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THE MYELOARCHITECTONICS OF THE HYPOTHALAMUS IN THE DOG

I. THE ANTERIOR NUCLEI

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The aim of this paper is to describe, on the basis of myeloarchitectonics, the division, topography and interconnections of the hypothalamic nuclei in the dog.

The hypothalamus has been a subject of many anatomical investigations. So far, however, no agreement has been achieved as to the division of the hypothalamus into nuclei and nucleus groups. The cytoarchitectonic elaborations make up the most numerous group of studies on the hypothalamus (Gurdjian 1927, Craigie 1925, Rioch 1929, Morgan 1930, Bodian 1939 and Bleier 1961). They have been carried out with the Nissl method and aimed at the description of cells which is, however, insufficient for the accurate identification of the hypothalamic nuclei. The Nissl method does not also allow one to determine the interconnections of the hypothalamic nuclei. The division into nuclei is made by some authors only on the basis of the size of cells in a given hypothalamic area. This is an unreliable criterion since paraffin sections are marked by deformations of cells (both with regard to shape and size), which may reach as much as 20 per cent.

Recently, an original division of the hypothalamus into nuclei has been given by Spatz (after Diepen 1962). Spatz applied the criterion of the myelinization within the hypothalamic nuclei, dividing them into the

well and poorly myelinized ones. Unfortunately, this division fails to show the functional organization of the hypothalamic nuclei.

Kuhlenbeck (1954) in his study on the hypothalamus in man used the methods for staining both the cells and fibers. Like earlier investigators, Kuhlenbeck distinguished the anterior, the middle and the posterior groups of hypothalamic nuclei, maintaining that an area, determined by him as a dorsal and entopeduncular group, should be included in the hypothalamus. Furthermore, Kuhlenbeck suggested that the entopeduncular nucleus, like the remaining nuclei of the hypothalamus, originated from the hypothalamic primordium of fish and amphibians.

Studies in which the areas of the hypothalamus concerned with neurosecretion (paraventricular nucleus, supraoptic nucleus and massa intermedia) are dealt with form a separate group. The hypothalamic nuclei involved in neurosecretion in the dog have been described by Morgan (1930). Laqueur (1954), Scharer (1963), Diepen (1962) and Schreiber (1963) are among the authors who described this region in other species.

Generally, little is known on the anatomy of the hypothalamus in the dog. In fact, Rioch (1929, 1931) is the only author who described the cytoarchitectonics and, in part, the myeloarchitectonics of the hypothalamus in the dog. The following groups of nuclei have been identified by Rioch: the periventricular area, the lateral area, the rostral or supraoptic area, the tuberal or infundibular area and the caudal or mammillary area. Because of a rather scant information, supplied by Rioch's paper, a necessity arose to study the hypothalamus in the dog on the basis of myelin sections.

MATERIAL AND METHOD

The following material was used: (1) 5 continuous series of frontal sections of the dog brains, stained by the methods of Nissl, Klüver-Barrera, Schultze and Weigert-Wolters; (2) two sagittal series, stained by the Klüver-Barrera and Weigert-Wolters and (3) one horizontal series, stained by the Weigert-Wolters method. In the Weigert-Wolters method, the brain was cut into 50 μ thick slices, while in all other methods this thickness amounted to 20 μ.

OBSERVATIONS

In applying the myeloarchitectonic criterion, the following groups of nuclei have been differentiated in the hypothalamic area of the dog: the anterior, the intermediate and the mammillary group (Fig. 1) Rioch identifies the lateral area as a separate section of the hypothalamus in the dog.

It has been shown by our analysis of the fibers in the lateral hypothalamic area that it is not uniform over its entire length and an anterior and a middle part are recognized within it.

The mammillary bodies (Fig. 1, c.m.) are the most unquestionable group of hypothalamic nuclei in the dog. This group also is the easiest one to identify in all series of sections. Situated posteriorly to the infundibulum, they are anatomically well-developed and, in frontal sections, they are marked by a ring of fibers, situated in the section plane. Two nuclei of mammillary bodies are disposed inside this ring and the remaining ones adhere to it on the outside (anteriorly).

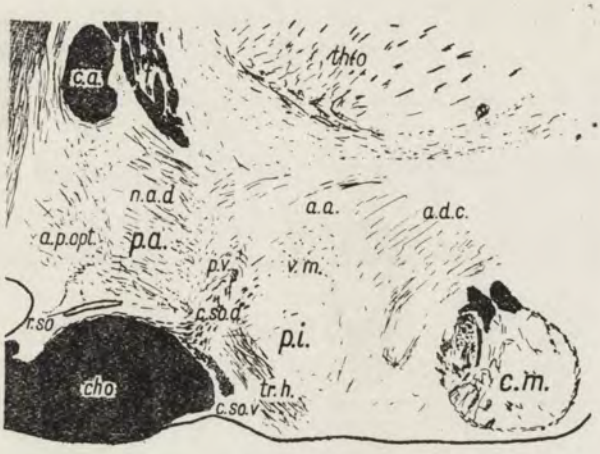

Fig. 1. Sagittal section through the medial hypothalamus in the dog. Weigert-Wolters stain

The intermediate part (Fig. 1, p.i.) is situated more anteriorly. Previously, it has often been called tuber cinereum. This part is located close to the infundibulum.

The anterior part of the hypothalamus is located in front of the intermediate part (Fig. 1, p.a.). A well-myelinized system of fibers of the dorsal supraoptic commissure and a system of fibers, belonging to the hypothalamic-tegmental tract, intersecting the former, runs on the boundary between the intermediate and anterior part. The demarcation of these two hypothalamic portions in myelin sections is quite distinct. The fiber systems, mentioned above, are related to a greater extent with the intermediate part and they will be discussed together with the latter.

According to some anatomists, the preoptic area, situated in front of the anterior part, is a subdivision of the hypothalamus. However, phylogenetically it belongs to the telencephalon and, therefore, it has been described separately (M i o d o ń s k i 1963).

In the present paper, the following areas have been differentiated in the anterior part of the hypothalamus in the dog : (1) the anterodorsal nucleus, (2) the anteroventral nucleus, (3) the suprachiasmatic nucleus, (4) the anterior supraoptic nucleus, (5) the massa intermedia, (6) the paraventricular nucleus, (7) the periventricular area, (8) the lateral nucleus.

The anterodorsal nucleus of the hypothalamus (Figs. 2, 3, 4, 6 and 9, n.a.d.)

Topography. The anterodorsal nucleus is situated in the middle of the anterior part of the hypothalamus. In frontal sections, this nucleus is seen posteriorly to the medial preoptic area. It stretches over the entire ante-

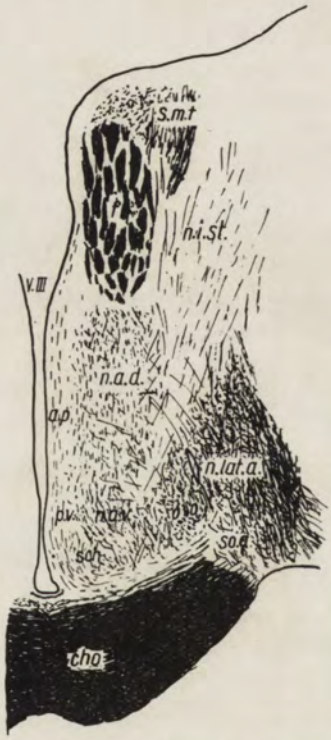

Fig. 2. Frontal section through the anterior hypothalamic nuclei

rior part of the hypothalamus, terminating, together with it, in the place where the optic tract divides. In the anterior and middle part, the anterodorsal nucleus has the shape of an ellipse the longitudinal axis of which runs in the vertical plane. In the caudal part, this ellipse loses its regular

shape on the ventral side since the anteroventral nucleus appears in this place. The height (a dorsocaudal dimension) of the anterodorsal nucleus amounts to about 3.2 mm, while the horizontal dimension amounts, in the frontal plane, to about 2 mm and, in the sagittal plane, fluctuates between 2 and 2.5 mm.

The anterodorsal nucleus, occupying the central position within the anterior part of the hypothalamus (Figs. 2 and 3, n.a.d.), is surrounded by the remaining hypothalamic areas. The lateral boundary is the easiest to be noticed of all boundaries of the anterodorsal nucleus. On its lateral side, there is the lateral hypothalamic area whose rich texture of fibers makes these areas distinctly different from each other. The determination of this boundary is also facilitated by the presence, between the anterodorsal nucleus and the lateral area, of fibers, coming out of the laterodorsally situated interstitial nucleus of the stria terminalis.

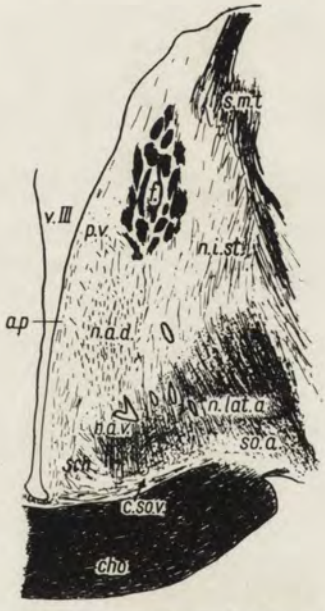

Fig. 3. Frontal section through the anterior hypothalamic nuclei

The determination of the dorsal range of the anterior nucleus is also simple since the fiber bundles of the fornix run dorsally to it. Somewhat more difficult is the determination of the medial and ventral range of the anterodorsal nucleus. The periventricular area is situated medially to it, the same as, in the caudal part, the paraventricular nucleus, while the anteroventral nucleus is located on its ventral side.

Architectonics. The main fiber system, running through the entire anterodorsal nucleus, displays an orocaudal direction with a slight downward deviation of fibers. This system (I) consists mostly of two types of fibers. The first, pronouncedly predominating, is represented by thin (below 1 μ in thickness) fibers, arranged in bundles about 12 to 15 μ in diameter. On the average, these bundles contain 5 fibers. The second system (II), less abundant, is represented by somewhat thicker (up to 2 μ in diameter) fibers, also grouped in bundles but containing less, that is, only 2 to 3 fibers each.

Fig. 4. Myeloarchitectonics of the anterodorsal hypothalamus in the dog. Weigert stain

In the anterior part of the anterodorsal nucleus, some fibers of both these systems get outside the boundaries of the nucleus and, without any change in the direction, run, through the nucleus bed of the anterior commissure (situated ventrally to the anterior commissure), towards the septum. A few of them intermingle with the fibers of the stria terminalis. Fibers that have not been scattered over the area of the nucleus pass, in the posterior part, to the anteroventral nucleus.

Some fibers from the periventricular area join the anterodorsal nucleus on the medial side. There are few fibers of this system and they mostly run lateromedially, some of them deviating ventrally or dorsally. The fibers of this system are short and may be found only on the medial side of the nucleus among the fiber bundles of system I.

The anterodorsal nucleus is joined by the fibers from the interstitial nucleus of the stria terminalis. Without forming bundles, they run by ones dorsoventrally and dorsomedioventrally. In the anterodorsal nucleus they display a uniform direction and terminate at different levels of this nucleus.

In addition to these systems, few thin and fairly long fibers, running lateromedially, take their origin from the anterodorsal nucleus. Finally, they reach the internal capsule where they disappear.

The cytoarchitectonic sections display, in the anterodorsal nucleus, the presence of a few types of cells oval or ellipsoidally elongated in shape. Oval cells are about 8 μ in diameter, elongated ones — 10 μ in diameter and to 25 μ long.

Previously, the medial preoptic area was related with the anterior nucleus of the hypothalamus and described as a single unit, called, the anterior hypothalamic region (Bleier 1961). This is due to the cytological similarity of these areas. Rioch (1929) did not find any strict boundary between the medial preoptic area and the anterodorsal nucleus and, consequently, he accepted a conventional boundary. The delimitation of these two structures may be carried out only in the myeloarchitectonic sections.

The anteroventral nucleus of the hypothalamus
(Figs. 2, 3, 5 and 9, n.a.v.)

Topography. The anteroventral nucleus of the hypothalamus is a small nucleus, situated between the anterodorsal nucleus, dorsally, and the suprachiasmatic nucleus, ventrally. Medially, this nucleus borders on the

Fig. 5. Fiber system of the hypothalamic anteroventral nucleus in the dog. Weigert stain

periventricular area, whereas laterally — on the lateral area of the anterior division of the hypothalamus. On the lateroventral side, also the lateral area (Figs. 2 and 3) adheres to the anteroventral nucleus. This nucleus has so far been neither described, nor even identified.

Architectonics. The anteroventral nucleus of the hypothalamus has specific connections which allow one to differentiate it. Principally, the fibers in this nucleus, have an orocaudal trace. They show a considerable posterior deviation and, in the ventral part, they turn laterally. Eventually, they terminate in the ventromedial part of the lateral area of the anterior hypothalamus. These are only thin fibers which do not form bundles but run loosely (Fig. 5). This fiber arrangement is typical of the entire area of the anteroventral nucleus.

The anteroventral nucleus receives a considerable number of fibers, running from the interstitial nucleus of the stria terminalis. These are long fibers, disposed in the plane of the frontal section. They run ventrally from the interstitial nucleus of the stria terminalis, passing by the anterodorsal nucleus and, hereafter, edge themselves into the area between the anterodorsal and the anterolateral nuclei. They disappear in the anteroventral and anterolateral nuclei. The fibers of this system reach the anteroventral nucleus over its entire surface.

The anteroventral nucleus is also connected with the suprachiasmatic nucleus. This connection is provided by thin lateromedial fibers which may be found only on a small area on the medial and ventral side of the anteroventral nucleus.

The cytoarchitectonics of the anteroventral nucleus is similar to that of the anterodorsal nucleus. Cells are mostly oval or elongated, their diameter being within limits of 8 and 10 μ and length reaching 25 μ. They are poorly stainable when the Nissl method is applied.

The paraventricular nucleus of the hypothalamus
(Figs. 2, 3, 6, 7 and 9, p.v.)

Topography. The paraventricular nucleus is a small nucleus, situated in the anterior part of the hypothalamus. This nucleus is concerned with neurosecretion (Diepen 1962, Scharrer and Scharrer 1963, Laqueur 1954, and others). In Nissl's sections this nucleus is distinctly differentiated and, therefore, it may easily be found. It consists of large, easily stainable cells so that, even slightly magnified, it may be located without any difficulty.

The paraventricular nucleus in the dog is shaped like a mace turned with its blunt end upwards and slightly posteriorly.

In the rostral part, the paraventricular nucleus is about 125 μ wide (a lateromedial dimension), while, in the dorsal part, the same dimension amounts to about 450 μ. A dorsoventral height of this nucleus is within limits of 3 and 4 mm.

The paraventricular nucleus is mediocaudally situated in relation to the anterodorsal nucleus described above. The ventral part of the paraventricular nucleus is situated dorsally to the suprachiasmatic nucleus and its dorsal part is located as far posteriorly as above the intermediate (tuberal) part of the hypothalamus. On the lateral side, the paraventricular nucleus borders on the anterodorsal nucleus and, on the medial side, on the periventricular area. The ependymal layer of ventricle III, in the place where the paraventricular nucleus is situated, displays a peculiar corrugation (Fig. 7). The fiber bundles of the fornix run laterodorsally to the paraventricular nucleus.

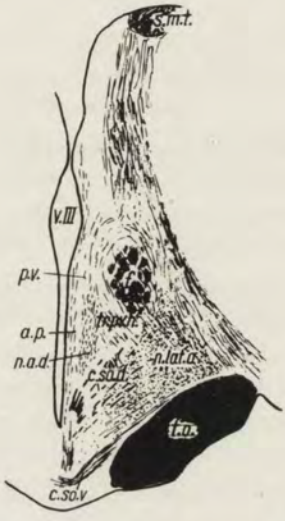

Fig. 6. Posterior sector of the anterior hypothalamus in the dog

Architectonics. The myelin sections display, within the paraventricular nucleus, only a small number of fibers. Similar conditions may be observed in the sections of the silver series where the picture of this nucleus is brighter than that of adjacent nuclei.

The paraventricular nucleus contains in fact two systems of fibers. The first consists of the dorsoventrally running fibers. In the dorsal part of the nucleus they run upwards and scatter in the nucleus reuniens of the thalamus. A part of them intermingles with the fibers of the stria medullaris of the thalamus. The second system consists of the laterally and lateroventrally running fibers which take their origin at various levels of the paraventricular nucleus. They are thicker than the fiber of the first system (diameter, about 3 to 4 μ). This system gets outside the limits of

the nucleus and, without any change in its principal direction, forms a paraventricular-hypophyseal tract. Within the limits of the hypothalamus the fibers of this tract do not form any compact pathway. After leaving the paraventricular nucleus, they run towards the supraoptic nucleus. A part of the fibers of this tract terminate in the supraoptic nucleus, while the remaining fibers reach pars nervosa of the hypophysis.

On the medial side, the paraventricular nucleus is connected with the periventricular area. (The periventricular area, presenting itself as a layer of nervous cells around ventricle III, is discussed below). These are few, short fibers that reach only the external parts of the nucleus and do not enter its deeper layers. The direction of these fibers is almost dorsoventral with a slight lateral deviation.

The paraventricular-hypophyseal tract (Fig. 6), getting out of the paraventricular nucleus, makes up a pathway, connecting this nucleus with the hypophysis. It has been shown (L a q u e u r 1954) that the neurosecretory substances, produced in the paraventricular nucleus are conveyed by this tract to the hypophysis. It has furthermore been shown that this tract in the dog runs through the supraoptic nucleus.

In Nissl's sections, the paraventricular nucleus is marked by large, well-stained cells. Their morphology is similar to that of the cells of the supraoptic nucleus. Two types of cells may be distinguished within the nucleus. These are oval cells about 25 μ in diameter and triangular, pyramidal cells about 35 $\times$ 25 μ. They have a large nucleus and a well-visible nucleole. Occasionally, fairly large vacuoles, containing the neurosecretory substance, may be seen within the cells of the paraventricular nucleus. These vacuoles frequently displace the Nissl bodies as far as the peripheral parts of the cells.

Vacuoles, filled with the neurosecretory substance, are stained blue-black according to the Gomori neurosecretion method. In using this method, L a q u e u r (1954) discovered that neurosecretion occurs not only inside the cells of the paraventricular nucleus. Like M o r g a n (1930) and other authors, he indicates that neurosecretion also occurs on the fibers of the paraventricular-hypophyseal tract. The presence of many enzymes has been discovered in the paraventricular nucleus, as well as in the supraoptic nucleus (which is also a neurosecretory nucleus). S c h r e i b e r (1963) found phospatase between the cells of the paraventricular nucleus in the cow embryo. Likewise, perioxydases, as well as the acetylcholine dehydrogenase and esterase have been found in the neurosecretory cells of the anterior part of the hypothalamus.

According to M e y e r (1935), the paraventricular nucleus phylogenetically derives from the preoptic area of fish and amphibians which also gave origin to the supraoptic nucleus of mammals. The cells of the

paraventricular and supraoptic nuclei in mammals display a similarity to the supraoptic nucleus in fish and birds. The concentration of cells, known as massa intermedia of the hypothalamus, may be a residue, formed as a result of the division of this originally single nucleus. The paraventricular nucleus has also been found in the hypothalamus of man where its size is about two times as large as in the dog. In the dog, the dorsoventral dimension amounts to 3 to 4 mm and, in man, according to Le Gros Clark et al. (1938) — to 7 mm.

With regard to the blood vessels, the paraventricular nucleus is the second to the supraoptic nucleus which, of all hypothalamic nuclei, has the largest number of blood vessels. This was shown by Craigie (1940) for the rat and by us for the dog.

