruption of the axonal pathway (Z e l e n a and L u b i ń s k a 1962).

In order to test this hypothesis quantitative biochemical experiments were devised to detect the movements of axoplasm indirectly. The displacements of acetylcholinesterase (AChE) containing particles, measured by shifts of AChE activity along the nerve, were used in the same way as in cells accessible to visual observation the movements of visible granules swept with the cytoplasmic currents are used to detect the streaming and analyze its character.

Changes of longitudinal distribution of AChE after nerve section were therefore investigated both in the central and in the peripheral stumps. In the latter only the changes occurring at early periods preceding the beginning of Wallerian degeneration are relevant for the study of axoplasmic movements.

Intact peripheral nerves exhibit a proximo-distal gradient of AChE activity (L u b i ń s k a et a l. 1962, B a r t o s z y ń s k i et a l. 1962) The value of the gradient varies with the type of nerve. In the present experiments the peroneal of dog was used. The decrease of AChE activity along this nerve amounts to about ten per cent per 100 mm. After nerve section local increases up to several hundred per cent are observed in a stretch of a few mm. Since AChE is an axonal component and seems to be absent from Schwann cells of normal nerves (T e w a r i and B o u r- n e 1960), the changes of distribution of this enzyme along the nerve reflect probably only axonal changes. The experiments were made in the
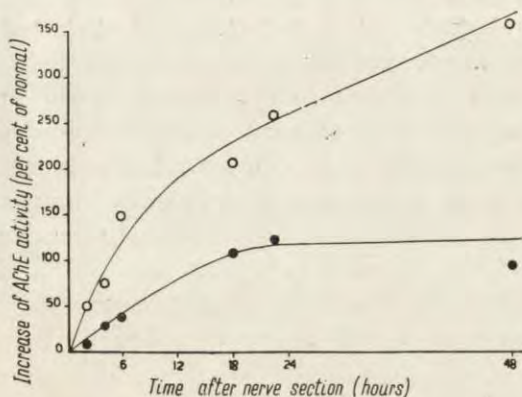

Fig. 1. Time course of increase of AChE activity (in per cent of the normal) in cut nerves in the proximal (circles) and distal (dots) segments adjacent to transection.

following way. Under nembutal anesthesia the nerve was cut in one or several places and small pieces were removed and analyzed to determine the normal level of AChE activity, by methods described previously. (Lu b i ń s k a e t a l. 1963). Then, at various time intervals, the rest of the nerve, both above and below the section was excised and cut into consecutive short pieces of 2-10 mm. Each piece was analyzed separately.

Very early, from two hours onwards, an increase of AChE activity was observed in short segments adjacent to transection both on the proximal and on the distal side, the increase on the proximal side being stronger. The accumulation of the enzyme increased progressively with time, on the distal side for about 24 hours, on the proximal side for many days. The time course of accumulation is shown in Fig. 1.

When the nerve was cut in two places and left in situ an increase of AChE activity was observed at four sites, above and below each lesion.

At each section the increase is stronger on the proximal than on distal side. The amount of the enzyme collecting at the ends of the isolated segment depends on its length. When it is long enough, of the order of 100 mm, the rate of accumulation of AChE and its spatial distribution in the terminal region is the same at the end of the stump connected with cell bodies and at the end of the isolated segment (Fig. 2). The similar course is maintained for 6 hours or more indicating that within this time interval the accumulation of AChE at the ends is independent of any activities of the cell bodies. At later stages the parallelism is disrupted, the rate of increase in the isolated segment slowing down.

Since there are indications (K o e n i g and K o e l l e 1961, Clouet and Waelsch 1961) that under certain circumstances AChE may be synthesized in the axon, it was important to ascertain whether the increase of AChE at the cut ends is not due to a local synthesis of the enzyme. This was done by comparing the total amount of AChE found in the stretch of the nerve contained between the cuts with the initial amount of the enzyme estimated from the length of the segment and the level of AChE activity found in pieces removed at the proximal and distal transection at the beginning of the experiment.

In 14 experiments in which the isolated segments were left *in situ* for periods ranging from 2 to 23 hours the AChE contents of the segment
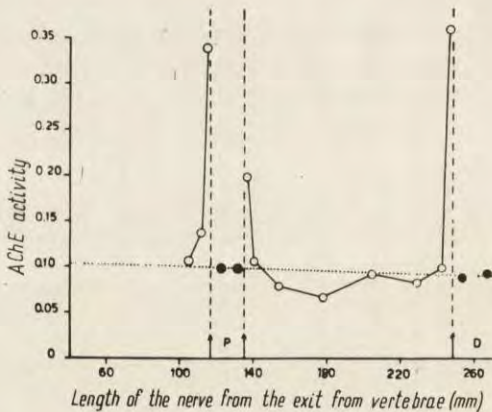

Fig. 2. Longitudinal distribution of AChE activity (micromoles of AThCh split by 1 mm of nerve in 2 hours) in dogs peroneal nerve cut at two levels. Arrows, sites of transection. Dots, AChE activity in pieces removed at the beginning of the experiment at the proximal (P) and distal (D) transection. Dotted line shows the initial gradient of AChE activity. Circles, AChE activity 6 hours after nerve section in the distal part of the proximal stump and in the segment contained between the cuts.

was 98.4 $\pm$ 2,0 per cent of the normal. The length of the isolated segment, which varied from 20 to 130 mm, did influence the increase of activity at the ends but had no effect on the total amount of AChE in the segment.

It may be inferred from these results that under experimental conditions described here no AChE is formed anew after nerve section and that the increase at the ends, compensated by a decrease in the middle of the segment, is due to displacements of the pre-existing enzyme in both directions along axons.