The massa intermedia of the hypothalamus (Fig. 7, m.i.)

Topography. The massa intermedia is represented by cells, disposed laterally or lateroventrally in relation to the rostrum of the paraventricular nucleus. The cells are located in the ventral and medioventral part

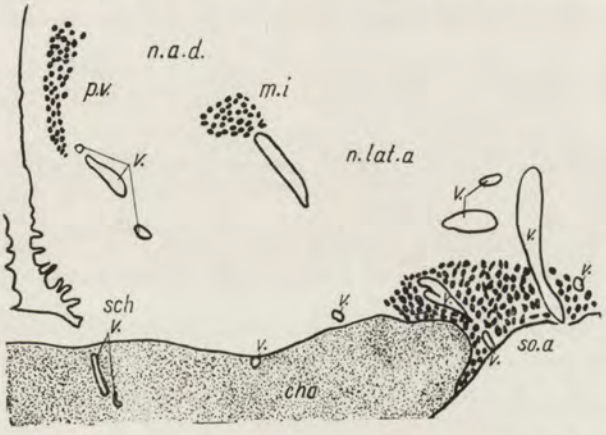

Fig. 7. Neurosecretory areas of the anterior part of the hypothalamus in the dog. Semidiagramatically, Nissl stain

of the anterolateral nucleus. Two or three concentrations of the cells may be seen of the massa intermedia. Each concentration whose diameter may reach to 200 μ contains many cells, usually, oval in shape. Their length comes to 30 μ with the width, reaching 12 to 15 μ. The nuclei of these cells are well-stainable and, owing to their considerable dimensions (diameter, to 7 μ), also distinctly visible.

In their size and stainability, the cells of the massa intermedia are similar to those of the paraventricular nucleus.

Myeloarchitectonically, it has been shown that the massa intermedia contains a small number of fibers which makes tracing their connections difficult.

The cells of the massa intermedia are mostly found close to the blood vessels (Fig. 7). In most cases, they are located on the dorsal side of a vessel. The location of the cells of the massa intermedia has induced some authors to assign these cells to the supraoptic nucleus and some others — to the paraventricular nucleus. Kuhlenbeck (1954) suggested that massa intermedia is involved in neurosecretion.

Phylogenetically, the massa intermedia may be a residue, formed as a result of the separation of the preoptic nucleus in fish and amphibians into two neurosecretory nuclei, that is, the supraoptic and the paraventricular nucleus in mammals. It is also possible that it was the displacement of a certain number of cells from the supraoptic nucleus by the blood vessels growing into the brain that caused the formation of these two neurosecretory nuclei. The location of the cell concentrations of the massa intermedia near the vessels which, coming out of the circulus arteriosus Villisi, grow into the hypothalamus through the brain base, might serve as a proof for such a hypothesis.

In the dog, the massa intermedia has been assigned to the tangential (supraoptic) nucleus (Rioch 1929). In man, it has been described by Diepen (1962) who called it " intermediäre Zellnester ". Koikegami (1938, cited after Diepen 1962) has described it in the macaque and in the cat, giving it the name of the paraventricular or supraoptic accessory. The massa intermedia in man has also been described by Brockhaus (1942) (cited after Diepen 1962) and Feremutsch (1955).

The anterior supraoptic nucleus of the hypothalamus (Figs. 2, 3, 7 and 9, so.a.)

Topography. The supraoptic nucleus in the dog is a nucleus which consists of two parts, separated one from another. Its anterior part, situated in the anterior part of the hypothalamus, occupies an area on the lateral side of the optic chiasm. The posterior part is located, medially to the optic tract, in the region of the intermediate part of the hypothalamus.

The division of the supraoptic nucleus into these two parts is often applied and they are differently called by different authors. The terms which are most often met with are, the tangential nucleus of the tuberal part and the tangential nucleus of the supraoptic part (Bodian 1939). A similar division and nearly the same terminology are applied by Bleier (1961).

In the present paper, only the anterior supraoptic nucleus is discussed below. Along its entire trace, the anterior supraoptic nucleus is situated ventrally to the lateral area and laterally to the optic chiasm. More posteriorly, in the caudal part of the optic chiasm, the cells of the supraoptic nucleus are shifted laterally by the fibers of the optic tract which diverge laterally. The anterior supraoptic nucleus disappears at the level of the complete divergence of the optic tract.

Fig. 8. Myeloarchitectonics of the periventricular area of the hypothalamus in the dog. Weigert stain

Architectonics. The rostral part of the supraoptic nucleus contains a thin layer of cells. More posteriorly, the cells huddle together, forming a compact group, while the anterior supraoptic nucleus takes a triangle shape. In the place of the most extensive development, this nucleus is (lateromedially) about 1,400 μ wide and (dorsoventrally) to 320 μ high.

In the Nissl sections, this nucleus displays a concentration of large cells with a diameter that comes to 30 μ. These cells are mostly oval but elongated cells 30 × 20 μ in size are also met with occasionally. According to Diepen (1962) and Schreiber (1963), similarly as the paraventricular nucleus the supraoptic nucleus is associated with neurosecretion. A large (diameter, to 7 μ (nucleus with a strongly stainable nucleole may easily be observed inside the cells of the supraoptic nucleus.

In myelin sections, a small number of fibers may be found in the supraoptic nucleus. The system of fibers from the optic chiasm is undoubtedly the best-developed fiber system of all that reach this nucleus. This system consists of fairly thick fibers, reaching 6 μ in diameter, branching off from the lateral and laterodorsal margin of the optic chiasm. Observing the location of these fibers within the optic chiasm, one may find two types of fibers. The first is represented by fibers which laterodorsally

come out of the optic chiasm. In the anterior part of the optic chiasm they form a small bundle which reaches the medial part of the anterior supraoptic nucleus. Fibers of the other type detach from the lateral part of the optic chiasm but they do not huddle together into a bundle, instead, in the form of a loosely arranged bundle, they also enter, on the medial side, the anterior supraoptic nucleus ventrally in relation to the fibers of the former type.

Both types of fibers, forming this system, intermingle with each other and scatter in the anterior supraoptic nucleus.

The second largest fiber system in the anterior supraoptic nucleus consists of fibers, reaching this nucleus from the anterolateral nucleus. This system is very well-developed and present in the entire anterior supraoptic nucleus. It forms a loose system of scattered fibers, running dorsoventrally. This system contains fibers with a diameter lesser than 2.5 μ.

Through the lateral nucleus, the anterior supraoptic nucleus is reached by fibers from the stria medullaris of the thalamus. This system contains a small number of fibers and is situated between the fibers which, on the dorsal side, enter the lateral nucleus.

Few fibers from the medial forebrain bundle, which may be traced on the sagittal sections, frontally enter the supraoptic nucleus. Accoyrding to De Vito and Smith (1964), the anterior supraoptic nucleus is connected via this bundle with the prefrontal cortex. A degeneration of the lateral region of the anterior supraoptic nucleus followed the lesion of the prefrontal cortex in Macaca nemestrina.

Escolar (1954) cited after Diepen 1962) presented evidence, showing that the amygdaloid complex is associated with the supraoptic nucleus. According to this author, this pathway runs through the substantia innominata. This connection takes its origin from Brockhaus' nucleus supraamygdaleus which, according to the English terminology (used in these Laboratories), corresponds with two nuclei of the amygdaloid complex, that is, medial and central nuclei. No details can be given on this connection since there is surprisingly little information on the anatomy of the substantia innominata in the dog.

On the dorsal side of the optic chiasm, there runs a system of fibers of the ventral supraoptic commissure. The fibers of this system are not connected with the anterior supraoptic nucleus. Diepen (1962) indicates that the ventral supraoptic commissure connects bilaterally the optic tract and the entopeduncular nucleus. Likewise, it has been shown by Gurdjian (1927) that, in the rat, the ventral supraoptic commissure runs over the supraoptic nucleus but is not connected with this nucleus. Neither in the dog, connections of these two structures have been found despite their close neighborhood.

The supraoptic-hypophyseal tract starts from the anterior supraoptic nucleus and runs caudoventrally towards the infundibulum. This tract is poorly visible in frontal sections since it runs almost vertically to their plane. However, it may easily be found in sagittal sections in which it may be seen that it starts between the cells of the anterior supraoptic nucleus and runs posteriorly, entering, through the infundibulum, the posterior portion of pars nervosa of the hypophysis. This tract has been confirmed by degeneration methods. It has been reported by O'Connor (1948) that, after the lesion of the infundibulum, a degeneration of cells occurs in the supraoptic nucleus.

Apart from large dimensions of cells, the blood vessels are the most striking anatomical detail in the anterior supraoptic nucleus. These are vessels, 7 to 60 μ in diameter, which enter the brain from its base (Fig. 7) and entwine the nerve fibers which is in conformity with Craigie's (1940) observations. Investigating the degree to which the hypothalamus of the rat is supplied with blood vessels, Craigie found nearly two times larger blood vessel network in the supraoptic and paraventricular nuclei than in all the remaining nuclei of the hypothalamus. In the dog, the number of capillaries in the area of the anterior supraoptic nucleus is much greater than in paraventricular nucleus.

Periventricular area of the hypothalamus. (Figs. 2, 3, 6, 8 and 9, a.p.)

Topography. The walls of ventricle III consist of a unilaminar ependymal epithelium, under which a thin layer of nerve cells is situated. These cells make up a periventricular region which has been called a periventricular nucleus (Bleier 1961) or a periventricular gray (Bodian 1939). This region is also seen in the hypothalamus of the dog in which, however, it can be hardly called a nucleus since it comprises a very large area of ventricle III and stretches not only over the hypothalamus but also over the thalamus and the preoptic area.

Architectonics. In the anterior part of the hypothalamus the periventricular area consists of the layer of a unilaminar ependymal epithelium which directly lines the walls of ventricle III. Underlying is a layer of nerve cells.

The ependyme is to 15 μ thick. In some places, particularly in the vicinity of the paraventricular nucleus, the ependyme is strongly corrugated. The folds are fairly large, reaching to 60 μ in height and to 90 μ in width. This corrugation is visible in sections of all series used.

The periventricular area is marked by fine (diameter, to 1 μ), well-myelinized nerve fibers, clearly visible in the sections of the silver and

of the Weigert series. The trace of these fibers within the periventricular area is almost vertical with a slight anterior deviation (Fig. 8). These fibers start in the dorsal part of the periventricular area, pass through the entire area and, in the ventral part, enter the suprachiasmatic nucleus. This is the strongest connection of the periventricular area in the anterior part of the hypothalamus in which most fibers of this connection terminate.

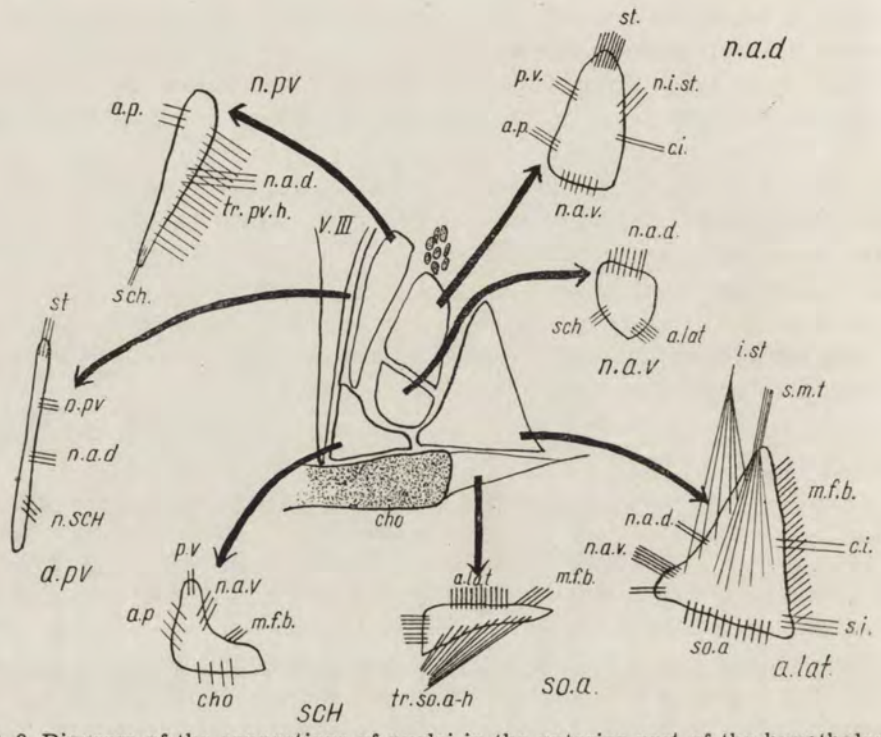

Fig. 9. Diagram of the connections of nuclei in the anterior part of the hypothalamus in the dog. Shaded spots denote the direction and density of fibers in particular systems (the paraventricular-hypophyseal tract, passing through the anterodorsal and the anterolateral nuclei is not marked in these nuclei)

In the dorsal part, the periventricular area is joined by fibers that are not associated with the stria terminalis and the fornix. The number of these fibers is very small and they are difficult to be traced. These connections in the cat, rat, guinea pig and monkey have been confirmed by Vallenstein and Nauta (1959) who identified them by means of the degeneration methods.

On the lateral side, some fibers of the periventricular area deviate lateroventrally or medially, reaching the anterior nucleus of the dorsal hy-

pothalamus and, in the posterior part, the paraventricular nucleus. These are short nerve fibers. Their length comes to 100 μ.

The cells of the periventricular area are small and, with Nissl method, poorly stainable. They are mostly oval, less frequently, elongated. Their diameter is ca. 5 μ. The cells of the periventricular area are partially situated between the parallelly arranged fibers. The rest of them occupy an area on the lateral side of these fibers.

The physiology of the periventricular system is little-known. Ford and Kantounis (1957) presented evidence showing that some cells of the periventricular system in the rabbit are involved in neurosecretion.

The suprachiasmatic nucleus (Figs. 2, 3, 9 and 10, sch.)

Topography. The suprachiasmatic nucleus is one of the smallest nuclei of the hypothalamus in the dog. Described also in other species, it is often called an ovoid nucleus (Gurdjian 1927, Rioch 1929). It occupies a small area in the ventral part of the anterior hypothalamus,

Fig. 10. Myeloarchitectonics of the suprachiasmatic nucleus. Weigert stain

bordering posteriorly on the anteroventral nucleus of the hypothalamus, medially and dorsally, on the periventricular area, laterally, on the lateral nucleus and anteroventral nucleus and, ventrally, on the optic chiasm.

The suprachiasmatic nucleus starts its trace, as a crescentiform nucleus, at the level of the anterior part of the optic chiasm. More posteriorly, it is rectangular with a shorter side of this rectangle pointing upwards. The suprachiasmatic nucleus terminates before the ventral supraoptic

commissure. The width of its rectangle amounts to about 500 μ, the height — to 1, 100 μ.

Architectonics. Fibers which make up the extension of the fiber system of the periventricular area form the basic system of the suprachiasmatic nucleus. The trace of this system is dorsoventral and, in the ventral part of the nucleus, it deviates laterally (Fig. 10). Most fibers of this system terminate in the region of the nucleus, few of them, getting out and running laterally, terminate in the lateral area of the hypothalamus. The fibers of the basic system are short and run in the plane of the frontal section.

On the ventral side, the suprachiasmatic nucleus is joined by many fibers, running from the optic chiasm. Two types of fibers may be distinguished in this system. The first type is represented by thick fibers, 5 μ in diameter and well-myelinated. They take their origin in the laterodorsal part of the optic chiasm, forming bundles a few fibers each. They may also be observed in the anterior part of the optic chiasm. The second type consists of fibers, starting from the dorsal part of the optic chiasm, scattered and forming no compact bundles. They are thinner than the former and less myelinated (their diameter comes to 2 μ). Both these types of fibers enter the nucleus from the ventral side.

The suprachiasmatic nucleus has only few associations with a part of the anteroventral nucleus. Small nerve fibers, running lateromedially from different levels of the suprachiasmatic nucleus make up these associations. They terminate on the ventromedial side of the anteroventral nucleus and form no distinct system.

A part of the fiber system of the suprachiasmatic nucleus reach the ventral regions of the lateral area of the hypothalamus where they scatter.

The suprachiasmatic nucleus is joined by few fibers, running from the medial forebrain bundle. Through the lateral nucleus they enter the suprachiasmatic nucleus. These are scattered fibers that terminate at different levels of the suprachiasmatic nucleus. They enter the suprachiasmatic nucleus frontolaterally. This connection has first been described in rat by Gurdjian (1927). According to this author, the suprachiasmatic nucleus in the rat is joined by fibers from the stria terminalis via its supracommissural component. In the dog, such a connection has never been shown.

Cytologically, the suprachiasmatic nucleus is built similarly as the periventricular area. Cells are small, oval to elongated. Their diameters fluctuate within limits of 5 and 7 μ. They are poorly stainable with thionine.

No data on the physiology of this nucleus are available in the literature.

The anterolateral nucleus of the hypothalamus

(Figs. 2, 3, 6, 9 and 11, n.lat.a.)

Topography. The lateral nucleus is situated on the lateral side over the entire length of the hypothalamus. Laterally to the anterior part of the hypothalamus, the anterior part of the lateral nucleus is located. Over its entire trace, the lateral nucleus has a complex system of connections because this is an area, passed by many nerve tracts.

The lateral nucleus may be divided into two areas : the first, situated on the lateral side of the anterior part of the hypothalamus, constitutes the anterior part of the lateral nucleus and the second, lateral to the intermediate part of the hypothalamus constitutes the posterior part of the lateral nucleus.

Fig. 11. Myeloarchitectonics of the anterolateral nucleus of the hypothalamus. Weigert stain

The anterior part of the lateral nucleus in the dog borders, posteriorly, on the lateral preoptic area and, anteriorly, reaches the intermediate part of the lateral nucleus. In the anterior part of the hypothalamus, medially to the lateral nucleus, the anterior nucleus of the dorsal hypothalamus is situated, while the anteroventral nucleus is situated in the ventromedial part. Laterally, the lateral nucleus is limited in this place by the descending fibers of the stria medullaris of the thalamus. On the dorsal side, the interstitial nucleus of the stria terminalis is situated on a small section in the anterior part, while the anterior supraoptic nucleus is located ventrally to the anterolateral nucleus.

The lateral nucleus of the hypothalamus has been shown in all mammals.

Architectonics. In frontal sections, the anterolateral nucleus is triangular in shape, the base of this triangle being 2.5 mm long and the height coming to about 2 mm.

The medial forebrain bundle is the principal and the strongest fiber system of the lateral nucleus. Its fibers run, as a scattered system, through the entire area of the lateral nucleus. The fibers of the medial forebrain bundle enter the lateral nucleus from the frontal side. They are well-myelinated and their thickness is from 2.5 to 4 μ. The medial forebrain bundle is a complex pathway, consisting of fibers from the lower portions of the olfactory regions, from the septum and from certain areas of the neocortex. They terminate mostly in the intermediate and mammillary parts of the hypothalamus.

The fibers, coming from the interstitial nucleus of the stria terminalis, situated dorsally to the lateral nucleus, are another fiber system, less numerous than the former, that runs through the anterolateral nucleus. These fibers run dorsoventrally. This fiber system enters the lateral nucleus from the dorsal and dorsomedial side. These are long fibers, with a diameter coming to 3 μ, scattered and forming no bundles.