Not all axonal components increase in the same proportion near the sites of section. For example, the increase of total proteins is much weaker than that of AChE. Thus in a group of 12 experiments made within 48 hours after nerve section, the average increase of AChE in the segments adjacent to the lesion was 306% on the proximal, and 118% on the distal side, whereas the total proteins increased by 28% and 31% respectively.

The selective character of accumulation of AChE as well as the time course of the process indicate that it cannot be regarded as a simple damming up of material at the interruption of the axonal pathway. Some insight into the mode of arrest of AChE containing particles is obtained by morphological examination of fibres at the sites of increased AChE activity. When crushed fibres are teased over the region of the crush and a few millimetres beyond it on both sides, so as to permit the comparison of changes on both sides of the lesion in the same fibre, the following picture is observed. Beyond the collapsed crushed part of the fibre and the regions of disorganized fibre contents on both sides of it the fibre reverts to an apparently normal appearance. It is in this region, some 200 — 500 μ from the border of the crush that several nours after infliction of the lesion following changes appear. In the middle of the fibre a tongue of optically different axoplasm becomes visible (Fig. 3). It appears granulated in fresh fibres in phase contrast and osmiophilic in fibres fixed in osmium tetroxide. At later stages the granulated axoplasm becomes denser and fills the whole lumen of the fibre. In many fibres the myelin turns inwards at the border between the unaffected and the disorganized part of the fibre and ensheaths the meniscus of axoplasm (Fig. 3 B). In these fibres the modified axoplasm does not reach the end of the cul-de-sac in the initial 24 hours. The granulated region extends over about 100 μ and fades progressively away without a clear-cut transition to the normal region of the fibre. The meniscus on the distal side is formed somewhat farther from the border of the crush and the length of the granulated zone is smaller. The location and dimensions of granu-

lated axoplasmic regions are similar to the sites of increased AChE activity in fibres stained for histochemical detection of AChE (Fig. 3 D).

The thickness of teased fibres prevents the analysis of structural details in the zone of granulated axoplasm. It corresponds probably to the region of fibre stuffed with mitochondria seen by W e i s s, T a y l o r and P i l l a i (1962) in electron microscope. An accumulation of mitochondria and other granules above the site of lesion was described also by other workers (E s t a b l e et a l. 1957, V a n B r e e m e n e t a l. 1958,
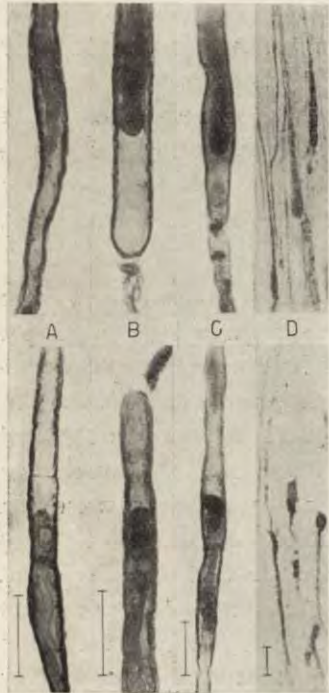

Fig. 3. Appearance of modified axoplasm, above and below the region disorganized by the crush in the sciatic nerve of rat. Proximo-distal orientation of fibres from top to bottom. Upper part, proximal; lover part, distal to the crush. A, B, C — teased fibres fixed in buffered osmium tetroxide. D — longitudinal section of the nerve stained for AChE activity by Koelle and Friedenwald (1949) method. A — five hours, B, C and D — 24 hours after crushing. In B the myelin sheath encloses completely the axoplasm separating the disorganized region of the fibre from the preserved part in A and C there is no clear-cut separation of the two regions. Scale 50 microns.

S c h l o t e and H a g e r 1960). The changes in the fibre on the distal side of lesion do not seem to have been looked for in electron microscope.

Our data are insufficient, as yet, to estimate the rate of flow in the axon from the rate of accumulation of AChE at the ends as the proportion of the enzyme containing particles stopping at the ends is not known. It seems certain, however, that this rate is much higher than that usually accepted for the proximo-distal movement of axoplasm, that is of 1 mm a day. In fact, in a terminal segment of about 6 mm above the lesion the amount of AChE is doubled in 4 to 5 hours. It would take several days to double if the rate were of 1 mm a day.

Our experiments provide no clues concerning the mechanism of axoplasmic streaming. On purely descriptive level they show a bidirec-

tional movement of axoplasm in surviving nerve fibres cut from their cell bodies and the settling of some of the particles carried by the stream near the cut ends, both central and peripheral. Since in tissue cultures the cut axons exhibit cytoplasmic motion (L e v i 1941, H u g h e s 1953) and *in situ* the fibres separated from their cell bodies maintain initially most of their physiological properties unaltered, it seems justifiable to consider the bidirectional movements of axoplasm in cut nerve fibres as remnants of the pattern existing in intact fibres. The deposition of particles at the ends is not a specific feature of cut fibres either. In the intact fibres the terminal region of axoplasm is modified and filled with structural particles (B o d i a n 1952). Collection of mitochondria, granules and vesicles was described at the central and peripheral ends of many types of axons: at all efferent nerve endings, at peripheral ends of afferent fibres in cutaneous receptors (C a u n a 1961) at the tips of regenerating fibres *in situ* (H a y 1957) and of axons grown *in vitro* (de R o b e r t i s and S o t e l o 1952). In many of these endings accumulation of AChE containing particles was also found (Ba r r n e t t 1962).