Somewhat further posteriorly, the anterolateral nucleus is joined, also from the dorsal side, by fibers from the stria medullaris of the thalamus. Similarly to the former system, they are scattered all over the anterolateral nucleus. Coming out of the stria medullaris of the thalamus, the fibers of this system run ventrally and enter the lateral nucleus from the dorsal side. Hereafter, a part of them disappear on the territory of the lateral nucleus and the rest of them turn anteriorly, getting eventually outside the lateral nucleus and reaching the olfactory regions. This is the olfacto-habenular tract.

In the anterior part, the lateral nucleus of the hypothalamus is also passed by mediolaterally running fibers. They start in the anterodorsal nucleus, pass through the lateral nucleus and terminate in the internal capsule. On account of a considerable concentration of fibers in the internal capsule, further tracing of these fibers is impossible.

The anterior supraoptic nucleus is another area, having connections with the anterolateral nucleus. The areas, occupied by these two nuclei border directly each on the other and the system, connecting them, occupies the entire border area. The fibers of this system start in the lateral nucleus and are directed dorsoventrally. They terminate among the cells of the anterior supraoptic nucleus. This well-visible system contains well-myelinated fibers about 2.5 μ in diameter.

The hypothalamic-tegmental tract starts between the anterior and intermediate parts of the lateral nucleus. This trace starts up as a compact system of well-myelinated fibers to 5 μ in diameter. They come out of

Gurdjian 1927 rat Rioch 1929, 1931 dog	Kuhlenbeck 1954 man	Westwood 1962 ferret	Bleier 1961 cat	Crosby and Humphrey 1962 man	Diepen 1962 man	Śmiałowski dog
area anterior hypothalami	N. anterior hypothalami	area anterior	area anterior hypothalami	area anterior hypothalami	n. anterior hypothalami	n. ant. dorsalis
xxx	xxx	xxx	xxx	xxx	xxx	n. ant. ventralis
n. filiformis	n. paraventricularis	n. paraventricularis	n. paraventricularis	n. paraventricularis	n. paraventricularis	n. paraventricularis
xxx	massa intermedia	xxx	xxx	xxx	intermediäre Zellnester	massa intermedia
n. ovoideus	n. suprachiasmaticus	n. suprachiasmaticus	n. suprachiasmaticus	xxx	n. suprachiasmaticus	n. suprachiasmaticus
n. tangentialis	n. supraopticus	n. supraopticus, rostral div.	n. supraopticus anterior comp.	n. supraopticus	n. supraopticus	n. supraopticus ant.
n. periventricularis hypothalami anterioris	xxx	n. periventricularis ant.	n. periventricularis ant.	periventricular gray	xxx	area periventricularis
n. lateralis hypothalami	n. lateralis hypothalami	xxx	area lat. hypoth., ant. div.	area lat. hypothalami	xxx	n. lateralis ant.

the lateral nucleus and run mediocaudally. Since this tract is situated practically in the intermediate part of the hypothalamus, it has been omitted from the present section.

According to E s c o l a r's (1954), the lateral nucleus is also joined by a bundle of fibers, coming from the amygdaloid complex. E s c o l a r (1954) found that these fibers start up in the Brockhaus supraamygdaloid nucleus which, according to the English terminology (used at these Laboratories), corresponds to the central and medial nucleus of the amygdaloid complex. This connection runs through the substantia innominata.

As an area through which many fiber systems pass, the lateral nucleus contains a small number of cells. The cells of this area are small and, with the Nissl method, are poorly stainable. In the anterolateral nucleus, triangular (diameter, about 12 μ) and elongated, rectangular (dimensions, 17 × 7 μ) cells occur.

SUMMARY

The anterior part of the hypothalamus in the dog is situated between the preoptic area (anteriorly) and the intermediate (tuberal) area (posteriorly). The posterior boundary is determined by the fibers of the dorsal supraoptic commissure which belongs in fact to the intermediate part. Using the myeloarchitectonic criterion of division, the following parts have been differentiated in the anterior part of the hypothalamus: the anterodorsal nucleus, the anteroventral nucleus, the suprachiasmatic nucleus, the anterior supraoptic nucleus, the paraventricular nucleus, massa intermedia, the periventricular area and the anterolateral nucleus. During a detailed, profound analysis, the fiber pattern within particular nuclei, as well as their connections with adjacent structures has been considered.

It was for the first time that the anteroventral nucleus of the hypothalamus has been differentiated and described. Also the massa intermedia of the hypothalamus belongs to the hypothalamic areas which have been infrequently described in the literature.

ABBREVIATIONS

A.d.,	dorsal area	c.so.d.,	dorsal supraoptic commissure (Ganseri)
a.d.c.,	dorsocaudal area	c.so.v.,	ventral supraoptic commissure
a.p.,	periventricular area	f.,	fornix
a.p.opt.,	preoptic area	m.f.b.,	medial forebrain bundle
c.a.,	anterior commissure	m.i.,	massa intermedia
cho.,	optic chiasm	n.a.d.,	anterior dorsal nucleus
c.m.,	mammillary bodies		

n.a.v.,	anterior ventral nucleus
n.i.st.,	interstitial nucleus of the stria terminalis
n.lat.a.,	anterolateral nucleus
p.a.,	hypothalamus anterior
p.i.,	intermediate part
p.v.,	paraventricular nucleus
r.so.,	recessus supraopticus
s.,	septum
sch.,	suprachiasmatic nucleus
s.i.,	substantia innominata (Reicherti)
so.a.,	anterior supraoptic nucleus
s.m.t.,	stria medullaris of the thalamus
s.t.,	stria terminalis
tho.,	thalamus
t.o.,	optic tract
tr.pv.h.,	paraventricular-hypophyseal tract
tr.so.h.,	supraoptic-hypophyseal tract
v.,	blood vessels
vm.,	ventromedial nucleus
v III,	ventricle III

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EXTREME CAPSULE IN THE DOG : MYELOARCHITECTONICS

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The extreme capsule in the brain of the dog is a thin layer of white substance, situated between the claustrum and the neocortex. The aim of this paper is to determine the range of the extreme capsule, to investigate its structure and to show its connections with the adjoining areas of the brain.

Continuous microscopic serial sections of seven dog brains were used. Three brains were stained according to the Weigert-Wolters method and cut frontally, horizontally and sagittally. The preparations were 50 μ thick. Four brains, stained according to the Klüver method, were cut frontally and sagittally into 20 μ thick sections.

The extreme capsule of the dog consists of fibers and cells. Its shape is correlated with that of the cerebral cortex, adjoining it and, consequently, variable since it corresponds with the arrangement of fissures and gyri of the cerebral cortex. In oral parts of the brain, the extreme capsule is shaped like a slightly deformed 3 and, in the left hemisphere, like a regular 3 (in the right hemisphere—an inverted 3). Further on, in the frontal section, it takes the form of an arc with its convexity turned towards the medial part of the brain. In the posterior part of the brain, the extreme capsule is strongly elongated and resembles a scythe. As compared with the external and internal, the extreme capsule is built of loosely disposed fibers with cells, scattered between them. It is also in the extreme capsule that more cells may be observed than in the external capsule and, moreover, they are more differentiated. Usually, they are spindle-like in shape, sometimes, pyramidal and more or less oval. The fibers

form a fine network in whose meshes cells are disposed. On the side of the claustrum, the fusiform cells are wedged between the fibers of the extreme capsule. The number of these cells is greater than that of cells, entering on the side of the cerebral cortex. Cells which, on the one hand, enter from the side of the claustrum and, on the other, from the side of the cerebral cortex, are met with over the entire length of the extreme capsule.

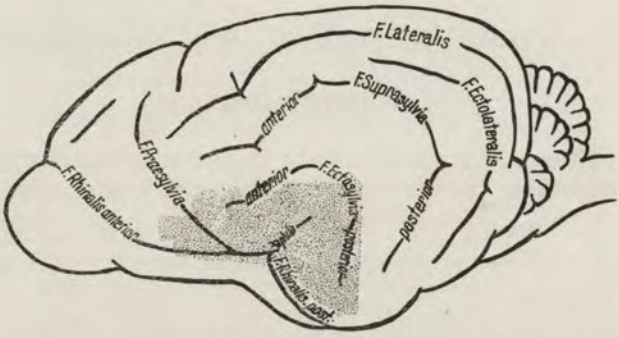

Fig. 1. Projection of the extreme capsule on the lateral surface of the dog brain

The range of the extreme capsule is more or less identical as that of the claustrum to whose external side this capsule adheres. A projection of the extreme capsule on fissures and gyri of the lateral surface of the brain dog is depicted in Fig. 1. This projection is similar to a formless figure, something that resembles two trapeziums, touching each other with their bases with the upper trapezium being about three times the size of the lower one. The projection of the upper margin of the extreme capsule reaches the central section of the ectosylvian fissure. It runs in the form of a straight line, parallel to the rhinal fissure, reaches the ectosylvian fissure, intersects it and, as a broken line, descends to the presylvian fissure. Further on, the projection of the extreme capsule intersects the presylvian fissure, runs across the orbital gyrus and reaches the rhinal fissure. From this place, the lower margin of the extreme capsule runs parallel to and somewhat below the anterior rhinal fissure towards the posterior part of the brain. Caudally of the sylvian fissure, the margin descends along the posterior rhinal fissure. Still further caudally, the projection of the extreme fissure runs parallel to the posterior ectosylvian fissure. The extreme capsule is, therefore, situated below the following gyri : below a small section of the sylvian gyrus, below the upper part of the posterior composite gyrus, below the upper part of the piriform gyrus and next, below the lower part of the orbital gyrus and below the poste-

rior part of the anterior composite gyrus. It forms a sort of a wedge between the arms of the presylvian and anterior rhinal fissures (T e n e r o w i c z 1960).

The extreme capsule is variable in shape and thickness :

Anteroposterior distances :	3.2 cm	3.7 cm	4.1 cm	4.6 cm
Dorsal part	220μ	900μ	470μ	560μ
1/3 of the width	300μ	620μ	930μ	420μ
2/3 of the width	1,100μ	520μ	900μ	340μ
Ventral part	330μ	370μ	600μ	390μ
Mean :	480μ	602μ	725μ	428μ

The table, shown above, is based on several measurements of the thickness of the extreme capsule, taken on sections that have been stained by the Weigert-Wolters method. The mean thickness fluctuates within limits from 500 to 600 μ.

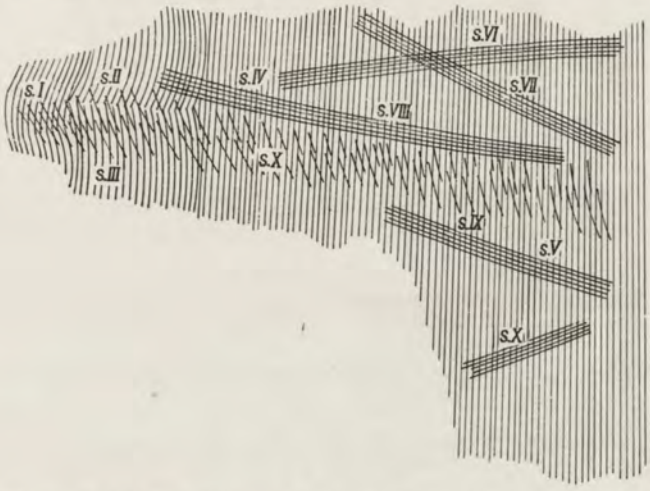

Fig. 2. Diagram of fiber systems running through the extreme capsule

The following myeloarchitectonic areas, determined by K r e i n e r (1964), are included in the projection of the extreme capsule on the lateral surface of the brain : posteriorly, a part of the ORB II area and the entire ORB III area. In the central part, the projection of the extreme capsule covers almost entire CE II and a part of the CE I areas, the entire SJ area, a small section of the allocortex, almost entire S and entire EP II areas. In the caudal part, the projection of the extreme capsule takes in small parts of the CPL II and CPM I, as well as a part of the small CPM II areas.

The extreme capsule consists of fibers medium in thickness, distinctly visible and, in the anterior and central parts of the brain, abundant. In the posterior parts of the brain where the extreme capsule takes the shape of a scythe, its fibers become indistinct in their central sector. They disappear either in the claustrum or in the allocortex but, in sections stained by the Weigert-Wolters method, this cannot be identified. Crosby et

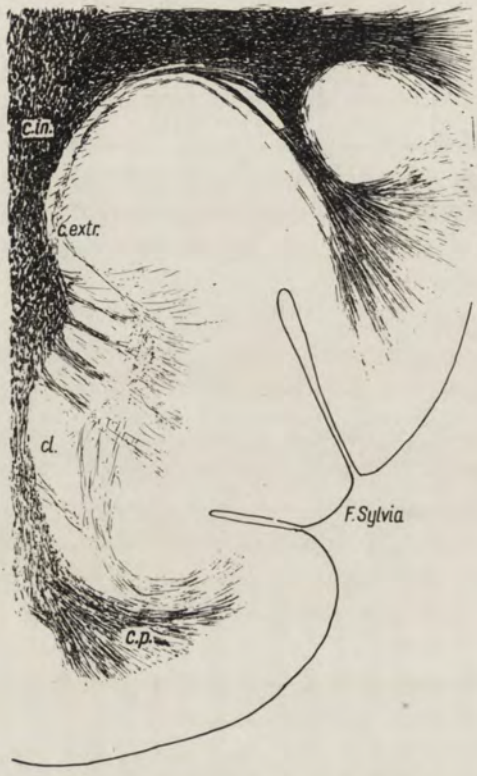

Fig. 3. Frontal section through the extreme capsule in the dog brain. Semischematic, Weigert-Wolters

al. (1962) maintains that, in mammals, on certain levels, the claustrum directly contacts the neocortex. It results from our observations, that, over its entire length, the extreme capsule separates the claustrum from the cerebral cortex.

Basically, the extreme capsule consists of five fiber systems, similar to each other in structure and arrangement but connecting different regions (Fig. 2). In the oral part of the brain, fibers, making up the bulk of

the extreme capsule form system I which connects the orbital gyrus with the piriform cortex. Within the piriform cortex, these fibers constitute a marginal part of the cortical radiation from which they run to the orbital gyrus, myeloarchitectonic area ORB III, where a part of them gets between the radial fibers, coming out of this gyrus. Another part runs further, encircles, in the arcuate manner, the radiation, coming out of the orbital gyrus and gets between the fibers of the internal capsule. As they run towards the posterior part of the brain, the fibers, forming the bulk of the extreme capsule, become disposed in the shape of the figure 3 in the left and the inverted 3 in the right hemisphere (Fig. 3). Viewed in the frontal section, the extreme capsule consists, in this place, of two fiber systems.

A system of long fibers, medium in thickness, that is, system II runs arcuately from the white substance of the anterior sylvian gyrus, where it makes up a part of the radiation of this gyrus, to the cortex of the sylvian fissure and to the myeloarchitectonic area ORB III where it also intermingles with the cortical radiation. A part of these fibers separates from this bundle, deflects towards the medial side of the brain, passes through the claustrum and gets between the fibers of the internal capsule in its central part.

The third system of fibers (system III) within the extreme capsule is formed by fibers getting out of the allocortex. Inside of the allocortex these fibers are disposed fanwise. A part of this fan consists of the fibers of the cortical radiation of the piriform cortex. Others diagonally pierce this radiation and enter deeper cortical parts. In the dorsal part, a part of the fibers of this system runs to the internal capsule and, another part, to the cortex of the sylvian fissure and to the area ORB III. In the dorsal part, many fibers, medium in thickness, which get out of the myeloarchitectonic area SJ (K r e i n e r 1964), break through between the fibers of system II. They run at an acute angle, are not grouped in bundles, break through between the fibers of the extreme capsule and claustrum and enter the internal capsule in its dorsal and central part. The ventral part of this system is pierced by the cortical radiation of the myeloarchitectonic area ORB III.

More posteriorly, the extreme capsule takes the shape of an arc with its convexity turned to the medial side of the brain. The fibers of system IV within this region, get out of the white substance of the anterior ectosylvian gyrus. They deflect ventrally from the radiation of this gyrus and run in the form of a loose band to the piriform cortex. In the piriform cortex, they reach deep inside the cortical radiation where they branch

off in the fanlike manner. Against the background of the system of fibers, making up the bulk of the extreme capsule, different systems are formed which we shall deal with below.

Finally, system V appears in the parts of the brain where the extreme capsule extends and, in cross section, takes the scythe-like shape. The fibers running in this region connect the posterior ectosylvian gyrus with the piriform cortex. Within the posterior ectosylvian gyrus, they deflect from the ventral part of the radiation of this gyrus. In the piriform cortex, the fibers of the extreme capsule enter myeloarchitectonic areas, determined by Kreiner (1964) as the areas CPM I and CPM II. Other systems which intersect this system will be dealt with below. In general, one may conclude that a considerable part of the extreme capsule connects insular areas and those, considered to be acoustic areas, with the allocortex.

Fibers, forming systems, described above, considerably differ in thickness. Fibers 2.5, 1.5 and 1.0 μ thick may be observed in sections stained by the Weigert-Wolters method. There are also much thinner ones. All fibers are arranged loosely, do not form bundles and fill out the entire area of the extreme capsule. As the arc, drawn by the extreme capsule, shifts downwards, the number of these fibers increases.

Regardless of the above division but considering the pattern of fibers, we may divide the extreme capsule into the following three parts : dorsal, central and ventral.

In the dorsal part, there are many fiber systems which connect this part either with the cerebral cortex or with the internal capsule. These systems consist of fibers different in thickness, loosely disposed and forming no bundles. They either intersect each other or run parallel.

In the central part, fibers that pass through the extreme capsule mostly make up the radial fibers of the cortex of sylvian fissure. It is also in this system that fibers are medium in thickness, loose and forming no bundles. In the ventral part, only few connections with the external capsule and with the cerebral cortex may be observed. In this part, systems consist of thinner and less visible fibers but they continue to be loosely arranged.

In the central part of the brain, the extreme capsule, viewed in the frontal section, takes the shape of an arc, deflected from the medial part of the brain. Fibers that make up its bulk have been described above. System VI, consisting of the fibers medium in size, loosely disposed and forming no bundles, may be seen against the background of the dorsal part of the extreme capsule. This fiber system gets out from the white substance of the anterior sylvian gyrus, obliquely breaking through the

radiation of this gyrus. Hereafter, it branches off dorsomedially from the white substance and, over a short section, intermingles with fibers that make up the bulk of the extreme capsule. After leaving the extreme capsule, this fiber system passes through the claustrum and, in the dorsal part of the internal capsule, enters between its fibers.

The next system, that is, system VII is very extensive. A part of its fibers constitutes the radiation of the myeloarchitectonic area SJ and, another part, the radiation of the area FS (Kreiner 1964). The fibers of this system come out of the white substance of the anterior sylvian gyrus, obliquely piercing the radiation. This system intersects the fibers of the former system. A part of the fibers of this system intersects the white substance of the anterior sylvian gyrus and, in the cortical part of the brain, directly enters the myeloarchitectonic area SJ. Shifting towards the medial part of the brain, the fibers of this system slightly change their trace. After passing through the white substance of the anterior sylvian gyrus, these fibers get between the fibers of the extreme capsule and hereafter, they reach the cerebral cortex. The next part of the fibers of this system is situated still closer to the internal capsule. These fibers intersect the white substance of the anterior sylvian gyrus, the claustrum and, through the extreme capsule, run to the sylvian fissure (area FS). The fibers of this system, occurring in abundance, are medium in thickness and loosely disposed.

Below these systems, system VIII, consisting of fibers which descend at an acute angle and, passing through the claustrum and internal capsule, probably enter the putamen, divides itself from the dorsal part of the extreme capsule. System VIII contains many fibers medium in thickness.

Fiber system IX intersects the former. It comes out of the dorsal part of the claustrum and its fibers describe an arc, deviating from the cortical parts of the brain. This system goes through the extreme capsule and enters the cortex of the sylvian fissure. It consists of a small number of fibers which are also medium in thickness.

Fibers of system X, coming out of the myeloarchitectonic area ORB III in the caudal section of the orbital gyrus, run parallel to the extreme capsule more or less half-way its length. These fibers perpendicularly intersect the extreme capsule in the plane of the claustrum and enter the internal capsule. Thus located bundle of fibers, constituting the cortical radiation of the area ORB III, is visible in the section, stained by the Weigert-Wolters method. In the sections, stained by the Klüver method, the fibers with this trace may be seen almost over the entire length of the extreme capsule. These fibers intersect with a dorsoventrally running system. In the ventral part of the extreme capsule, they are less

abundant and finer. In this region, the number of systems, passing through the extreme capsule is smaller than those in the dorsal and medial parts. Only fine systems, containing few fibers, run through this area.

Below system X, discussed above, a system of fine, poorly visible fibers, detach from the extreme capsule. The fibers of this system are loosely disposed and, at an acute angle, they descend, entering between the fibers of the external capsule. It is worth while mentioning that a fine

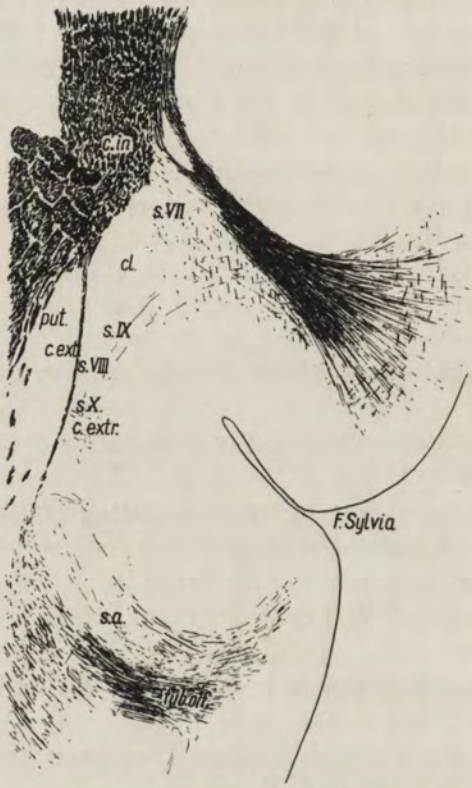

Fig. 4. Frontal section through the extreme capsule in the dog brain, 0.8 cm distant from section 2. Semischematic Weigert-Wolters

fiber bundle comes out of the internal capsule, passes in the ventral part, through the claustrum and enters between the fibers of the extreme capsule. They run loosely disposed and form no bundles. In the caudal part of the brain (Fig. 4 and 5), the extreme capsule begins to extend and takes a scythe-like shape. Fibers, that form its bulk, make up system V. They connect the posterior ectosylvian gyrus with the cortex of the piriform lobe and with myeloarchitectonic areas CPM I and CPM II. Only

the fibers located in the dorsal part are distinctly visible. In the medial part they occur in ever lesser number and are very poorly visible. Once more, they become better visible in the ventral part. In the ventral part, the fibers of the extreme capsule run very near the internal capsule. In this section, single fibers deflect from the extreme capsule and enter

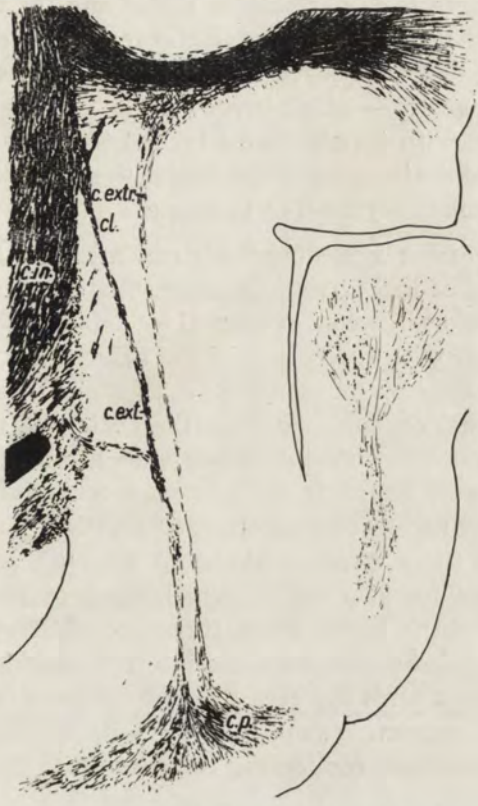

Fig. 5. Frontal section through the extreme capsule in the dog brain, 0.5 cm distant from the section shown in Fig. 4. Semischematic, Weigert--Wolters

between the fibers of the internal capsule. Fiber systems, determined as systems VI and VII are visible against the background of fibers which constitute the bulk of the extreme capsule in its dorsal part.

Finally, fiber system X, accompanying the extreme capsule should also be mentioned. This is a fiber system which connects the orbital gyrus with the olfactory tubercle. This system accompanies the extreme capsule over a very short section and consists of fibers medium in thickness, running loosely disposed and forming no bundles (S y c h 1960).

SUMMARY

The extreme capsule in the brain of the dog is a thin layer of white substance, situated between the claustrum and the cortex. It consists of fibers which form a network with cells disposed in its meshes.

The extreme capsule is variable in shape and, in the frontal section, in the oral parts of brain, it appears in the form of a deformed " 3 " and, somewhat further, takes the shape of a regular " 3 " in the left hemisphere (in the right hemisphere — of an inverted " 3 "). Next, it may be seen in the form of an arc with its convexity turned towards the medial part of the brain. In the posterior part of the brain, the extreme capsule strongly elongates and becomes scythe-like in shape.

Five successive fiber systems which run more or less dorsoventrally constitute the bulk of the extreme capsule. System I connects the orbital gyrus with the piriform cortex, system II — connects the white substance of the sylvian gyrus with the cortex of the sylvian fissure and, moreover, with the myeloarchitectonic area ORB III. System III connects the allocortex with the internal capsule and with the cortex of the sylvian fissure. System IV connects the anterior ectosylvian gyrus with the allocortex and, finally, system V connects the posterior ectosylvian gyrus with the piriform cortex and myeloarchitectonic areas CPM I and CPM II. Against the background of the systems, making up the bulk of the extreme capsule, other systems are also visible which connect the former with the adjoining regions of the brain. Thus, there are fiber systems which connect the gyri, described above, with the internal capsule, with the cortical parts of the brain and with the area SJ. The extreme capsule is also crossed by the system, connecting the claustrum with the cortex of the sylvian fissure and by the system, connecting the area ORB III with the external capsule.

Small, fine fiber systems run through the extreme capsule and connect the internal capsule with the cortical part of the brain. The extreme capsule is also a place from which fibers come out running to the internal and external capsules.

ABBREVIATIONS

c. ext.,	external capsule	F. Sylvia,	sylvian fissure
c. extr.,	extreme capsule	put.,	putamen
c. in.,	internal capsule	s. a.,	accompanying system
cl.,	claustrum	tub. olf.,	olfactory tubercle
c. p.,	piriform cortex	s. I, I, III ...	system I, II, III, etc.

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MYELOARCHITECTONICS OF STRIA TERMINALIS IN THE DOG

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The aim of this paper is to investigate the structure, route and terminations of stria terminalis in the dog.

The work has been carried out on the basis of series of frontal sections of the dog brain stained by the Weigert method, as well as series of frontal sections, stained alternately by the Klüver-Barrera method and the Schultze silver method. The results have been checked on the basis of sagittal and horizontal sections of the dog brain, stained by the Weigert, Klüver-Barrera and Schultze methods. A total of six series have been used for this work.

Gross anatomy

The stria terminalis is a bundle of fibers which run from the anteromediodorsal portions of the amygdaloid complex to the anterior commissure region. It at first runs in the vicinity of the dorsal parts of the optic tract and, after encircling the posterior margins of the internal capsule, it runs between the thalamus and the internal capsule. The stria terminalis is not uniform. It consists of three bundles, the fibers of which diverge in different directions at its both ends. They differ from each other in the density of the fiber disposition, in the fiber thickness and in the reactivity to the stain.

The supracommissural component is the largest bundle of the stria terminalis. It consists of thin and palely staining fibers. It makes up a connection of the hippocampal gyri (Miodoński 1965), as well as of the basal, medial, cortical and central nuclei of the amygdaloid complex with the medial praeoptic gray (Young 1936).

The commissural component connects the nucleus of the lateral olfac-

tory tract of one hemisphere with the corresponding nucleus of the contrateral hemisphere. It runs from one to the other hemisphere, joining the bundles of the anterior commissure.

The stria medullaris component is the only component of the stria terminalis, having no connections with the amygdaloid complex (Miodoński 1965). Its fibers appear at the level of the posterior boundary of the olfactory tubercle among the fibers of the medial forebrain bundle. After passing posteriorly through the substantia innominata to the region, adhering to the lateral boundary of the supraoptic nucleus, these fibers form a compact bundle running over the dorsolateral surface of the optic tract posteriorly, dorsally and laterally towards the vicinity of the remaining bundles of the stria terminalis. The stria medullaris component of the stria terminalis, together with the remaining bundles, reaches the vicinity of the medial parts of the anterior commissure where they join the stria medullaris.

The bundles of the stria terminalis are accompanied by the cells of the interstitial nucleus of the stria terminalis. This nucleus is best-developed in the neighborhood of the anterior commissure but its cells are scattered along the fibers of the stria terminalis, both anteriorly and caudally. In the frontal part, they reach the preoptic area and the anterior parts of the hypothalamus.

Myeloarchitectonics

The fibers of the stria terminalis are poorly stainable and, therefore, they are well visible only in compact bundles. Only the fibers of the stria medullaris component are strongly stainable.

A considerable part of the fibers of the supracommissural component takes its origin in the hippocampal gyrus. In the form of a compact bundle they run anterodorsolaterally within the wall of the inferior horn of the lateral ventricle. As it runs upwards, this bundle is joined by fibers coming from the amygdaloid complex. They form a flat lamina, situated between the basal and medial nuclei of the amygdaloid complex. This lamina is composed of fibers which, within the basal nucleus, form a medioörodorsally running system, inside the medial nucleus, run lateroörodorsally and, in the cortical nucleus, anteromediodorsally. Fibers, coming from the cortical nucleus, form a loose layer on the boundary between the nucleus and the ventral part of the basal nucleus (Figs. 3 and 4, cf. Maksymowicz 1963, Miodoński 1965). This boundary, approaching the lower parts of the lamina of fibers between the basal and medial nucleus, turns upwards. In the place where the supracommissural com-

ponent of the stria terminalis borders on the central nucleus of the amygdaloid complex it is joined by fibers which run caudomediodorsally and which come from the same nucleus (Figs. 2, 3 and 4).

The fibers of the supracommissural component of the stria terminalis, separating from the amygdaloid complex are arched upwards above the optic tract where they meet the remaining two bundles. The supracommissural component is conspicuous, among the bundles of the stria terminalis, in its size and stainability. It is the largest and palest bundle. As

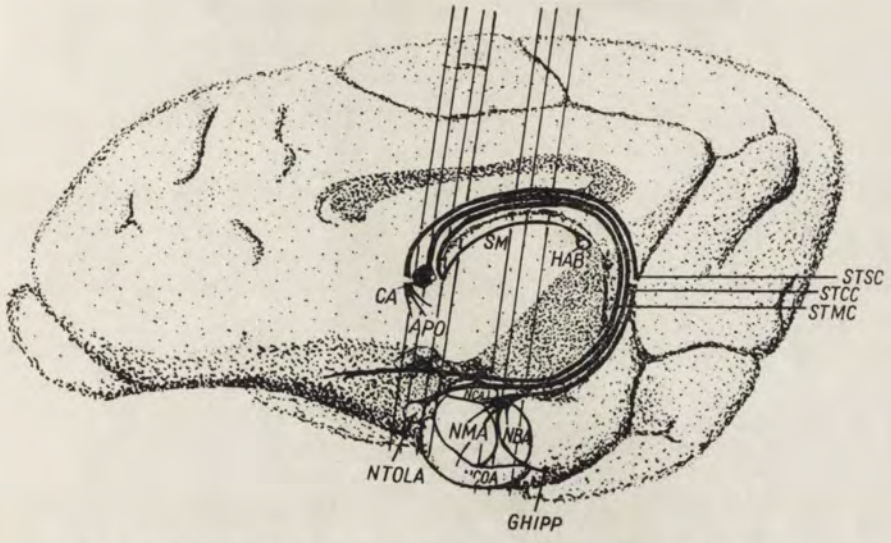

Fig. 1. Distribution of the stria terminalis in the dog's brain

it encircles the posterior margin of the internal capsule, it takes the ventral, caudal and, finally, dorsal position in relation to the remaining bundles and, therefore, it describes a larger arc than they do (Figs. 1 and 2).

As it approaches the medial part of the anterior commissure, the supracommissural component of the stria terminalis loosens and deviates anteriorly from the remaining parts (Figs. 1 and 7). Some loose fibers, coming from the supracommissural component deflect ventromedially and reach the anterior parts of the hypothalamus. The remaining fibers, pass over the anterior commissure, descend in the region of the anterior boundary of its medial part, turn downwards and scatter in the medial preoptic area (medial preoptic gray of Young, 1936), forming a system which runs medioventrally.

The commissural component consists of fibers which, within the nucleus of the lateral olfactory tract run ventrodorsally and, after leaving this nucleus, caudodorsomedially, concentrating into a compact bundle (Figs. 5 and 6). After passing through the mediodorsal parts of the medial nucleus of the amygdaloid complex, the commissural component of

Fig. 2. Frontal section of the dog's brain. Weigert's method

the stria terminalis reaches a point above the optic tract where it is situated over the supracommissural component. Encircling the internal capsule, it runs inside an arc, described by the supracommissural component.

As it approaches the level of the anterior commissure, the commissural component deviates medially and, after disintegrating into a few small

bundles (Fig. 7), it joins the caudal parts of its medial section from which, however, it differs distinctly over its entire trace up to the contralateral hemisphere. In the contralateral hemisphere, the fibers of the commissural component of the stria terminalis, after covering a road similar to that described above, reach the nucleus of the lateral olfactory tract.

Fig. 3. Frontal section of the dog's brain. Weigert's method

The stria medullaris component is the only component of the stria terminalis having no connection with the amygdaloid complex. The fibers of this component appear among the fibers of the medial forebrain bundle at the level of the posterior boundary of the olfactory tubercle and, through the substantia innominata, run posteriorly, forming within the latter a laterocaudally stretching system. Between the lateral boundary

of the supraoptic nucleus and the medial boundary of the nucleus of the lateral olfactory tract (Figs. 6 and 7) these fibers form a loose bundle which turns laterocaudodorsally, parallel to the optic tract and very near its laterodorsal surface. A small distance from the surface of the optic tract and a considerable degree of similarity between the fibers of both

Fig. 4. Frontal section of the dog's brain. Weighert's method

these systems present difficulties in perceiving the stria medullaris component of the stria terminalis over a fairly long stretch (Figs. 2, 3 and 4).

After reaching the region of the amygdaloid complex, the stria medullaris component takes a medial position in relation to the remaining two bundles of the stria terminalis and, together with them, encircles the internal capsule. As it approaches the level of the medial part of the

anterior commissure, the stria medullaris component deviates more medially and ventrally and, after joining the fibers of the stria medullaris, it turns upwards and intermingles with these fibers. No fibers, coming from the stria terminalis, may be distinguished from other ones within the stria medullaris (Fig. 6).

The interstitial nucleus of the stria terminalis is a concentration of cells, accompanying the fibers of the stria terminalis. The largest amount of these cells occur in the vicinity of the anterior commissure. However,

Fig. 5. Frontal section of the dog's brain. Weigert's method

they are disposed anteriorly and posteriorly along the fibers of the stria terminalis. Anteriorly, they reach the preoptic area and the anterior parts of the hypothalamus.

The interstitial nucleus of the stria terminalis (Figs. 5, 6, 7 and 8) is, as seen in cross sections, a triangular nucleus, bordering laterodorsally on

the caudate nucleus, lateroventrally — on the internal capsule, medially adhering to the dorsal parts of the hypothalamus and, dorsomedially, bordering on the free space of the lateral ventricle.

Longitudinally, two portions may be differentiated in the nucleus. Both are composed of polymorphous cells which, however, are different in size.

Fig. 6. Frontal section of the dog's brain. Weigert's method

The magnocellular part is disposed dorsomedially and its cells surround the supracommissural component of the stria terminalis. They accompany the fibers as far as the preoptic area.

The parvocellular part, situated lateroventrally, is associated with the commissural component of the stria terminalis. Its cells, together with

fibers, descend to the caudal boundary of the medial section of the anterior commissure and, in this place, intermingle with the cells of the anterior part of the hypothalamus.

The stria medullaris component of the stria terminalis is situated outside the area of the interstitial nucleus of the stria terminalis (Figs. 3, 4,

Fig. 7. Frontal section of the dog's brain. Weigert's method

5 and 6). It runs along the boundary between the nucleus and the thalamus within the wall of the lateral ventricle.

Thin, poorly stainable fibers are visible among those of both parts of the interstitial nucleus of the stria terminalis. Their trace is parallel to that of fibers which form compact bundles. Posteriorly, they reach the central nucleus of the amygdaloid complex. Those, running anteriorly, terminate in the medial preoptic area and in the anterior parts of the hypothalamus.

Fig. 8. Frontal section of the dog's brain. Weigert's method

DISCUSSION

The stria terminalis in the dog consists of three parts, all of them together encircling the internal capsule but, both in the region of the amygdaloid complex and in the vicinity of the anterior commissure, diverging and running in different directions.

The supracommissural component of the stria terminalis has previously been studied in different species (Craigie 1925, Gurdjian 1928, Humphrey 1936, Young 1936, Fox 1940, 1943).

In the dog, the supracommissural component of the stria terminalis connects the medial preoptic area and the anterior parts of the hypothalamus with the hippocampal gyrus and with the basal, medial, cortical and central nuclei of the amygdaloid complex.

The commissural component of the stria terminalis makes up a connection between the nuclei of the lateral olfactory tract of both hemispheres. It passes from one to the other hemisphere together with the fibers

of the anterior commissure. In other species, its route is similar (Craigie 1925, Gurdjian 1928, Humphrey 1936, Young 1936, Fox 1940, 1943).

The group of nuclei of the amygdaloid complex, connected with the stria terminalis (the basal, medial, cortical and central nuclei and the nucleus of the lateral olfactory tract of the corpus amygdaloideum) should be opposed to the nuclei which are not associated with the stria. These are the lateral and putaminal nuclei of the amygdaloid complex (Maksymowicz 1963, Miodoński 1965).

The stria medullaris component of the stria terminalis in the dog is not connected with the amygdaloid complex. Its fibers constitute a branching of the medial forebrain bundle. Running posteriorly, they considerably approach the lateral surface of the optic tract and almost disappear against its background. Thus, they pass by the amygdaloid complex. Like the remaining two bundles, after detaching from the surface of the optic tract, they descend around the internal capsule. After reaching the region of the anterior commissure, the stria medullaris component joins the anteroventral part of the stria medullaris. This area is strongly myelinated and hence the great divergence of opinions in the literature, dealing with this problem.