These facts indicate that both at natural endings of axons and at artificial ends produced by transection some local conditions prevail favouring the settling of particles carried by the stream of axoplasm. It is tempting to suppose that the change of rate and direction of streaming at these sites is the determining factor. This hypothesis is to some extent supported by the finding that near the nodes of Ranvier the amount of mitochondria and profiles of endoplasmic reticulum is larger than in the internodal axoplasm (R o b e r t s o n 1960), although much smaller than at nerve endings. Since the diameter of the fibre at the node is about half of that of the internode, the rate of flow presumably changes near the node and some tendency to arrest of particulate components of axoplasm becomes apparent.

If this description of the axoplasmic movements and of arrest of particles is correct, other components built in into the membranes of mitochondria or of endoplasmic reticulum, besides AChE, should also accumulate at the cut ends whereas the concentration of components dissolved in the axoplasmic matrix should not exhibit appreciable changes.

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SENSORY CUES IN RETURN REACTION

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In one of the previous papers of this series (Ł u k a s z e w s k a 1959),
it was shown that the returning behaviour of white rats in the horizontal
plane is different from that in the perpendicular plane. On the horizontal
T maze, the rats returned correctly to the starting place in about 90 per
cent cases, whereas on perpendicular maze they were unable to solve the
task. The route taken on the perpendicular maze apparently did not
provide the proper information necessary for the returning by the same
route to the starting place.

Both types of mazes differed basically in two respects: a) in the
perpendicular maze, the rats did not turn sideways as they did on the
horizontal maze, they went only up and down; b) running in a straight
line on perpendicular maze, the rats could not use the extra-maze
visual cues, whereas the horizontal maze offered such possibility.

To test which of these differences were responsible for the failure on
perpendicular maze two experiments on different groups of rats were
carried out on horizontal T maze. First, the perception of side turnings
was considerably diminished by reducing the angle between the maze
arms, and, secondly, the animals were deprived of vision.

MATERIAL AND METHODS

Information concerning animals and experimental series is given in Table I.
Rats in experiment B were blinded by electrocoagulation two weeks before
the experiment.

The scheme of the horizontal T maze is shown in Fig. 1. Fig. 2 illustrates
successive stages of reducing the angle between the arms of the maze.

Table I

Informations concerning animals and maze

Experi-ment	Animals					The angle between the arms of T maze		
	No. of group	num-ber of ani-mals	sex	age in month		series		
						a	b	c
A	1	6	♂	3	normal	180°	90°	15°
	2	15	♂	5		15°	180°	—
B	1	7	♀	3	blind	180°	—	—

As in all experiments of this type, the rats were required to come out of the cage which was placed on one of two starting platforms, reach the cup on the maze stem, grasp the food and return to the cage where they were allowed to eat it. Full description of the method was given previously (Ł u k a s z e w s k a 1961).
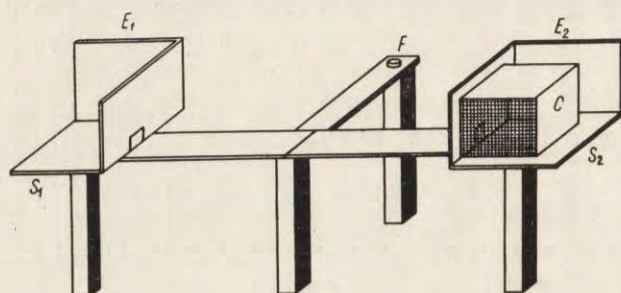
Fig. 1. Horizontal T maze.
S_1, S_2 — starting platforms; C. — cage; F — cup with food;
E_1, E_2 — wooden screens.

Each series consisted of 10 experimental sessions. During each session the rats performed 3 runs from the same starting platform, S_1 and S_2 on alternating days. Experiments were carried out in day light, the room was visually heterogenous.
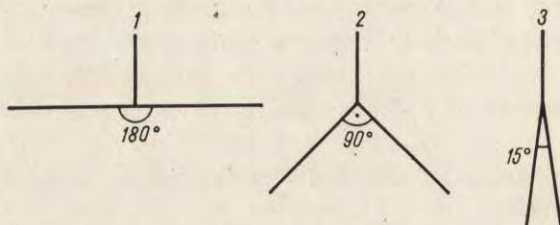

Fig. 2. Stages of lessening the angle between the arms of T maze.

RESULTS

Experiment A

Group 1

Series a. Angle 180° between the arms. The correct return reaction was at the same level as previously described (Łukaszewska 1961), i. e., in above 90 per cent of cases (Fig. 3a).

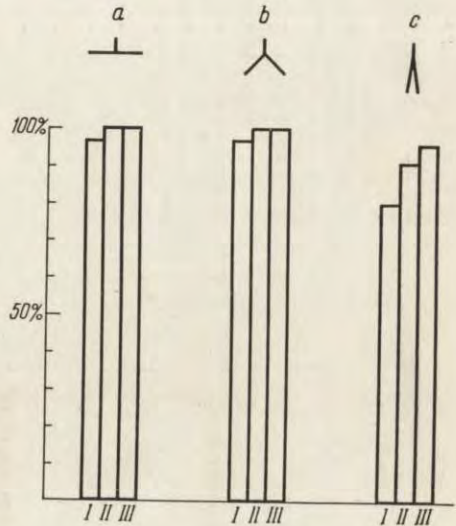*Series b.* Reducing the angle to 90° did not influence the return ability of rats (Fig. 3b).

Fig. 3. The influence of lessening the angle between maze arms on return reaction.

a, b, c, — series of experiments with angle 180°, 90° and 15° respectively; I, II, III — successive trials. Each column represents the percentage of correct return reactions in the respective trials.

Series c. Reducing the angle to 15° caused a statistically significant ($p < 0,02$, test χ^2) decrease in correct reactions in the first trial of each experimental session. However the return ability was, in large part, preserved. In trials II and III only a few errors appeared (Fig. 3c).