According to Humphrey (1936), in the bat, there exists a habenular component of the stria terminalis. It might connect the posterior parts of the amygdaloid complex and areas, adjoining the hippocampus through the medium of the stria medullaris with the habenula. Fukuschi (1952) ascertains that the habenular component comes from the cortical nucleus and from the central nucleus of the amygdaloid complex, as well as from the periamygdaloid cortex. Fox (1943), Adey and Meyer (1952), Lammers and Magnus (1955) do not at all find the stria medullaris component of the stria terminalis in the experimental material. It was only Bürgi (1954) who, after a unilateral lesion of the stria medullaris, has observed degenerated fibers passing through the habenular commissure and running to the contralateral stria medullaris, to the stria terminalis and to the amygdaloid complex. The fibers, connecting the interstitial nucleus of the stria terminalis with the anterior part of the hypothalamus correspond with a part which has been called by Young (1936) an interstitiohypothalamic tract (amygdalo-hypothalamic tract).

The loose fibers, detaching from the supracommissural component of the stria terminalis and running downwards, posteriorly to the medial part of the anterior commissure, to the anterior parts of the hypothalamus, might correspond with the part, described by the name of the preoptic component (Fox 1940, 1943, Young 1936).

SUMMARY

The stria terminalis is a tripartite bundle, running from the amygdaloid complex to the anterior commissure region. The three components of the stria terminalis differ from each other in both the structure and terminations : (1) the supracommissural component, the largest of them and composed of fine fibers, connects the hippocampal gyrus and the amygdaloid complex (the basal, medial, cortical and central nuclei) with the medial preoptic area and with the anterior parts of the hypothalamus ; (2) the commissural component connects the nuclei of the lateral olfactory tracts of both hemispheres and (3) the stria medullaris component associates, through the stria medullaris, the olfactory regions with the habenula.

The interstitial nucleus of the stria terminalis is a concentration of cells, situated along the bundles of the stria terminalis. Fibers, disposed among them, run parallel to those, crowded in compact bundles, and terminate in the anterior parts of the hypothalamus and, posteriorly, in the central nucleus of the amygdaloid complex.

ABBREVIATIONS

APO, preoptic area
CA, anterior commissure
CE, external capsule
CHO, optic chiasm
CYPR, piriform cortex
HAB, habenula
HIPP, hippocampus
INST, interstitial nucleus of the stria terminalis
NBA, basal nucleus of the amygdaloid complex
NBDA, dorsal part of the basal nucleus
NBVA, ventral part of the basal nucleus
NCA, central nucleus of the amygdaloid complex
NCD, caudate nucleus
NCOA, cortical nucleus of the amygdaloid complex
NLA, lateral nucleus of the amygdaloid complex
NMA, medial nucleus of the amygdaloid complex
NO, optic nerve,
NPA, putaminal nucleus of the amygdaloid complex
NSO, supraoptic nucleus
NTOL, nucleus of the lateral olfactory tract
PUT, putamen
SIN, substantia innominata
SM, stria medullaris
STCC, commissural component of the stria terminalis
STMC, stria medullaris component of the stria terminalis
STSC, supracommissural component of the stria terminalis
TO, optic tract

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STRIA MEDULLARIS OF THE THALAMUS IN THE DOG

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The aim of this paper is to describe the anatomical connections of the habenular nuclei, running anteriorly through the stria medullaris of the thalamus in the dog brain.

Eight series of sections of the dog brain, that is, three frontal, two sagittal and three horizontal, stained by Klüver-Barrera and Weigert-Wolters methods, as well as by Landau silver method were used.

Topography

The stria medullaris of the thalamus in the dog is a broad and well-developed bundle, consisting of a few fiber systems. It makes up an arcuate pathway, stretching on the surface of the thalamus and constitutes a boundary between its medial and dorsal surface. A chorioid lamina of ventricle III, called taenia of the thalamus, is attached to the sharp, upper margin of the stria. In the frontal section, the stria makes up a single oval bundle, medially rounded and laterally tapering off. In the broadest place, it is 0.5 mm thick and 2 mm wide.

In its principal trace, the stria fibers are concentrated and form a sort of a tract, while in peripheral parts, on the side of the thalamus, they are more loosely arranged. At the end of its mediodorsocaudal trace, the thalamic stria reaches the frontal and dorsal parts of the habenula where—mostly in lateral nuclei—some fibers terminate and other ones, passing through the habenular commissure, become interlaced with the fibers of the contralateral stria.

Anteriorly, the stria deflects from the wall of ventricle III, sharply turning downwards and slightly anteriorly (Fig. 2). In this stage, on one side, it marks out the boundary of anterior thalamic nuclei and on the other side, it adheres to the interstitial nucleus of the stria terminalis and passes through the dorsal hypothalamus. In this area, the stria begins to lose its compactness and, as it descends slightly laterally, its fibers, ever more divided from each other, scattered and forming no distinct systems, reach the olfactory region.

Just below the intraventricular foramen, the stria is joined by a considerably sized bundle of fibers, which, detached from the descendent columns of the fornix and turning ventrocaudally, link on the stria. On the opposite side and somewhat posteriorly, a fiber bundle, turning upwards, deflects medially and laterally from the stria terminalis and runs posteriorly together with the fibers of the stria medullaris of the thalamus.

Myeloarchitectonics

The fibers of the stria medullaris of the thalamus slightly differ in thickness, but fairly thick fibers predominate. In sections, stained by the Weigert-Wolters method, their thickness amounts to about 2.5 μ. They are easy to stain by all the methods used, their trace is compact and they run parallel to each other.

They have been divided into seven systems, forming connections of the olfactory region with the habenula.

Septo-habenular tract. The fibers of this tract (Fig. 1) derive their origin from the commissure of the anterior portion of the fornix (Singer 1962). In this area, they form a fine system of somewhat darker fibers. They reach the lateral side of the descendent columns of the fornix and descend together with its fibers. Just below the intraventricular foramen, they deviate from the columns in the form of a loose, more darkly stained system (Fig. 3). Joining the stria medullaris of the thalamus, they run dorsocaudally and somewhat medially. A few hyperchromatic cells (Miodoński 1965), constituting a nucleus of this tract, are situated in the place where the septal-habenular route branches off from the descendent columns of the fornix. This is a small nucleus whose cells, compared with those of the adjoining nucleus of the fimbria, are larger and better stained.

An identically named tract has been described for other mammals. In the case of the bat, Humphrey (1936) derives the origin of this route from the interstitial nucleus of the hippocampal commissure and describes certain associations with the medial septal nucleus, situated more anteriorly. In the case of oppossum (*Didelphis virginiana*), the interstitial

nucleus of anterior commissure has been added by Loo (1931) to these fibers. As described by Herrick (1933) for reptiles and by Huber and Crosby (1929) for birds, the septal-habenular tract consists of the fibers of the interstitial nucleus of anterior commissure and the septum, as well as, in the case of birds, of the interstitial nucleus of the hippocampal commissure. After destroying habenular nuclei, degenerated fibers, passing through the columns of the fornix to the septum, have been observed by Mitchel (1963).

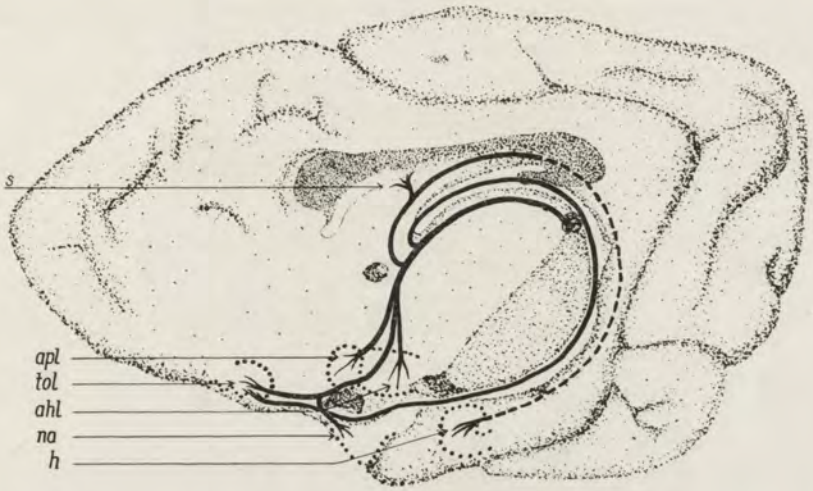

Fig. 1. Diagram of the branching of the stria medullaris of the thalamus

Medial cortico-habenular tract. Fibers which form this tract run from the hippocampus (Fig. 1) together with the columns of the fornix. In the place where dorsocaudal columns are situated, a large corticohabenular tract separates and, together with the system described above, passes slightly medially and dorsally and, hereafter, joins the stria medullaris (Fig. 3). Compared with the fibers of the septal-habenular tract, the fibers of the cortico-habenular tract form a tangled system of thin fibers less intensive in stain and situated below the former ones. The observation of their trace together with column fibers is impossible because of a slight differentiation of fibers and a peculiarly tangled structure of the descendent columns of the fornix. In place of the detachment, they " extricate " in a certain manner from the tangle of the remaining fibers of columns from which they differ in a slightly more intensive stain. The fibers of this tract are thinner than the remaining fibers of the stria medullaris (about 1.25 μ). Almost all investigators are unanimous as to the existence of this tract. Young (1935) for the rabbit, Humphrey (1936) for the

didelphis, as well as other authors derive the origin of this tract from the hippocampus. Its existence has not been confirmed only by Ramon y Cajal (1911).

Anterior olfacto-habenular tract. Fibers of this tract form a scattered system, originating from the lateral preoptic area (Fig. 1). These rather thin fibers run upwards from the anterior part dorsally and somewhat caudally, together with the posterior olfacto-habenular tract. In relation to this tract, the fibers take a more medial position.

Posterior olfacto-habenular tract. This tract derives its origin (Fig. 1) from the lateral hypothalamic area. Its fibers are thick and intensive in

Fig. 2. Parasagittal section through the diencephalon of the dog (Weigert-Wolters, semischematic)

stain. Few fibers, getting out of the anterior hypothalamic nuclei join this tract. Anterolaterally, they pass upwards, unite with the fibers of the preoptic area (Figs. 1 and 4) and join the main bundle of the medullary stria. Among all fibers, reaching the wall of ventricle III, the fibers of these two systems take the most medial position. They do not display any

differences from each other, are rather thick (about 2.5 μ) and intensively stained.

Most authors show these systems as one tract and it is only L o o (1931) who divides them into two routes, that is, the medial olfacto-habenular tract and the paraventricular olfacto-habenular tract. The first approximately corresponds with the anterior olfacto-habenular tract and the second—with the posterior olfacto-habenular tract. The fibers, coming out of these two areas, probably make up the original component of the stria

Fig. 3. Cross section through the diencephalon of the dog (Weigert-Wolters, semischematic)

medullaris of the thalamus. According to H u m p h r e y (1936), the fibers of this system run most closely to the wall of ventricle III and, reaching the habenula, they become exactly medial in relation to other fibers of the stria and enter the medial habenular nuclei.

Lateral olfacto-habenular tract. The more laterally situated fibers (Fig. 4) closely contact the tract, described above. They derive their origin from the olfactory tubercle of which they get out together with the fibers

of the medial forebrain bundle. They run caudally and medially to the optic tract where they turn dorsally and intersect with more dorsal fibers of the medial forebrain bundle (Fig. 2). In this place they are joined by the fibers which run from the olfactory tubercle among more dorsal fibers of the medial forebrain bundle. They are directed upwards, slightly posteriorly and medially, uniting with the fibers of the medial olfacto-habenular tract. A few fibers of this system originate in contact with large cells of the supraoptic nucleus. Upon taking a lateral position to the descending columns of the fornix, the fibers of the lateral olfacto-habenular tract form a fibrous, spindle-like capsule. Among the fibers of this capsule, cells are visible whose shape and size indicate their association with the interstitial nucleus of the terminal stria. Most likely, this is a part of this nucleus, separated by the fibers of the lateral olfacto-habenular tract.

This tract has been identified by all authors. Humphrey (1936) describes it in the bat as a very small system. Craige (1925) supports Herricks view that this tract is the largest component of the stria medullaris in the rat which, however, was not confirmed by Young (1935) in his descriptions of the guinea pig and rabbit. A degeneration, caused by the lesion of the olfactory tubercle, stretching through the stria medullaris of the thalamus to the lateral habenular nuclei (in rabbit and cat) was observed by Kusama and Hagino (1961).

Medial cortico-habenular tract. This tract consists of a small number of fibers which, together with the medial and lateral olfacto-habenular tracts, reach the stria medullaris in the vicinity of the mediodorsal part of the anterior thalamus (Fig. 1). This tract descends together with the fibers of the lateral olfactory tract, intersects with the medial forebrain bundle and reaches the height of the posterior part of the supraoptic nucleus. Next, the fibers of this tract run somewhat caudally to the anterior areas of the amygdaloid complex. In the anterior part of this complex they take the most medial position. This place is also reached by the fibers, coming out of the piriform cortex which, together with the former, run to the medullary stria.

After destroying the anterior part of the amygdaloid area, Kusama and Hagino (1961) observed a degeneration of axons, running through the stria of the thalamus to the lateral habenular nuclei. A part of them passed through the habenular commissure and joined the contralateral stria. However, it has not been noticed precisely in which area these fibers terminate.

Stria terminalis, pars ad striam medullarem. In addition to the fibers of the lateral olfactory tract, connecting the habenula with the olfactory tubercle, the habenula has still other connections with this area through

the fibers that make up a component of the stria terminalis which joins stria medullaris of the thalamus and, together with its fibers, reaches the habenula (Fig. 1).

The fibers of this system, together with the medial olfactory tract, take their origin from the olfactory tubercle. In the laterocaudodorsal direction, they run posteriorly through the Reichert's substantia innominata. Reaching the lateral part of the supraoptic nucleus, they bunch and adhere

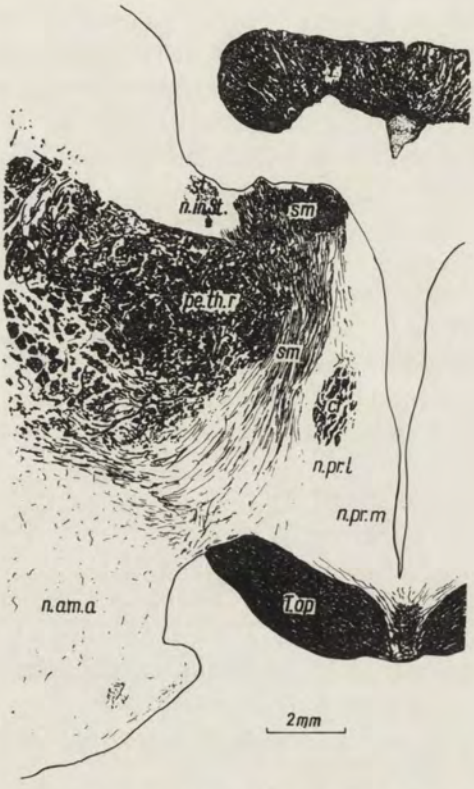

Fig. 4. Frontal section through the diencephalon of the dog, 1.5 mm distant from cross section 3 (Weigert-Wolters, semischematic)

to the optic tract, Further on, they run posteriorly towards the vicinity of the amygdaloid complex. From this place, together with the remaining two bundles of the stria terminalis they encircle the internal capsule, sharply turn upwards along the ventral wall of the interventricular aperture and laterally (Fig. 1) join the stria medullaris of the thalamus. The fibers of this bundle differ from the remaining fibers of the stria termi-

nalis in the intensity of staining and in a fact that they are thicker. This is the only system of the stria terminalis devoid of connections with the amygdaloid complex (Miodoński 1966).

Both their staining and their thickness indicate that they are similar to the fibers of the stria medullaris of the thalamus and not to the stria terminalis ; the remaining fibers of the stria terminalis are poorly stainable and thinner.

This tract is described by most authors with considerable reservations. Humphrey (1936) finds only a small number of fibers which get out of the stria medullaris. She derives them from the posterior parts of the amygdaloid complex. A habenular component of the stria terminalis has been observed by Young (1931) and derived by Fukuschi (1952) from central and cortical nuclei of the amygdaloid complex. Fox (1943), as well as Adey and Meyer (1952), have not confirmed the existence of the habenular component of the stria terminalis. Bürgi (1954) is the only author who, after a unilateral lesion of the stria medullaris, observed fibers, passing through the habenular commissure to the contralateral stria medullaris and, hereafter, to the stria terminalis and terminating in the nuclei of the amygdaloid complex. This divergence of opinions is difficult to explain. A great accumulation of intersecting systems with fibers that do not differ much from each other is one of the reasons why tracing the passage of fibers between these two striae is so difficult.

The connections through fibers that get out of the interstitial nucleus of the stria terminalis are given by many authors as accessory connections between the stria terminalis and stria medullaris of the thalamus.

It is over a considerably stretch that the interstitial nucleus contacts the fibers of the stria medullaris. Fibers, running to the hypothalamus, come out of the cells of this nucleus in its medial part. It is quite possible that fibers, coming out of the most dorsal part (Fig. 3) of this nucleus, enter the anterior part of the terminal stria. This would make up another connection of these two systems.

These tracts converge in the vicinity of the dorsomedial part of the anterior thalamus and, in the form of a single bundle, reach the habenula. Some part of fibers terminate in habenular nuclei, while others, disposed more medially, pass through the habenular commissure and intermingle with the fibers of the contralateral stria.

SUMMARY

The stria medullaris of the thalamus makes up a complex bundle whose fibers form 7 systems, providing connections between some telencephalic areas and the habenula. The anterior olfactohabenular tract derives its

origin from the lateral region of the preoptic area. The posterior olfacto-habenular tract originates in the lateral hypothalamic area. A small number of fibers of the anterior hypothalamic nuclei also join this tract. The lateral olfacto-habenular tract comes out of the olfactory tubercle. Fibers, coming out of the supraoptic nucleus, run towards this tract. The lateral cortico-habenular tract forms a connection with the anterior nuclei of the amygdaloid complex and of the piriform cortex. These four systems run close to each other and, hereafter, converge forming the stria medullaris of the thalamus.

The septum is connected with the habenula through the septo-habenular tract. The hippocampus is connected with the habenular nuclei through the medial cortico-habenular tract. The fibers of these two tracts run together with those of the fornix and, hereafter, join the stria.

The system, related with the stria terminalis, makes up another connection with the olfactory tubercle. This tract, after encircling the internal capsule, laterally unites with the stria medullaris.

In the vicinity of the dorsomedial part of the anterior thalamus, all these systems converge and, in the form of a single bundle, reach the habenular nuclei where a part of fibers terminate and another part, passing through the habenular commissure, intermingles with the fibers of the contralateral stria.

ABBREVIATIONS

ahl,	lateral hypothalamic area	n.pr.m.,	medial preoptic nucleus
apl,	lateral preoptic area	n.in.St.,	nucleus of the terminal interstitial striae
c.a.,	anterior commissure		
c.f.,	column of the fornix	n.Sl.,	lateral septal nucleus
ch,	optic chiasm	pe,th,r.,	rostral pedunculus of the thalamus
c.call,	corpus callosum		
f,	fornix	s.m.,	stria medullaris of the thalamus
h,	hippocampus	st.,	stria terminalis
n.am.a.,	anterior amygdaloid nucleus	th.,	thalamus
n.hab.,	habenular nucleus	t.mth.,	mammillo-thalamic tract
na,	anterior nucleus	tol.,	olfactory tubercle
n.pr.l,	lateral preoptic nucleus	T.op.,	optic tract

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SALIVATION AND INSTRUMENTAL RESPONDING TO AN INSTRUMENTAL CS PRETRAINED USING THE CLASSICAL CONDITIONING PARADIGM

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In our previous paper (Ellison and Konorski 1965) we found that the salivary CR and the instrumental response could be separated in time when special training procedures were used. In our procedure, two CS's — an instrumental CS and a classical CS — were presented on each trial, and the instrumental CS came to elicit only the instrumental response while the classical CS came to elicit only salivation.

It is only with such special procedures that these two responses can be separated, however, and in the procedures usually followed in instrumental conditioning the same CS serves as both the classical CS and the instrumental CS in that it both just precedes food and also serves as the signal for instrumental responding. With these usual procedures the two responses occur at the same time, showing a high positive correlation (Konorski and Miller 1936).

In the present paper we will attempt to demonstrate that the two responses can be shown to be distinct even when they are elicited by the same CS and thereby occur at the same time. The method of demonstrating this follows the procedures of Konorski and Wyrwicka (1950), where it was shown that the learning of an instrumental response to a CS originally trained using classical conditioning procedures occurs extremely slowly, and that instrumental responding to such an altered CS remains

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weaker, even after extensive training, than that to another CS which had always been trained as an instrumental CS. In the present paper this finding will be replicated and it will additionally be shown that the effects of such retraining on the salivary CR are the converse of those on the instrumental response.

METHOD

Three dogs were used as subjects. Two of the Ss (Nos. 1 and 2) were experimentally naive prior to the experiment. Salivary recording in these Ss was accomplished by means of the shortened duct method described by Sołtysik and Zbrożyna (1957), and the instrumental response trained was that of lifting the right forepaw to a high level and returning it to the floor immediately. The third S had previously served as S No. 3 in the experiment reported by Ellison and Konorski (1965). For this S the lever-pressing response was used as the instrumental response, and salivation was recorded by means of an artificial fistula similar to that described by Sheffield (1957).

The procedure for all Ss was as follows : first a good classical CR was trained to a CS which will henceforth be called CS_1. During the early presentations of this stimulus the CS—US interval was 2 seconds ; this interval was then slowly lengthened to 10 seconds. After a consistent salivary CR had developed with the 10 second CS—US interval, 200 overtraining trials were given. This training procedure was followed in order to develop a strong classical CR to CS_1.

In the next stage of training, CS_1 was never presented while an instrumental response was being trained to a new stimulus, henceforth called CS_2. In order to train the instrumental movement, a response was first elicited in the absence of CS_2 and immediately reinforced, and when the animal began to actively perform the required movement, CS_2 was sporadically presented and only those responses made during it were rewarded. Then the time between presentations of CS_2 and the time between onset of CS_2 and food presentation were gradually lengthened. The intertrial interval averaged four minutes during the final stages of training, and the time between CS onset and presentation of food was 10 seconds. The food was presented exactly at the 10th sec. if one or more responses had occurred during the action of the CS. If no responses occurred, food was withheld until the first response did occur. The CS overlapped 5 sec. with food presentation. Under this contingency, the Ss always made several responses before the 10th sec. of CS action, and the CS—US interval was consequently always 10 sec.

At least 100 further trials were then given with CS_2 so that a strong, stable instrumental response and a consistent salivary CR occurred on each trial. Then CS_1 was reintroduced and trials were alternated between CS_1 and CS_2 with the instrumental reinforcement contingency now applied to both conditioned stimuli. That is, reinforcement was now withheld to CS_1 until an instrumental response occurred and until the CS had been on for at least 10 sec. On the first such CS_1 trial the dog would usually wait patiently for food until after the normal time of food presentation, and then would become impatient and perform the trained instrumental response. This response was immediately reinforced. Several days of this training were sufficient to reach a state where at least one instrumental response was always made before the 10th sec. of CS action, whether CS_1 or CS_2 was presented.

Further training consisted of merely alternating CS_1 and CS_2 trials. The

reinforcement schedule was the same for both stimuli. A daily session consisted of 4 presentations of CS_1 and 4 of CS_2 with intertrial intervals varied around a mean of 4 min. Which of these two stimuli were presented first on any given day was determined by chance. This training was continued daily for at least 200 trials after all Ss were performing the instrumental response well to both stimuli.

The nature of the instrumental response, the method of training, and the specific conditioned stimuli used with each S are presented in Table 1.

Table 1. Methods of training and conditioned stimuli used for each individual S.

Dog	CS_1	CS_2	Method of training
No. 1	Metronome	Buzzer	Passive flexion
No. 2	Buzzer	Metronome	Tactile stimulus to paw
No. 3	Buzzer	Light	Baited lever

RESULTS

The data to be reported will concern the 200 trials given after each S was performing the instrumental response well to both conditioned stimuli. An inspection of the records from these 200 trials revealed a long-lasting difference between the CR's evoked by the two conditioned stimuli. The instrumental response was stronger to CS_2, but the salivary CR was stronger to CS_1.

These results are presented graphically in Fig. 1 for the salivary CR, and in Fig. 2 for the instrumental response. Considering only Fig. 1, it can be seen that a good salivary CR occurs to CS_2, but that its amplitude is much lower than that to CS_1. This effect was long-lasting, continuing over the entire block of 200 trials. The source of this lowered amplitude of salivary CR to CS_2 did not appear to be a lowered CR frequency to CS_2. The frequency of response, whether to CS_1 or CS_2, was always above 95%. Rather, these results reflected a tendency of CS_2 to elicit a consistently lower rate of salivary flow than CS_1.

The results with instrumental responding, as seen in Fig. 2, were just the opposite. This graph depicts the average number of instrumental responses made during the initial 10 sec. of action of the CS. The average number of responses was always well above one for both stimuli, but at least twice as many instrumental responses were consistently made to CS_2 than to CS_1.

These differences in rate of instrumental responding and conditioned salivation reflected a difference in the gross behavior of the dogs to the two conditioned stimuli similar to that described by K o n o r s k i and W y r w i c k a (1950). Upon presentation of CS_1 S would stare intently

at the food bowl, salivating profusely. Occasionally shifts in body position were made, but few of these developed into instrumental movements. When instrumental movements did occur, they were usually performed while the dog was staring into the food bowl. On the contrary, to CS_2 the attention of the dog was less strongly focused on the food bowl. The body was shifted more frequently. Conditioned salivation occurred with a latency and form similar to that to CS_1, but the maximal rate of salivation was much lower.

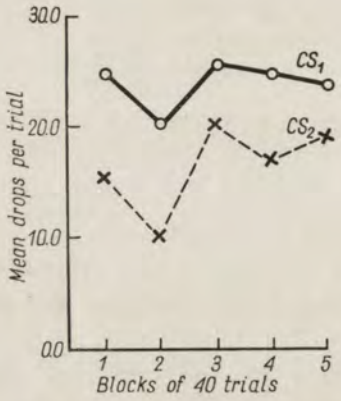

Fig. 1. Mean salivary CR in drops for each conditioned stimulus as a function of training. The amplitude of the salivary CR to CS_1 remains substantially above that to CS_2 throughout training

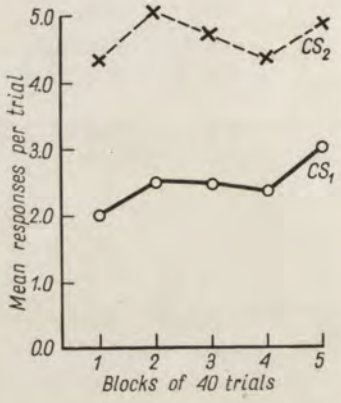

Fig. 2. Mean number of instrumental responses per trial for each conditioned stimulus as a function of training. More responses are made to CS_2 than to CS_1 throughout training

In order to present more clearly the individual results from each dog and the progressive changes in the individual S's records, these data were replotted in terms of a ratio between the responses to the two conditioned stimuli. For each individual S, the ratio between amount of salivation to CS_2 divided by that to CS_1 was calculated for each block of 20 trials. A similar score was computed for the instrumental data : number of responses to CS_1 was divided by the number of responses to CS_2 within each trial block. Figs. 3 and 4 present these data. For each dog, the ratios begin at less than one and slowly rise. These figures show a tendency for the effect to diminish as training progressed which was not apparent in Figs. 1 and 2.

The most persistent difference in instrumental responding was obtained in the dog No. 3 taken from the experiments previously reported by Ellison and Konorski (1965). In this dog, the leverpressing curve

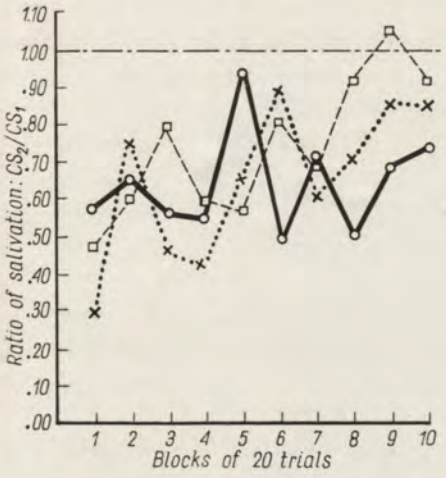

Fig. 3. Individual curves for each S showing the ratio of salivation to CS_2 divided by salivation to CS_1 as a function of training. The dashed line drawn through 1.00 indicates the point of equal CR strength to each stimulus. Legend : filled circles — No. 1 ; open squares — No. 2 ; X's — No. 3

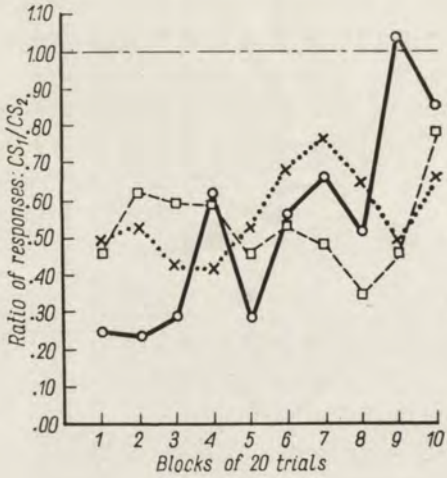

Fig. 4. Individual curves for each S showing the ratio of instrumental responses to CS_1 divided by responses to CS_2 as a function of training. Legend as in Fig. 3

appeared to have reached an asymptote with CS_1 clearly inferior to CS_2 (cf. Fig. 4). In this S the classical CR was even more strongly established than in the other two Ss owing to the extremely protracted training given with this CS.

DISCUSSION

In the present experiment fewer instrumental movements but a larger salivary CR were elicited by a CS originally trained with classical conditioning procedures and then retrained using instrumental methods than by one always trained with instrumental procedures. Although this effect slowly decreased with further retraining, an inspection of Figs. 1 and 2 indicates that differences in amount of classical or instrumental training *per se* cannot be invoked as the sole explanation for these effects. Shifting the CS_2 curve forward or backward 100 trials would not change the conclusions to be drawn from either Fig. 1 or Fig. 2.

An important question which might be raised is whether the decreased salivary responding to CS_2 might have been due solely to increased inhibition of delay. The answer to this question seems clearly to be negative, for the form of the salivary CR was not greatly different for the two

CS's, and furthermore the frequency of CR's remained high to both CS's (cf. Ellison, 1964). These arguments also indicate that the decreased number of instrumental responses to CS_1 was not due to merely a more accurate estimation of the time of reinforcement.

The interpretation favored by the authors is that the strength of the process underlying instrumental responding (the " drive CR ") was greater to CS_2 in these experiments, while the strength of the process underlying the salivary CR (the " consummatory CR ") was greater to CS_1. This was reflected in differences in the general behavior of the dogs to the two CS's : during CS_2 there were more frequent changes in body position, barking, and a higher rate of instrumental responding, while to CS_1 the dogs stood more still, staring intently at the food bowl, and they salivated more profusely.

The reason that decreased salivary responding to an instrumental CS when compared to an equivalent classical CS has not been reported earlier may be related to the finding that the effects of intensity of CS on the elicited CR, for example, are much greater when these effects are compared within subjects rather than between subjects. It should also be noted that the behavior elicited by the classical CS must be clearly the " waiting " type of behavior as seen to CS_1 in this study. For example, in a study by Ellison and Williams (1962) it was found that when dogs were alternated between instrumental and classical trials of comparable length, conditioned salivation was the same on both types of trials. During the " classical " trials presented by these authors, however, the behavior of the animals was more like that seen in the present experiments to CS_2 — the animals would bark at the food bowl and move about on the conditioning stand. Merely the use of the Pavlovian classical conditioning procedure will not, then, guarantee the strong classical CR necessary to observe this effect. Such a strong CR was obtained in the present experiments by the use of initially short CS—US intervals and a preferred food reinforcement, and because the classical CR was trained first and well-trained.

These results further substantiate a separation of the drive CR and the consummatory CR. In our previous communication (Ellison and Konorski 1965) it was found that eventually the salivary CR and instrumental responding were negatively correlated. In that study the experimental procedures to some extent dictated this negative correlation, in that two distinct CS's were used and the place of feeding was clearly differentiated from the place of instrumental responding. In the present experiments, no clear incompatibility was dictated between the salivary CR and the instrumental response. Each CS served both as the signal for food and as the signal for instrumental responding, and the instrumental

response of lifting the leg was not physically incompatible with that of looking into the food bowl and salivating. Nevertheless, even after extensive instrumental training CS_1 showed a weaker instrumental response and a stronger salivary CR than CS_2. While the relations between these two processes need further study, these findings suggest that antagonistic relations between these two processes may be a more general property of learning than has been previously suspected.

SUMMARY

Conditioned salivation and instrumental responding to a CS originally classically trained and then switched to instrumental were compared with the same responses to a CS always trained as instrumental. Conditioned salivation was greater to the originally classically trained CS, while instrumental responding was greater to the CS always trained as instrumental. These effects persisted after further training with both stimuli similarly reinforced. The relationship between these two responses is discussed.

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RETENTION OF THE AVOIDANCE REFLEX AFTER PREFRONTAL LOBECTOMY IN CATS*

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Most theories of avoidance conditioning assume that the classically conditioned fear response is crucial for the evocation of the instrumental avoidance response (Konorski and Miller 1933, Konorski 1948, Mowrer and Lamoreaux 1946, Mowrer 1960, Schoenfeld 1950, Solomon and Wynne 1954, Sołtysik and Kowalska 1960). Thus, one may expect that the effects of lesions in the frontal cortex, which exerts control on the autonomic nervous system and affective behavior (cf. Brutkowski 1964), would have a parallel effect both on the classically conditioned defensive reflexes and on the instrumental avoidance reflex. However, the experimental data hardly support such a simple hypothesis.

It has been shown that fear responses acquired during preoperative conditioning are either reduced (Streb and Smith 1955), or not changed (Maher and McIntire 1960) after frontal lesions in the rat. " Feeding inhibition " and anxiety symptoms acquired by dogs as a result of shock applications while eating were lost following bilateral prefrontal lobotomy ; however, they may be relearned (Lichtenstein 1950). A test of " displacement behavior ", in which the approach response was acquired by food reinforcement and the avoidance response by punishment of the approach response, showed that in frontal rats, opposite to intact animals, the approach was stronger than the avoidance response

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(Maher et al. 1962). When both alimentary and defensive instrumental reflexes were trained in the same monkeys (food versus fear discrimination), the latter were more impaired after prefrontal lobectomy than the former (Waterhouse 1957), but delayed responses were abolished whether motivated by food or by shock (Miles and Rosvold 1956).

These data generally indicate that lesions in the frontal pole of the cortex in rats, dogs, and in monkeys reduce fear or raise the threshold to noxious stimulation. Thus, one may expect deterioration of the avoidance reflex in frontal animals because excitation of the fear center is thought to be a precondition for the development and perhaps the maintenance of the avoidance response.

However, there is also evidence showing that the threshold of responsiveness to shock is lowered after removal of the lateral frontal cortex in monkeys as tested in the Sidman-type avoidance procedure (Weiskrantz and Wilson 1958). Hyperreactivity to noxious and tactile stimuli was observed after medial prefrontal lesions in rabbits (Brutkowski and Wojtczak-Jaroszowa 1963). Moreover, it was found that the classical defensive conditioned reflexes (both acid-defensive and electro-defensive) in dogs were more intense and their latent periods shortened after prefrontal lobectomy (Auleytner and Brutkowski 1960). A marked disinhibition of the inhibitory defensive reflexes (both differentiation and conditioned inhibition) was also observed by Auleytner and Brutkowski (1960). Shortening of the latency of the classical defensive reflexes in dogs after prefrontal lobectomy was observed also in another study ; however, the heart rate during the ITI's and tachycardia evoked by the shock applications were diminished after lesion (Jaworska and Sołtysik 1964). These data were interpreted as indicating an increase in emotional excitability after lesions in the frontal pole of the cortex (Brutkowski 1965, Brutkowski 1966). It was suggested that the medial part of the frontal cortex together with hypothalamic nuclei constitute one basic system which participates in mediating the type of inhibition referred to as "drive inhibition" (Balińska et al. 1966), and after destruction of a link in this system, the phenomenon of " drive disinhibition " should be observed. The deterioration of the avoidance reflex observed by some authors after prefrontal lobectomy was explained as a result of an increase in defensive-agressive emotional responses, which interfere with the avoidance response (Brutkowski and Wojtczak-Jaroszowa 1963, Brutkowski 1965, Brutkowski 1966).

Impairement of the avoidance reflex after lesions in the frontal pole of the cortex was observed in a number of studies using the two-compartment shuttle-box technique. Removal of the anterior cingulate cortex in

rats resulted in slow acquisition and long latency of the avoidance response, whereas lesions in the precentral agranular cortex did not exert any effect on the acquisition and latency of the avoidance response (Peretz 1960). Frontal operated monkeys made in the beginning of training a smaller percentage of avoidance responses than did temporal operated and normal animals (Smith et al. 1956). Immediate extinction of the preoperatively acquired avoidance reflex was found in several groups of monkeys after lesions in medial frontal and cingulate cortex, in frontotemporal region, in Ammon's formation, and in anterofrontal region. In control groups subjected to lesions in occipital region, in inferotemporal region, or sham-operated such changes were not observed (Pribram and Weiskrantz 1957). A small effect in decreasing resistance to extinction, but no effect on the acquisition and retraining of the avoidance response, was found in cats after dorsofrontal decortication, which includes the anterior third to half of the lateral gyri and underlynig structures to the level of the corpus callosum (Thompson 1959).

In some studies the lack of the relation of the postoperative changes in the avoidance reflex to the fear reaction was noticed. In cats a widespread lesion including anterior commissure, claustrum, internal capsule, and rhinal sulcus resulted in failure either to retain or relearn the avoidance response in spite of the fact that autonomic disturbances related to the onset of the CS and the escape response to the shock were similar to those in normal cats (Brady et al. 1954). Also in cats the preoperatively acquired bar-pressing avoidance response was impaired after removal of the proreal and orbital gyri but no noticeable changes in emotional behavior were observed (Zieliński 1963). In rats severe impairment of the avoidance response after lesions of the orbitofrontal cortex was shown but some components of the fear reaction to the onset of the CS and the escape response to shock applications were maintained (Thompson 1963, Thompson 1964).

From this review it is evident that previous studies on the effects of lesions in frontal cortex on the defensive conditioned reflexes yield very controversial results. One reason for this controversy is differences in species, experimental procedures, site of lesions, and operative techniques. Thus, it was decided to carry out a series of experiments in which subjects of the same species, apparatus, and frontal lesion would be used, to study the effect of the removal of the prefrontal cortex on the avoidance reflex. The independent variables were differences in the experimental procedure (change of the CS—US contingency, introduction of inhibitory trials, and so on).