Group 2

Series a. Angle 15°. The results obtained on this group were quite different. As can be seen in Fig. 4a, there were in trial I only about 60 per cent correct responses which was just a little above the chance level. But, the choices of return route were not simply random. A comparison of reactions of individual rats shows that in trial I the animals mostly chose the same return route independent of the route leading to the food (Fig. 5).

The preference for one route was so strong that the rats revealed only a small improvement in the succeding trials. As is seen from Fig. 4a,

in trial II, the correct responses increased by 3 per cent, and, in trial III, by 7 per cent. This increase is statistically insignificant.

Series b. Enlarging the angle to 180°. In some rats the tendency to choose the same return route remained even after the angle was enlarged
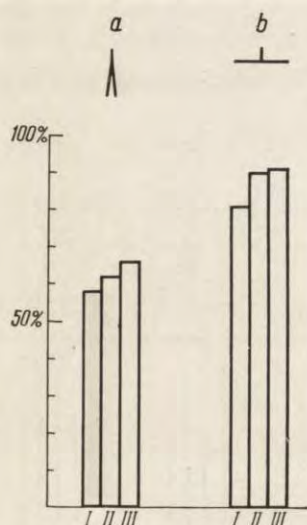

Fig. 4. Return reaction on maze with angle 15°
and after enlargement of the angle.
a, b — series of experiments with angle 15° and 180° respectively. Remaining denotation as in the preceding figure.

to 180° which caused a smaller number of correct reactions than observed up to now in maze with this angle. However, under these conditions 8 rats out of 15 solved the task without error. The difference in results of trial I in series a and b is statistically confirmed (p < 0,01, test χ^2).
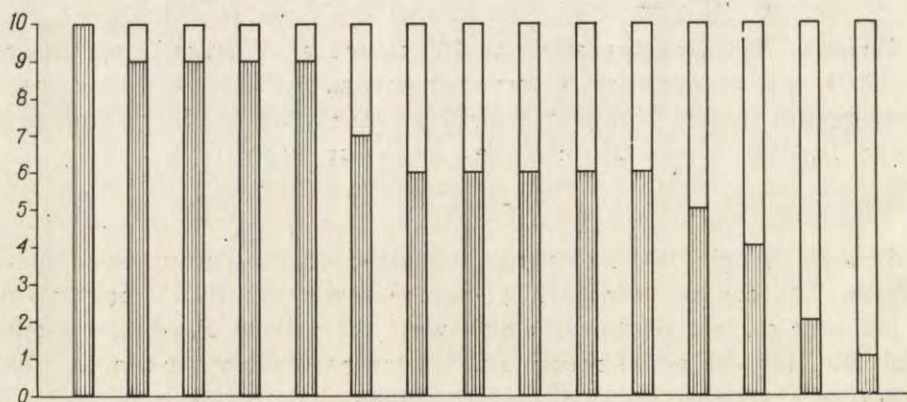

Fig. 5. The preference in choice of return route in rats on maze with angle 15°
(Group 2, series a).
Each column denotes the reaction of one rat in trial I during 10 experimental sessions. Dashed parts of column representes number of choices of left route, white parts — right route.

The above experiments suggest that rats cannot return by the same way as that previously taken to the food, when the proprioception of the turning angle is too small. However, it must be pointed out that decreasing the angle between the arms made the maze like a straight type, thereby eliminating the possibility of using visual extra-maze cues. This could be the reason for the poor performance of the task. This hypothesis was tested in experiment B.

Experiment B

The results of experiments carried out on blind rats are presented in Fig. 6. As is seen, the blind rats made only a few errors. Their return
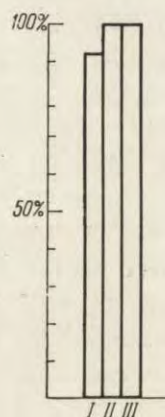

Fig. 6. Return reaction in blind rats.
Denotation as in Fig. 3 and Fig. 4.

ability did not differ statistically from that of normal rats (Ł u k a s z e w-s k a 1961). This indicates that visual cues are not necessary in choosing the correct return route.

DISCUSSION

The above results show that return to the starting place by the same route is possible when the rat has sufficient information about the side turning in the choice point. If the proprioception of turning is too weak, as in the maze with a small angle between its arms, the task becomes unsolvable. Under these conditions, the choice of return route is determined by the preference of one of the arms.

If experiments with the given group of rats do not start with the angle 15° between the arms, but the angle is lessened in steps from 180° on, the return ability is preserved to some degree. This shows that in such a case the discriminative ability of the rats is increased.

It is interesting that in the choice of return route rats can utilize only turnings in the horizontal plane. As was mentioned above the animals were not able to return by the same route in the perpendicular maze in which they could walk only up and down. It should be pointed out that lack of this ability is not connected with difficulties in discrimination of inclined plane. According to R u c h (1927, 1930) rats can discriminate a difference of 4 degrees. Nevertheless, they are not able to seize the rule that if they go up in one direction, they have to go down on the return route. The difference in return behaviour in horizontal and perpendicular plane may be explained by the rat's experience in early period of life. In fact, there is ample evidence to show that the more varied is the environment in the childhaod, the greater the animal's ability to solve particular problems (F o r g a y s and F o r g a y s 1952, H y m o v i t c h 1952, B i n g h a m and G r i f f i t h s 1952). For instance, young rats living in cages without anything to pick up or remove showed no tendency to build a nest in adult age (W i e s n e r and S h e a r d 1933). It is possible that the rats living in a cage, in spite of its small size, have the opportunity to utilize side turnings in their return reactions. However, since the animals move only in the horizontal plane, they are not able to return on a perpendicular maze.