The aim of the present experiment, which is the first of a series, was to investigate the retention of the avoidance reflex after prefrontal lo-

bectomy in two groups of cats differing in the method of shaping of the avoidance response. In one group of cats a strong classical defensive reflex to the CS was established prior to any instrumental training, whereas the other group acquired first the escape response from shock and only afterwards the CS was introduced. It is known from previous studies that the first method results in stronger emotional changes to the CS and the experimental situation, more rapid acquisition of the avoidance reflex and its higher resistance to extinction than the second method (Sołtysik and Zieliński 1963, Zieliński and Sołtysik 1964). Both speed of acquisition and resistance to extinction are indices of the strength of the CR ; thus a differential effect of frontal lesions on the retention of the avoidance reflex in the two experimental groups may be expected.

MATERIAL AND METHODS

Eight adult male cats were used. Experiments were carried out in a cage, 65 cm × × 55 cm × 40 cm, with a floor-grid to apply electric shock to the paws of the animal. In the middle of an oblong wall of the cage, 10 cm above the floor, a bar, 10 cm × 2 cm, was located. The bar could be removed trough a slit in the wall. Its automatic return was secured by means of a spring. The cage was placed in a sound--proof CR-chamber.

The CS was a mild tone of about 60 db. and 2000 c.p.s., applied through a loud--speaker from a tone-generator. Alternating current of 50 c.p.s. and about 20 to 30 volts from a transformer was used as the unconditioned stimulus (US). Avoidance (or escape) response was the bar-pressing reaction, which automatically and immediatelly terminated the CS and/or the US. When the avoidance movement did not appear during 5 sec. of the CS, the US was switched on and both stimuli were on until the animal responded.

Each experimental session consisted of 10 trials, the intertrial intervals lasting about 1 min. with the range from 30 to 90 secs. Each trial was recorded on a kimograph, speed of tape 0.5 cm per sec. The latencies of the bar-pressing responses were read from the records.

Some cats remained sitting with the paw still on the bar after the trial was terminated. In these cases, the bar was removed for a while and put back when the animal took its paw away from the slit.

In four animals the experiments began with conditioning fear CR to the CS. The classical defensive conditioning procedure was used : each trial started with the CS, and 5 sec. later the US was added for another 0.5 to 1.0 sec regardless of what the animal was doing. After 30 trials (3 experimental sessions) of such pretraining the regular avoidance procedure was introduced : the CS or the CS and US lasted until the bar-pressing response (either avoidance or escape) was performed. To make the acquisition of bar-pressing easier, in the beginning of training, a platform, 25 cm × 25 cm, was used as a prolongation of the bar. Then this platform was changed to a smaller one (25 cm × 12 cm, and subsequently, 12 cm × 7 cm). After 10 to 20 trials, the bar-pressing response was established, and no platform was then necessary. These four cats constitute the group with classical pretraining.

In another four cats (the group with escape pretraining) no CS was applied in

the beginning of experiments and the animals were first tought to escape from shock using the same prolongations of the bar. After three days (10 trials daily) of such escape pretraining, the regular avoidance procedure was introduced.

Except for the beginning of training, all Ss were treated indentically. The avoidance conditioning training was carried out until the criterion of 90 correct responses in 100 consecutive trials was reached. By the criterion number we mean the number of trials from the moment when regular avoidance procedure was applied and excluding the 100 trials during which the 90 per cent level was reached ; the latter trials constitute the criterion period. Then a 10-day pause in experiments followed, after which the avoidance reflex was trained for additional 10 days (control period). After this the prefrontal region (proreal and orbitalis gyri) was removed bilaterally in one stage. The operation was done by suction under Nembutal anesthesia in aseptic conditions. 10 days after operation experiments were resumed with the regular avoidance procedure and lasted 10 experimental sessions (post--operative period).

After finishing the experiments, Ss were killed with overdoses of Nembutal and their brains were subjected to histological analysis. Reconstructions of the lesions are presented in Figs. 1 and 2.

RESULTS

Comparison of performance in the two experimental groups. Clear difference in the speed of the acquisition of the avoidance reflex was observed between the two experimental groups. The mean criterion number for the group with classical pretraining was 34 trials, and for the group with escape pretraining — 98 trials ; medians were 24 and 112 trials, respectively ($p=.052$, Mann-Whitney test, two-tailed).

In spite of this marked difference between experimental groups in the speed of the avoidance reflex acquisition, differences in the level of performance during the criterion, control, and postoperative periods were negligible. Corresponding data are presented in Table I for each consecutive block of 50 trials. Statistical analysis of the data using analysis of variance, mixed design, type I, with two experimental groups and six blocks of trials as main effects, has shown that groups effect and interaction term were on chance level, whereas blocks differed at $p<.005$ level (Lindquist 1953).

From the data presented in Table I it is evident that in both groups the prefrontal lobectomy impaired the performance of the avoidance reflex. Comparison of the number of avoidance responses performed during the last block of 50 trials of the control period and during the first block of the postoperative period showed difference significant at $p<.01$ level (analysis of variance, mixed design, type I, Lindquist 1953). The experimental groups and interaction effects were not significant. Analogous comparison for the last block of the criterion period and the first block of the control period showed no effect of any factor.

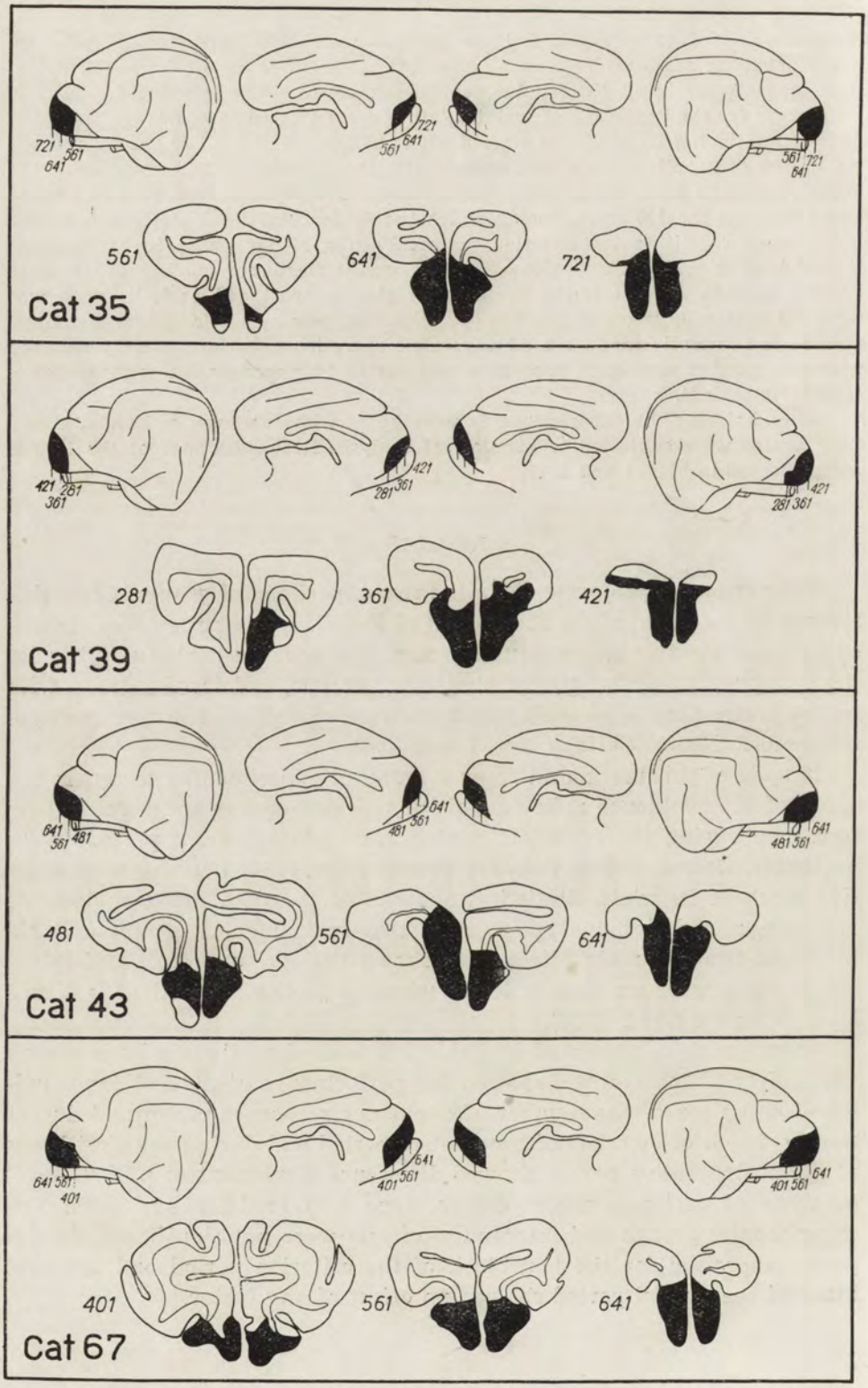


Fig. 1. Reconstructions of the lesions in cats from the group with classical pretraining

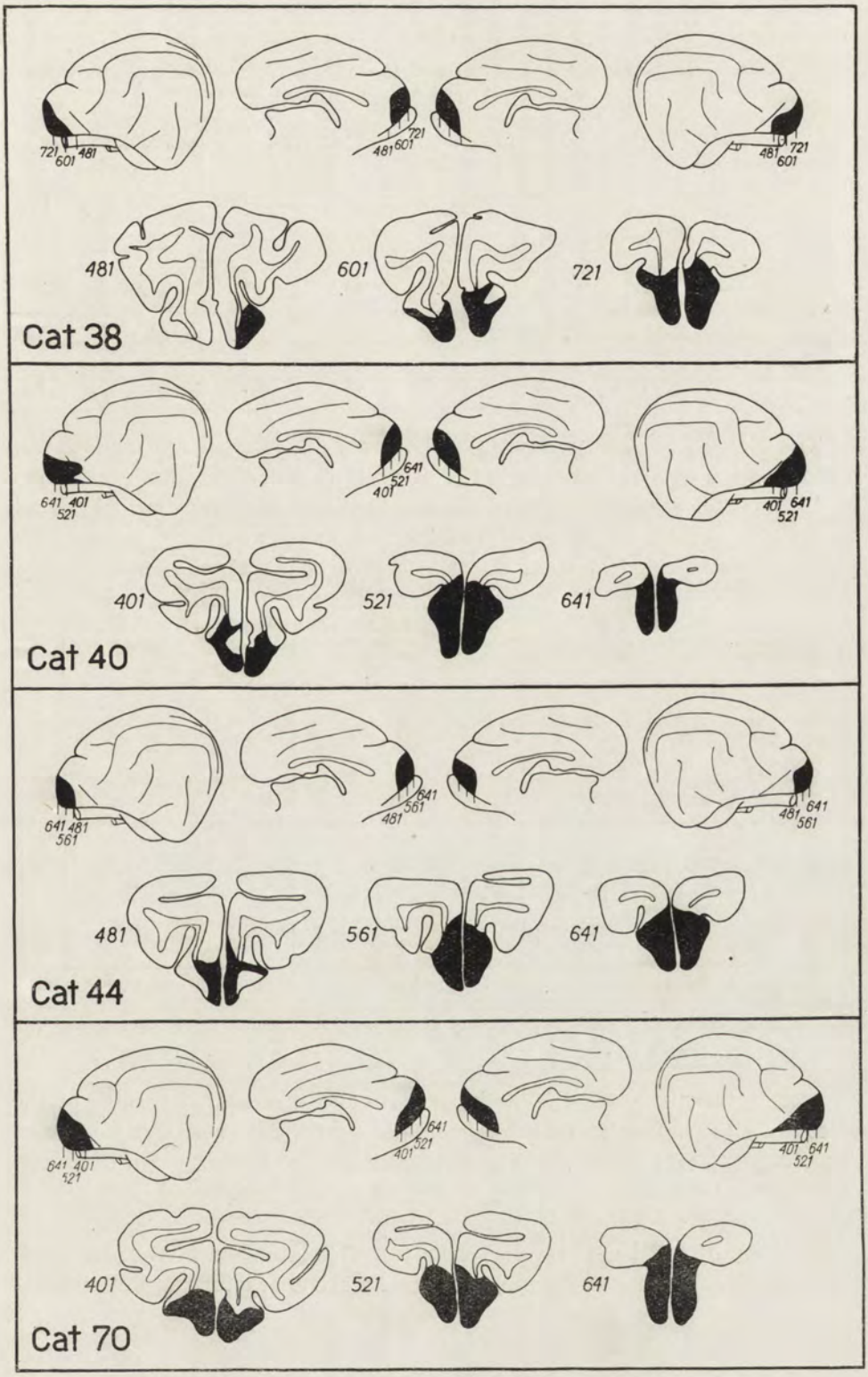


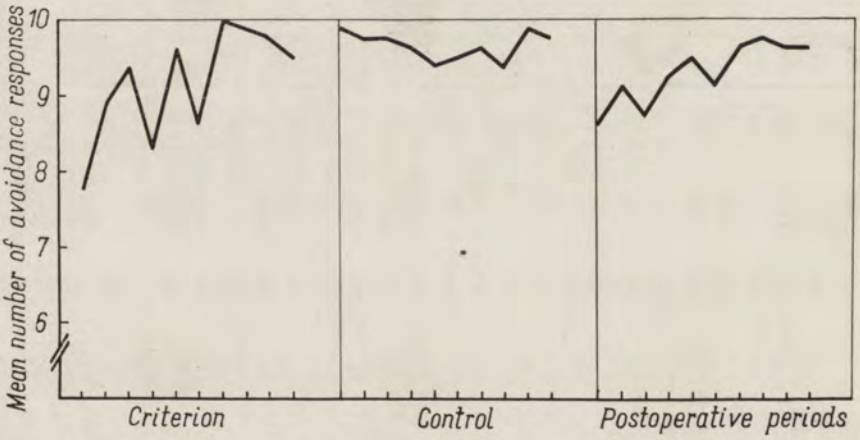
Fig. 2. Reconstructions of the lesions in cats from the group with escape pretraining

Table I

Numbers of avoidance responses performed in consecutive 50 trials blocks during criterion, control, and postoperative periods

Group	Pretraining		Criterion period		Control period		Postoperative period	
			1—50	51—100	1—50	51—100	1—50	51—100
1	classical	Mean	44.5	48.0	48.0	48.0	44.5	47.8
		Mdn.	45.5	48.5	48.5	48.5	44.5	49.5
2	escape	Mean	43.2	47.5	48.8	48.2	46.0	47.8
		Mdn.	42.5	48.0	49.0	49.5	46.0	48.0

The effect of the prefrontal lobectomy on the performance was a shortlasting one and already in the second block of the postoperative period the performance level corresponded to that during the control period. Comparison of the numbers of avoidance responses in two blocks of the postoperative period showed difference significant at the $p<.02$ level



Figs. 3. Changes of the avoidance reflex performance in consecutive sessions of the criterion, control, and postoperative periods (both experimental groups pooled)

(Wilcoxon test, two-tailed). The immediate and transient character of the effect of the prefrontal lobectomy on the performance of the avoidance response is clearly seen from Fig. 3, in which there is illustrated the mean numbers of avoidance responses performed by all cats pooled over corresponding experimental sessions.

Latency of the bar-pressing responses. The latencies of the bar-pressing (either avoidance or escape) responses were characterized for each cat

and block by the single value, namely by the median latency in a given block of 50 trials. From these values means and medians for each group were obtained, which are presented in Table II. Latencies in the six blocks taken into account differed at $p<.001$ level, whereas effect of groups and interaction were on chance level (analysis of variance, mixed design, type I, Lindquist 1953). Inspection of Table II shows that in the first half of the criterion period latencies were long, but in the course of training they become shortened, and the first and second halves of the criterion period differed at $p<.05$ level (Wilcoxon test, two-tailed). Prefrontal lobectomy resulted in the lengthening of latencies and had a more pronounced effect in the group with classical pretraining than in the group with escape pretraining. Comparison of the latencies observed in the blocks of trials just before and just after the operation showed that this interaction effect between experimental groups and two blocks of trials was significant at $p<.025$ level, effect of blocks—at $p<.05$ level, effect of experimental groups was on chance level (analysis of variance, mixed design, type I, Lindquist 1953).

Table II

Latencies (in secs.) of the bar-pressing (either avoidance or escape) responses in consecutive 50 trials blocks during criterion, control, and postoperative periods

Group	Pretraining		Criterion period		Control period		Postoperative period	
			1—50	51—100	1—50	51—100	1—50	51—100
1	classical	Mean	1.8	1.0	1.3	1.3	2.2	2.2
		Mdn.	1.6	1.1	1.2	1.3	2.2	2.0
2	escape	Mean	1.7	1.3	1.2	1.6	1.3	1.8
		Mdn.	1.7	1.1	1.1	1.6	1.9	1.8

See explanation in the text.

It should be noted that comparison of the latencies in the two blocks of trials of the control period has shown no significant effect of any factor or their interaction. However, when the effect of the frontal lobectomy on the latency scores was analysed basing on median latencies estimated for each S for the whole control and the whole post-operative periods, the effect of training periods was significant at $p<.001$ level but the interaction effect (training period vs. experimental group) was smaller, with $p<.10$.

The distribution of the latency scores for each individual cat was

strongly positively skewed, and due to the small percentage of escape responses, their influence on the median latency on the bar-pressing response was extremely small. Thus, we may consider the analysis presented above as analysis of the latencies of the avoidance bar-pressing responses.

Now, we will present data on the latencies of the escape responses alone. Due to the small number of escape responses, especially during the control period, only two scores were used for each cat : the median latency of escape responses performed during the criterion and control periods (pooled), and median latency of escape responses performed during the postoperative period. It is worth mentioning that within the criterion and control periods, as well as within the postoperative period, no systematic changes of the latencies of the escape responses were observed in any individual cat (one-sample run test, two-tailed, S i e g e l 1956). The data presented in Table III indicate that in all cats but one the median latencies

Table III

Median latencies (in secs.) of the escape bar-pressing responses during criterion and control periods (pooled) and the postoperative period

Group	Pretraining	Cat	Criterion and control periods	Posto-perative period
1	classical	35	1.4	0.2
		39	1.8	1.1
		43	0.6	0.4
		67	1.5	0.6
2	escape	38	1.4	0.4
		40	0.8	0.2
		44	0.2	0.5
		70	5.7	1.0

Latencies were measured from the beginning of the US onset.

of the escape responses were shortened after the prefrontal lobectomy. Comparison of these median latencies showed that they differed at $p<.02$ level (Wilcoxon test, two-tailed). When we leave out of account the cat 70 with extremely long latencies of the escape responses before operation, the shortening of latencies was still significant ($p<.05$, two-tailed test).

From the above data a parallelism of changes of the performance scores and latencies of the bar-pressing (avoidance) responses is evident. The Spearman rank order correlation coefficient (r_s) between these indices had a negative sign in each block of trials : short latencies of the bar-pressing (avoidance) responses were related to high performance scores. The high-

est values of the r_s were observed just before and just after the prefrontal lobectomy (r_s=—.66 with $p<.10$ for the last block of the control period, and r_s=—.75 with $p<.05$ for the first block of the postoperative period, two-tailed tests). A positive, although not significant correlation was observed between the criterion numbers (speed of acquisition) and the median latencies of the bar-pressing (avoidance) responses during the first block of the criterion period (r_s=.595, $p<.10$, two-tailed test).

Behavioral changes in the course of the experiment. Marked differences in the emotional state were observed between the two experimental groups in the beginning of the avoidance training. After the classical pretraining Ss showed a clear defensive response to the CS, while after the escape pretraining fear of the CS developed slowly and did not reach the same strength. In the beginning of training the cats were excited, performed many intertrial responses, more numerous after classical than after escape pretraining, changed their position in the cage, often defecated and urinated. These reactions disappeared together with stabilization of the avoidance reflex and all cats acquired a new mode of behavior, consisting in the preparatory response sitting near the bar during the intertrial intervals. Typically, during the last sessions of the criterion period and during the control period the Ss were alert, but no marked autonomic changes were observed in intertrial intervals.