As was proved on blind rats, the visual cues do not play a dominant role in return reaction. On the other hand, it is known that rats learn elevated maze mainly by visual cues. This two facts do not contradict each other because in our experimental situation the return reaction does not require any learning (Ł u k a s z e w s k a 1961). Besides, it must be taken into account that the same way may look different view from opposite directions. Utilization of visual cues would require identifying objects seen from different sides which may prove too difficult for rats.

Making use of the proprioceptive cues in the return route may also seem to present some difficulty since it involves taking the opposite turning to that taken at the same point on the route to the food. However, there is some evidence suggesting that task consisting in turn alternations are extremely easy for rats. Thus, in H u n t e r' s experiment (1940) rats using only proprioceptive cues mastered the maze with simple alternation in 9 to 16 trials. D e n n i s and H e n n e m a n (1932) and S n y g g (1947) found that some rats ran errorless a path with alternating left and right turns already in the first trial. In experiments by D a s h i e l l (1930, 1959) who used the checkerboard maze the rats ran from the beginning almost without error. According to the author's view the animals revealed here the space orientation. On the other hand, it is also

possible that the solution of the problem is due to the alternation of side turnings.

We did not test the significance of touch and olfaction in the return reaction but according to our evidence these cues can be discarded as useless. If they played any role in return reaction, the rats would be able to solve the task on perpendicular maze and on the maze with small angle because in both of them tactual and olfactory cues were also present. Some of the blind rats had the vibrissae cut. Unfortunately, we could not carry out normal experiments on these rats because as a rule they fell down from the maze and, later on, they did not want to leave the cage. However, in 11 cases in which the rats did run the maze safely, we did not observe any errors. It then may be concluded that proprioception connected with side turnings is the only factor necessary to return to the starting place.

The problem of which receptors are responsible for giving information about turnings is still open. At present, it is impossible to decide what role is played here by the vestibules, neck muscle receptors or skin and tendons. B e r i t a s h v i l i and K h e r k - h e u l i d z e 1958a, b, and B e r i t o f f (1959) stress the importance of vestibular sense in similar tasks. In their experiments children guided along a certain line (straight, zigzag, triangle and so on) could follow the same route in the opposite direction even with closed eyes. On the other hand, deaf children (with damaged vestibules) were unable to solve this task without vision. It is quite possible that in return reactions such as studied in our experiments the role of vestibular sense is equally important.

SUMMARY

The role of kinaesthetic and visual cues in return reaction of white rats was investigated on elevated T maze.

1. Elimination of vision did not impair return ability.

2. Reduction of the angle between the maze arms from 180° to 15° caused considerable decrease in the number of correct reactions.

3. By the reduction of the angle in three steps the rats preserved in some degree return ability.

4. Rats which began experiments from the angle 15° were not able to return correctly. Under these conditions, they revealed preference to one of the return paths.

5. It is concluded that return ability is based on the perception of side turnings. It is likely that this kind of perception is connected with vestibular sense.

6. The involvement of other cues (tactual, olfactory) is discussed.

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DELAY IN RETURN REACTION IN RATS

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In our studies on the so called return reaction in rats (Łukaszewska 1961) the animal is required to make a choice between two routes according to the turn performed in its way to food. The interval between the turn in the route to the food and the choice of return route (herein-after called the "delay period") may play an important role in return reaction. In our earlier experiments it amounted up to 3-4 sec, and nearly 100 per cent correct responses were obtained. It then was interesting to test the return reaction under conditions of delay period longer than 4 sec. In fact, such experimental has already been done (Łukaszewska 1961, 1962), but the results have not seemed to be reliable since the animals were previously experienced with a shorter delay. The purpose of the present investigation therefore was to test the return reaction of naive rats in a situation in which the delay period was about 7 sec.

MATERIAL AND METHODS

Experiments were performed on two groups of rats. Each group consisted of 10 naive male animals about 90 days old.

As the method is described in full elsewhere (Łukaszewska 1961), only the details necessary for understanding the course of experiments will be given. Briefly, the rats were required to go out of the cage, grasp the food and return along the same way to the cage. The horizontal T maze, described previously, was used. The only difference consisted of the elongation of maze stem from 40 to 100 cm. (Fig. 1). In consequence, the delay period was extended from 3 to about 7 sec.

Two series of 10 experimental sessions were carried out. In series I, each experimental session consisted of 3 trials in which the cage was placed on one of

the starting platforms. On alternate days, the cage was located either on S_1, or on S_2. Series II experimental sessions consisted of 5 trials. In each session after two runs from one platform the cage with the rat was transfered to the second platform from which the animal started for the next 3 runs. In trial I, the cage was always
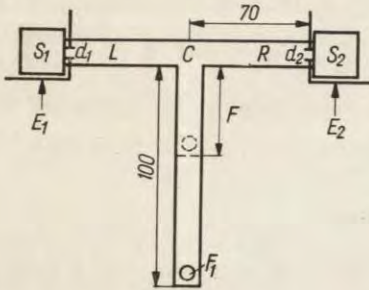

Fig. 1. The floor plane of T maze.
S_1, S_2, starting platforms; E_1, E_2, wooden screems; d_1, d_2, two way doors in the screens; R, right path; L, left path; C, choice-point of the return route; F, F_1 cups with the food in situations in which the delay period was 3 sec. or 7 sec. respectively.

placed on the platform used in the last trials of the previous day. The intertrial intervals depended on the rate of eating: generally, after finishing one food portion the rat immediately went for a second. The correction method was used, i. e. the animals were permitted to correct an error in the same trial.

RESULTS

Series I

a) *Experimental sessions separated by 24-hr. intervals*. The results obtained under conditions of an extended delay period differ significantly from those previously obtained with a shorter delay (Ł u k a s z e w s k a 1961). As far as the number of correct responses in trial I is concerned, only in the first session did the return reaction reach the previous level, i. e. 90 per cent. On the following days, the performance decreased, and then, in some rats a preference for one route (right) occurred (Table I). Only 3 out of 10 animals were able to solve the task (rats

Table I

The number of correct and incorrect return reactions in trial I of successive experimental sessions (24-hr. intervals).

No. of experiment	1	2	3	4	5	6	7	8	9	10
Path	L	R	L	R	L	R	L	R	L	R
Correct responses	9	7	2	7	2	7	4	10	4	9
Incorrect responses	1	3	8	3	8	3	6	0	6	1

Table II

The number of correct and incorrect return reactions performed by all the rats during series I (24-hr. intervals).

No. of rat Path	1		2		3		4		5		6		7		8		9		10	
	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−	+	−
Right	5	0	5	0	5	0	5	0	5	0	4	1	4	1	2	3	2	3	2	3
Left	4	1	3	2	3	2	1	4	1	4	1	4	1	4	4	1	2	3	1	4
Together	9	1	8	2	8	2	6	4	6	4	5	5	5	5	6	4	5	5	3	7

+, correct reaction; −, incorrect reaction

Nos. 1, 2, 3, cf. Table II) at the performance level of 1 to 2 errors altogether during 10 days. The reactions of the remaining animals were incorrect in about half the cases.

In spite of the inability to return correctly in trial I, the rats were doing well in the succeeding trials. Thus, in trial II the correct responses increased to 97 per cent, and in trial III to 100 per cent (Fig. 2a). It should be emphasized that in these trials the return route was, in fact, a repetition of the route in trial I.
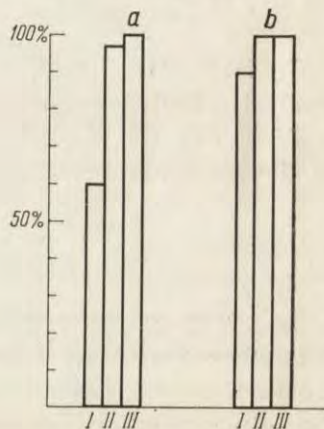
Fig. 2. The effect of intervals between the experimental sessions on return reaction.

a, the intervals between the experimental sessions are 24-hr; b, the intervals between the experimental sessions are 1 or 2 weeks; I, II, III, successive trials. Each column represents the percentage of correct return reactions in the respective trials.

The great number of errors performed in trial I at each session throughout the whole course of experiments contrasts with the perfect return ability in the first experimental session. This shows that when rats are not influenced by the memory traces of return performance from the preceding day their response may be correct.

b) *Experimental sessions separated by 1 or 2 week intervals*. To test above hypothesis, 3 experimental sessions at intervals of 1 or 2 weeks were carried out. The results obtained showed that the level of the return reaction was at 90 per cent of performance (Fig. 2b).

Series II

As seen in Fig. 3, a change of the starting place in trial III resulted in a considerable increase in the number of errors, which amounted to 74 per cent while in experiments with shorter delay it was only about 50 per cent (Łukaszewska 1962). This difference is statistically significant (p < 0,01 test χ^2).
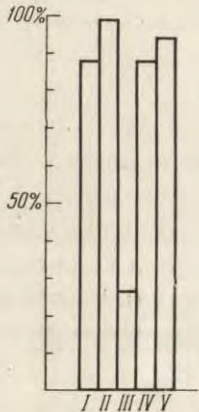

Fig. 3. The effect of the change of starting platform on return reaction.

I, II, trials before changing the starting platform; III, IV, V, trials after changing the starting platform. Other denotations as in Fig. 2.

In trials IV and V, the animals were doing markedly better, and reached a high level of performance (Fig. 3). Also in trial I and II the performance was mostly correct due to the fact that the cage was placed on the same platform as in the last trials of the previous day.

DISCUSSION

In our previous paper (Łukaszewska 1961) it has been shown that when the interval between the turn in the route to the food, and the turn in the choice point in the return way did not exceed 3-4 sec., the return reaction was mostly correct. If, however, the delay period of return reaction was extended up to 7 sec, as was the case in the present experiments, a marked decrease in performance occurred. However, even in this series all rats but one reacted correctly in the first experimental session, and only on the following days did their performance deteriorate significantly (series I). Likewise, in experimental sessions separated by 1 or 2 weeks intervals almost all choices were correct. This indicates that rats are, in fact, able to return to the starting place on elongated maze too, but they are disturbed by the memory of the return route taken on the preceding day. Longer intervals in experiments eliminate the disturbances and allow the animals to react correctly.

Since in experiments on shorter maze the return reaction was not affected by the daily change of the starting platform, it may be concluded that with the prolongation of the delay period the memory traces of the turn performed in route to the food are weakened and may be easier suppressed.

The same explanation accounts for the increased number of errors in the trial given after changing the starting platform in the same session in series II. In this trial the antagonistic relations between the strength of return reaction (i. e. the response based on memory traces of route taken to the food) and the tendency to repeat the return route chosen in the preceding trial are manifested. Due to the extention of the delay period the strength of the first factor was decreased and this caused the preponderance of the second factor.

In contradistinction to the deteriorating effect of the extention of the delay period on the return reaction, the ability to repeat the turn chosen in the previous trial was not affected. In fact, in all trials in which the starting platform had not been changed (trials II, III in series I and trials I, II in series II) the responses were correct irrespective of the delay period. It then may be concluded that the return reaction and repetition of the previously reinforced route are based on two different principles. Whereas the return reaction depends on proprioceptive cues, the repetition of the previous return run may also involve other cues. It is possible that the memory traces of latter cues are more longlasting than those of the first ones and, in consequence, the extention of the delay affects selectively only the return reaction.

The extended delay period did not affect the return ability of rats who were previously experienced with shorter delay (Ł u k a s z e w s k a 1961). This may be explained by the supposition that gradual elongation of the path between the food and the choice point applied in those experiments allowed the rats to adapt to gradual weakening of memory traces of turns taken in the run to the food.

SUMMARY

White rats which were required to choose the return route after the delay period of 7 sec. displayed a markedly worse performance than rats tested at a 3 sec. delay period schedule.

It has been shown that 7 sec delay animals are not unable to return to the starting place, but they are more susceptible to disturbing agents. It is concluded that the procedure of extending the delay period affects the memory traces of cues utilized by rats while choosing the return route (proprioceptive cues).

After the change of the starting place the 7 sec. delay rats made more errors than those with shorter delay. As the ability of repeating the choice reinforced in the preceding trial was not impaired by the extended delay, it seems that this reaction involves cues different from those in the return reaction.

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REVERSAL LEARNING IN REVERSAL TO THE PATTERN OF REVERSAL IN A THREE-UNIT-DOUBLE-CHOICE APPARATUS

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In a recent paper (D ą b r o w s k a 1963) concerning the problem of reversal learning evidence is given that the serial multiple choice habit represents a single kinaesthetic stereotype which is transformed as a whole, even if only one of its elements is changed. These data are in contradiction with the results reported previously by K o g a n (1951) who found that each element of the multiple unit maze was mastered separately, and the reversal learning in one element did not affect the other ones. In view of these controversial data it was necessary to elucidate the sources of the discrepancies.

MATERIAL AND METHODS

20 white rats were used in these experiments. The apparatus, experimental procedure and age of animals were the same as in our previous paper (D ą b r o w- s k a 1962), except that the apparatus had 3 instead of 4 transversal partitions. Animals were divided into four groups. In each group 5 rats were used. The animals mastered successively three tasks. The first task was named OL, original learning; the second task, RL, reversal learning; and the third task, R, relearning. OL-task and R-task were the same. Table I shows various way-patterns applied in experiments performed with different groups of animals. In this Table the left and right of each partition is designated by L and R respectively. To show which task the animals had to learn the letters for successive unlocked doors are given.

RESULTS

Table II shows that in our experimental conditions the general principle of reversal learning of maze habits was preserved, namely the animals learnt the RL-task more rapidly than the OL-task, and the R-task

Table I

Tasks mastered by four groups of animals

Group	OL	RL	R
1	LPL	LPP	LPL
2	LPP	LPL	LPP
3	LPL	PPL	LPL
4	LPP	PPP	LPP

Table II

Number of runs needed to master various tasks

Group	1				2				3				4			
Animal No.	OL	RL	R	NO.	OL	RL	R	No.	OL	RL	R	No.	OL	RL	R
1	18	17	8	6	18	17	4	11	17	10	3	16	17	14	10
2	11	3	4	7	17	10	1	12	9	10	3	17	16	21	5
3	8	6	1	8	11	11	3	13	15	11	8	18	9	2	2
4	10	3	5	9	14	11	6	14	6	4	2	19	9	5	9
5	8	14	17	10	14	15	6	15	14	11	3	20	11	5	6
mean	11	8,6	7		14,8	12,8	4		10,2	9,2	5		12,4	9,4	6,4

Table III

Number of errors made in changed and unchanged choice points

Group	Task	Changed point	Unchanged point
1	RL	11	26
1	R	13	8
2	RL	26	22
2	R	15	4
3	RL	21	33
3	R	11	9
4	RL	18	7
4	R	18	3

Table IV

Number of errors in the unchanged choice points for each animal

Group Animal No.	1		2			3			4		
	RL	R	Animal No.	RL	R	Animal No.	RL	R	Animal No.	RL	R
1	10	1	6	3	0	11	17	1	16	5	2
2	1	2	7	8	0	12	9	3	17	2	1
3	2	0	8	3	0	13	3	5	18	0	0
4	1	0	9	2	2	14	2	0	19	0	0
5	12	5	10	6	2	15	2	0	20	0	0

was mastered even more quickly. The Table also shows that the difficulty in reversal learning did not depend on the change of the choice point. When we analyse the errors in reversal learning (Table III) we find that they occur both at partitions in which the unlocked door was changed, and in those in which it remained the same. However, as seen in Table IV, some animals did not commit errors in the unchanged choice points, particularly in the relearning series.

DISCUSSION

In our previous paper concerning the mechanism of reversal learning in a four-unit-quadruple-choice apparatus it has been shown that the change of the pathway at one partition affects the whole habit, and the animal must learn it anew (D ą b r o w s k a 1963). The same appeared to be true in respect to the three-unit-double-choice apparatus used in the present paper. The only difference between the course of both original and reversal training in two apparatuses was that in the previous one the course of training was much more regular, as judged by the number of trials to reach criterion (comp. Table II of the present paper with Table II, Dąbrowska 1963).

When analysing the performance of the animals in reversal learning by comparing the number of errors in each animal with the character of errors, we see that some animals commit errors only in the changed choice points, and in those the number of errors is very small. Analogous results were obtained in another paper (D ą b r o w s k a 1962) in which the number of units was reduced. This shows that, when the maze is relatively simple, each element may be mastered separately, whereas in a more complex maze the task is solved as a whole.

Comparing the experimental conditions in K o g a n' s study with ours we clearly see the difference which could account for the discrepancy of

results. As seen in Fig. 1, in K o g a n' s maze the animal making a choice could not know whether it was correct or not, until he reached the end of the respective alley. If the choice was wrong the rat had to withdraw to the choice point, and then the correct alley was in front of him. In contradiction to this, in our maze the wrong choice was quickly recognized by the rat, since both doors were close to each other and the rat after discovering the locked door could immediately turn to the right one. In consequence, the animals had much more opportunity to integrate the whole serial habit than it was the case in K o g a n' s maze.

It seems that whether or not the animal does integrate the whole serial habit into one kinesthetic stereotype depends on various conditions such as the prevalence of kinesthetic cues, the accidental switching from the wrong to the right response, and so on. This problem is dealt with in our present studies.

SUMMARY

1. The present paper is concerned with the course of reversal learning in a three-unit-double-choice apparatus.

2. It was found that the errors committed in the reversal learning are not limited to the partitions in which the unlocked door was changed.

3. These resuts confirm our earlier data that in this type of maze the animals solve the task as a single kinesthetic problem.

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Book Review

Atlas of Electroencephalography on the Developing Monkey Macaca Mulatta. William F. CAVENESS. Addison-Wesley Publishing Co., Inc., Pergamon Press, London--Paris. Pages 145, 1962, illustrated.

One of the indicators of the development and degree of maturity of the central nervous system is the picture of the bioelectrical activities of the brain. C a v e-n e s s presents a detailed pattern of the bioelectrical activities of the brain of monkey in its ontogenetic development, from birth to puberty, that is, to the 24th month of life. The Atlas will be of interest, in the first place, to electrophysiologists working on monkeys, electroencephalographists and all those who are concerned with comparative physiology and the problems of the development of the central nervous system.

This work is based on 434 electroencephalograms obtained from 47 monkeys. In 10 monkeys the EEG investigations were carried out systematically throughout the whole 24 month period of observations; in the remainder, the investigations were carried out at different stages of development. The number of investigations and observation periods are shown in seperate histograms for each monkey. Investigations were carried out by bipolar method, recording the activity of the frontal, temporal and occipital regions. The Atlas is devided into sections, dealing with the following problems: 1° the appearance and bio-electrical patterns of the waking rhythm in various stages of development; 2° the development of the arousal response; 3 the bioelectrical pattern of transition from waking to sleeping in various stages of development; 4 the bio-electrical picture of drowsiness, light and deep sleep at various age levels from birth to puberty. The author compares the results of his own investigations with those obtained by L i n d s l e y in 1939 on the human brain (up to the age of 12). It should be noted that while this Atlas has only some pages of printed text, it contains 96 reproductions of 5 second sections of EEG. Electroencephalograph reproductions are of normal size, speed of paper 3cm/sec. In addition there are 13 tables, graphs or histograms (6 relating to the bio-electrical changes in the human brain, taken from the 1st volume of the G i b b s' Atlas, 1950). At the end of the Atlas can be found a recapitulation of the electroencephalographic material, comprising 64 EEGrams reduced to nearly half normal size. As a final Appendix there is a Bibliographical Reference section with 37 items and a short Index.

The considerable space alloted in the Atlas to graph recordings as compared with written text has much to recommend it and is in fact necessary in this type of work. The aboundance of forms and the variability of the EEG recordings in each fraction of a second is almost impossible to describe in words. It is much easier to reproduce them, so enabling comparison. A written description of a EEG

can only give and usually only does give a rough sketch of the pattern, which comprises changes too subtle to be adequately brought out. Also interpretation of EEG recordings continues to be, as D a v i s put it in his Introduction to the Atlas „more of an empirical art than an exact science". This description fully applies here, as the author evaluates the recordings „ad oculos", without making use of frequency analysers or electronic computers. Employing such equipment would undoubtedly help in attaining more precise and objective results in the investigations. This would, however, involve a more extensive use of this type of aids in EEG laboratories than has been the practice hitherto.

All who conduct EEG investigations in humans or animals prior to the puperty period are aware how far extended the physiological limits in individuals can be for the same age group. It is therefore right that besides the most typical pattern of bioelectrical maturity, the author includes also extreme patterns for slow and quick development. The EEG recordings are summarised in comparative tables, graphs of frequencies and amplitudes, giving the mean values (unfortunately, it is not said how these mean values were calculated, how many waves were taken into consideration, from which regions etc.) and also the extremes. Such a comparison enables the readers to get some idea as to the physiological limits of the recording at various stages of development.

Comparing the EEG pattern of the brain of monkey with that of man, the author comes to the conclusion that there is a very close similarity in the morphological picture of recordings at corresponding stages of development; it should be noted however, that bio-electrical maturation in monkey is six times faster than in man. Only in young monkeys is the amplitude greater than in man at the equivalent stage of development; in adult individuals both the amplitude and the frequency are of the same order. The excitatory reflex appears only in the second or third week after birth, first to tactile, then to auditory stimuli; a reflex to visual stimuli appears only in the 4-th week.

The waking rhythm becomes apparent by the second week after birth in the shape of waves at first 3 to 4 cycles per second, this frequency gradually increasing. The amplitude of these waves at first increases from 30-70V to 80-200v in the 6th to 10th week after which a decline is observed, lasting till the 24th month. At first, the recordings are asynchronous both as regards the anterior and posterior leads on the same side and also between the two brain hemispheres. Synchronisation is discernable in the 5th week and becomes pronounced in the 9th. Maturation of the activity begins from the posterior leads.

In subsequent chapters the author compares the EEGgrams of monkey and man in the state of drowsiness, light sleep and deep sleep; a good deal of space is given over to spindles, characteristic for light sleep.

In conclusion, due to the systematic investigations (possible to such an extent only on animals) the C a v e n e s s' Atlas in an original and valuable contribution to a better knowledge of the patterns of bioelectrical maturation of the brain of monkey. Noting of analogous regularities in man makes it also a useful aid in clinical EEG.

The general arrangement and graphical presentation of the Atlas are to be commended.

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