The general behavior of the cats did not indicate any increase in emotionality after prefrontal lobectomy. No hypermotility was observed. The Ss sat on the grid-floor near the bar, similarly as during the criterion and control sessions. The number of intertrial responses was even reduced in comparison with the preoperative control period, but this difference cannot be easily estimated, as cats more often than before remained sitting with the paw still on the bar after the trial was terminated and the bar had to be occasionelly removed.

DISCUSSION

The results of the experiment clearly demonstrate that prefrontal lobectomy in cats has a differential effect on the latencies of avoidance and escape bar-pressing responses : latencies of the avoidance responses are longer whereas latencies of the escape responses are shorter after the surgery. These effects are more permanent than the small and transient postoperative impairment of the avoidance reflex performance, which is presumably due to the shift of the median latencies of bar-pressing responses to the right.

These results cannot be explained by the hypothesis assuming a direct relation of the strength of the instrumental avoidance response to the

strength of the classically conditioned fear response. It is evident first of all from the lack of relation between postoperative deterioration of the avoidance reflex and the general emotionality of Ss, which did not change markedly after operation. The lack of a difference between the two experimental groups during the postoperative period gives additional arguments against this hypothesis. The differences in the speed of acquisition of the avoidance reflex related to the kind of pretraining procedure were assumed to be a result of the difficulty in acquisition of the classically conditioned fear response to the CS after the instrumental escape response has been established. Similarly, the lower resistance to extinction after escape pretraining than after classical defensive pretraining was assumed to be a result of a weaker fear response to the CS in the former group during the criterion period (Sołtysik and Zieliński 1963, Zieliński and Sołtysik 1964). Thus, if the postoperative impairment of the avoidance reflex performance and lengthening of the latency of avoidance responses are results of the weakening of the fear response, these changes ought to be more pronounced in the group with the escape pretraining than in the group with the classical pretraining.

It must be pointed out that the importance of the classically conditioned fear response to the CS for the maintenance of the avoidance reflex is questionable because it has been shown that the fear-evoking properties of the CS decrease in the course of avoidance training (Kamin et al. 1963).

Let us consider now the " drive disinhibition " hypothesis. This hypothesis assumes that the deterioration of the avoidance reflex after frontal lesions is a result of overexcitement of the Ss to the CS, which brings up in action other forms of defensive reactions, interfering with the performance of the bar-pressing avoidance response. Although the lengthening of the latencies of the avoidance responses seems to support this point of view, the shortening of the latencies of escape bar-pressing responses is in full contradiction with it. If, according to this hypothesis, the frontal animals become overexcited when the fear-evoking CS is presented, the more such an overexcitement and allied maladaptive defensive reactions (e.g. flight behavior, often observed in our cats in the beginning of training) would be evoked by the painful US. Postoperative shortening of the latencies of the escape responses indicate no interference of other reactions on the escape bar-pressing response. Moreover, our Ss did not show any other defensive reaction during the CS-US interval after the operation.

The main assumption of the " drive disinhibition " hypothesis consists in the increase of motivation after frontal lesions. Thus, if one observed postoperative improvement of the avoidance reflex performance, this re-

sult would also be in agreement with this hypothesis. In any case, the differential effect of the prefrontal lobectomy on the latencies of avoidance and escape responses contradicts the " drive disinhibition " hypothesis.

From the above discussion we may conclude that neither the hypothesis which assumes direct correspondence between the strength of the classically conditioned fear and the instrumental avoidance responses nor the " drive-disinhibition " hypothesis explain deterioration of the avoidance reflexes trained with a warning stimulus after lesions in the frontal pole of the cortex.

From the review given in the introductory part of the paper it is evident that, independently of the procedural and species differences, the impairement of the conditioned defensive reflexes was found when either extinction or retention of the previously established instrumental avoidance reflex was studied. In any of these situations (including " feeding inhibition ", " displacement behavior ", " food versus fear discrimination ") the Ss, if responded correctly, have opportunity to avoid the noxious stimulation completely and toward the end of the preoperative training the noxious stimulus was used only occasionally. On the contrary, when a noxious stimulus was applied in every trial (classically conditioned defensive reflexes), or the instrumental response was elicted by the noxious stimulus (escape trials in avoidance training) reflexes after frontal lesions were not deteriorated but often even enhanced. This differential effect shows once more a complex role played by the frontal cortex and a necessity of search for more discrete hypotheses to explain frontal lesion effects on different classes of reflexes.

SUMMARY

The effect of prefrontal lobectomy on the retention of the bar-pressing avoidance response was investigated in two groups of cats, 4 Ss each. In one group a strong fear response to the CS was established prior to any avoidance training (the classical defensive pretraining group) ; in the other group escape from the US was acquired before introduction of the CS (the escape pretraining group).

The prefrontal lobectomy resulted in lengthening of the latencies of the avoidance responses, shortening of the latencies of the escape responses, and in a small and transient but definite impairment of the avoidance reflex performance.

No group differences were noticed during the postoperative period except for a slightly more pronounced lengthening of the latency of the avoidance response for the classical than for the escape pretraining group.

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THE EFFECT OF FOOD REINFORCEMENT ON THE LEVEL OF ALIMENTARY EXCITATION

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In previous papers (Wyrwicka 1952, 1958, 1960) a paradigm of alimentary conditioned reflex type II (called also motor or instrumental reflex) was proposed. That theoretical model depicted the brain centers which are engaged in the alimentary motor conditioned reaction and the functional connections between them. In that model (Fig. 1) *A* represents the feeding center considered as " a compound of centers responsible for a state of alimentary excitation " (Wyrwicka 1960) ; *S* denotes the brain centers which represent conditioned stimuli, i.e. the experimental situation plus sporadic stimulus, or the experimental situation alone if no sporadic stimuli are used ; *M* corresponds to the center of instrumental reaction, consisting of all the sensory-motor centers responsible for the performance of the reaction.

Owing to the repetition of the procedure : conditioned stimulus → instrumental reaction → food reinforcement, functional connections between the centers *S*, *A*, and *M* have been established. The action of a conditioned stimulus (e.g. a tone) initiates a corresponding activation of the *S* center (e.g., acoustic). The center *S*, in turn, sends its excitatory impulses to the centers *A* and *M* through the connections *SA* and *SM*. Next, the center *A* sends its impulses to all the centers which are related to it, among others to the salivary glands, as well as to the motor centers including the center of the trained motor reaction *M*. Therefore, the center of the instrumental reaction receives excitatory impulses from two sources : directly from the center *S* on the way *SM* and indirectly through the

feeding center *A* on the way *SAM*. Owing to that, the excitatory level of the center of the motor conditioned reaction becomes higher than that of other motor centers and the trained instrumental reaction may appear.

A number of experimental facts seems to support the above view. 1). After a complete extinction, the instrumental reaction to a conditioned stimulus may be recovered spontaneously by only offering food in the presence of the same conditioned stimulus (Wyrwicka 1952, 1960). (The explanation of that fact in terms of the presented model is the following : Extinction blocks the connection *SA* ; the presentation of food again

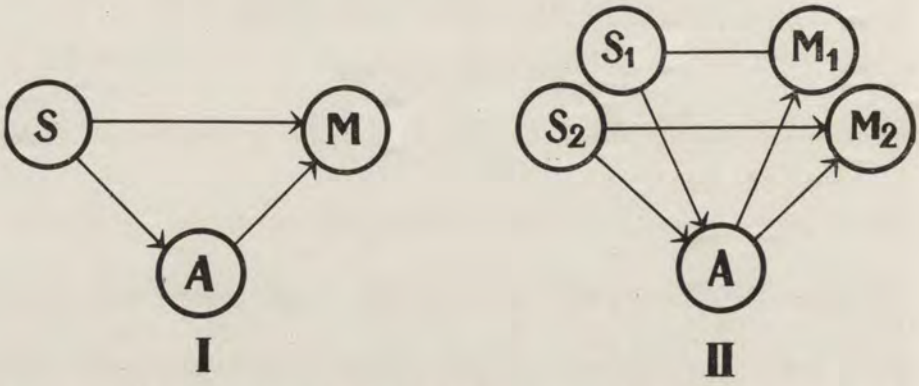

Fig. 1. I—Scheme of probable interrelations between brain centers in the course of an alimentary instrumental conditioned reflex. II—The same in the case of two different instrumental reactions trained to two different stimuli respectively. A, alimentary center ; *M*, M_1, M_2, centers of instrumental reactions ; *S*, S_1, S_2, centers of conditioned stimuli. Lines denote functional connections between the brain centers. The arrows indicate the direction of the excitatory impulses. (cf. Wyrwicka 1952, 1960)

recovers that connection). 2). The instrumental reaction does not appear after complete satiation (Wyrwicka 1950). (Expl. : The feeding center has become insufficiently excitable because of the action of internal " satiety factors " ; see the further part of the text.). 3). Electrical stimulation of the hypothalamic feeding center of a completely satiated animal elicits the previously trained instrumental reaction and eating (Grastyan et al. 1956 ; Miller 1957 ; Wyrwicka et al. 1959, 1960). (Expl. : Electrical stimulation raises the excitability of the center " A "). 4). Destruction of the hypothalamic feeding area causes not only aphagia (Anand and Brobeck 1951) but also disappearance of the instrumental reaction (Wyrwicka 1957, 1960 ; Morgane 1961b). (Expl. : An injury in *A* as well as a break of connections *SA* and *AM* takes place).

The evidence supporting the existence of the direct connections are

the following. 1). The instrumental reaction which has been trained to a "strongly motogenic" (Konorski and Wyrwicka 1952) conditioned stimulus for a long time, may appear in a satiated animal which refuses to take food (Wyrwicka 1950; Dobrzecka and Wyrwicka 1960). (Expl.: Impulses passing through *SM* may sometimes provoke the instrumental reaction without impulses from the feeding center). 2). It is possible to establish two or more conditioned reactions of different instrumental patterns reinforced by the same kind of food, to different conditioned stimuli respectively in the same animal (Konorski and Miller 1933, 1948; Voronin 1948; Wyrwicka 1956, 1958). (Expl.: There must be established by training two different connections, S_1M_1 and S_2M_2 between centers S_1, S_2 and M_1, M_2 respectively; each of the two instrumental reactions appears to the corresponding stimulus (see Fig. 1, II). 3). The above may be demonstrated by electrical stimulation of the hypothalamic feeding center in a satiated animal in which two different instrumental reactions have previously been established in two different situations respectively (i.e. placing the foreleg on the feeder was trained in one situation and kneeling down in another situation). Both movements were reinforced by the same kind of food. Electrical stimulation of the same hypothalamic site in each situation provoked that instrumental reaction which had previously been trained in it (Wyrwicka et al. 1960).

It must be stressed that the above paradigm applies to the conditions in which the instrumental conditioned reflex has been previously established, and we deal with the events occurring during the CS—US interval only.

The aim of the present paper is first to consider the organization of the feeding center and secondly to discuss the possible changes in the excitatory state of the feeding center during the act of consuming food, given as a reinforcement of the instrumental response.

Let us consider the problem of the structures which may constitute the feeding center. The structures related to feeding are found not only in the lateral hypothalamus but also extra-hypothalamically, e.g., in the preoptic area (Robinson and Mishkin 1962, Robinson 1964), substantia innominata (Brutkowski et al. 1962, Lewińska and Brutkowski unpublished data), pallidum (Morgane 1961, Oleshko 1964), ventral tegmentum (Robinson 1964), thalamus (Andersson and Jewell 1957, Pfaffman et al. 1961), mesencephalon (Wyrwicka and Doty 1962), medulla (Larsson 1954, Anand 1963), frontal lobes (Anand 1963, Brutkowski 1966). Taking the above into account, under the term "feeding center" we must understand a system of all the brain structures responsible for the

alimentary excitation and capacity for food intake. Therefore, in our further considerations we will use the term " feeding " or " alimentary system " instead of " alimentary center ".

It is obvious that the feeding system must be composed of both afferent and efferent structures. The afferent structures (Fig. 2, Aa) may receive — probably through some indirect pathways — the taste, smell, tactile, thermal and other signals deriving from the food. If a given conditioned stimulus always precedes the presentation of food, functional connections are established between the center of that conditioned stimulus and the afferent part of the feeding system. Therefore the action of the conditioned stimulus activates the afferent alimentary structures (eliciting the memory traces of the food stimuli).

Here, it should be added that the afferent elements of the feeding system in a hungry animal are also stimulated by some internal stimuli. This will not, however, be considered wider in this paper.

Another part of the feeding system consists of the efferent structures (Fig. 2, Ae). They are responsible for the " appetite to eat " and " seeking food ", i.e. for what may be generally considered as alimentary " drive ", and for the act of eating itself.

It is obvious that the afferent structures of the feeding system are connected with its efferent part. The efferent part is in turn linked with the motor system, where the motor reactions related to feeding are generated (Ms). The connections between the afferent parts and efferent parts of the feeding system as well as between the efferent part and the motor system are probably inborn or acquired in the early stages of the animal's life.

If no definite conditioned reactions were yet established in an animal in a given situation, activation of the efferent part of the feeding system provokes some general excitation in the motor structures. By training we may establish some functional connections from *Ae* to the center of a definite movement, e.g., flexion of the hind leg (*M*). The general connections *g* to the motor system remain active and may cowork with the specific ones (*sp*).

Now we shall discuss the problem of possible changes in the excitatory state of the feeding system at the time of consuming food offered as a reinforcement of the conditioned motor reaction. For simplicity we will consider an instrumental reaction established to the compound of stimuli of the experimental situation. This is a simple procedure in which each performance of the instrumental reaction is immediately reinforced by food. Here the excitatory process occurs all the time, in contrast to the case when sporadic stimuli are used ; the latter involve definite intervals

between successive trials, during which intervals the instrumental reaction must be inhibited.

Let us imagine that the animal has just performed the trained movement and has been consuming the food given as a reinforcement. The stimuli deriving from the food (Fig. 2, Fs) excite the afferent structures of the feeding system *Aa*. In turn, through the existing connections *Aa* → → *Ae* the efferent part of the feeding system as well as the center of the instrumental reaction are activated and the trained reaction should appear again. However, usually, this cannot happen since the animal is just in the course of performing another reaction, i.e. eating food. The presentation of food is a specific strong stimulus and the response to it is one of the earliest and best established reactions of the animal. Therefore, the

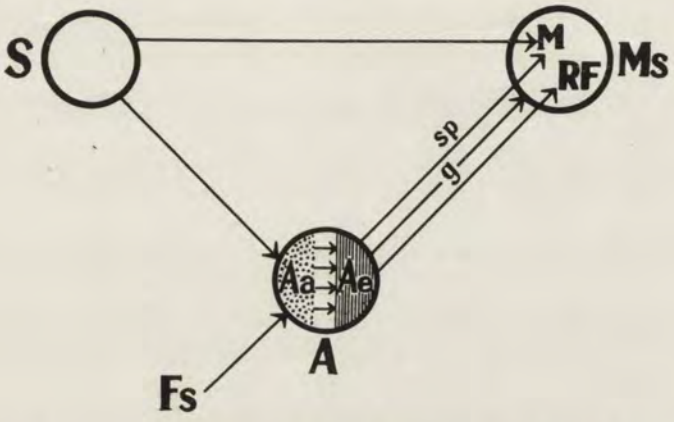

Fig. 2. Scheme illustrating the effect of food reinforcement on the excitatory state of the alimentary and motor systems. *A*, alimentary system, *Aa*, afferent part (stippled), *Ae*, efferent part (striped) ; *Ms*, motor system, *M*, center of instrumental reaction, *RF*, center of motor reaction to food ; *Fs*, stimuli deriving from food ; *S*, center of conditioned stimulus ; *g*, general connections, *sp*, specific connections. Other connotations as in Fig. 1

activation of the motor centers corresponding to the reaction to food (Fig. 2, *RF*), gains a higher level than that of the center of the instrumental reaction *M*. As a result, the instrumental reaction has been temporarily suppressed. As we see, the suppression of the instrumental reaction during eating takes place inside of the motor system.

As soon as the reaction to food becomes less intensive the instrumental reaction my appear again. The corresponding fact was observed in our experiments on goats in which a motor conditioned reaction had been established and daily trained. The goats received food (oats) after each performance of the trained movement. We found that after a few weeks

of training the animals ate only part of each portion and performed the next reaction to get a new portion, despite the fact that the previous one has not yet been eaten (Wyrwicka and Dobrzecka, unpublished data).

Owing to a special experimental procedure the instrumental reaction may remain unsuppressed by the reaction to food during eating. E.g., in the method used by Skipin and his collaborators (Plonska 1959) the dog presses the pedal not only during the action of the conditioned stimulus but also during eating, since otherwise the food is not available. Another example was shown by Struchkov (1960) : in his experiments the dogs were trained to perform instrumental reaction (lifting the hind leg) during eating.

The above considerations suggest that the presentation of food as well as the act of eating are excitatory factors securing the sufficient level of activity in the feeding system and, through it, in the center of the instrumental reaction (on the way $Fs \rightarrow Aa \rightarrow Ae \rightarrow sp \rightarrow M$, as shown in Fig. 2). Therefore the sensory input deriving from food (and perhaps producing " pleasure ") is the origin of repeating the instrumental reaction. This conclusion is in accordance with ideas of other authors (Pfaffman 1960, Teitelbaum 1962). Strong support to that view has been lent by experiments with self-stimulation (Olds and Milner 1954, Olds 1958). The excitatory role of the food reinforcement was also pointed out by Pavlov (1949) ; his opinion was based on the fact that conditioned salivation is always poor at the beginning of testing session and reaches its maximum value gradually in the next trials. Similar facts concerning alimentary instrumental reactions were found by Sheffield and Campbell (1954) and lent support to the " drive induction theory of reinforcement " put forward by Sheffield (Sheffield 1954, Sheffield et al. 1954). That theory claims that " rewards increase excitement ", which is in accordance with our ideas.

On the other hand, our view does not seem to be in harmony with the " drive-reduction theory of reinforcement " (Hull 1943, Miller 1959) as well as with the recent view held by Konorski (Konorski 1964, Konorski, to be published). According to the latter, the alimentary consummatory reflex produces an inhibitory effect upon the " hunger center " which is reactivated, often with rebound, immediately after the termination of the act of eating.

Now a question arises as to whether or not the excitatory effect of reinforcement must always be produced in all circumstances. Common observation as well as some experimental facts show that it is not the case. After satiation the conditioned instrumental reaction disappears and the animal refuses to eat any more. Here, we do come to the problem of the

inhibitory effect of consuming food upon the level of excitation of the feeding system, i.e., to the reduction of " drive ".

The experiments of Janowitz and Grossman (1949) showed that inhibition of the act of eating was the result of streching the stomach by either food, an inedible mass or a balloon filled with air (cf. Bulygin 1963). Another factor which might suppress eating is prolonged mastication and swallowing of food. Janowitz and Grossman (1949) found that the dogs with oesophagal fistula, in an experiment with sham-feeding, could eat continuously about 6 times as long as in normal feeding, but eventually stopped eating. This seems to indicate that there is some kind of fatigue of the peripheral or central structures which may stop the act of eating.

The above mentioned as well as other suppressive factors, e.g., thermal (Brobeck 1948, Andersson 1963) or humoral ones (Mayer 1955), appear only after the consuming of some amount of food. As long as the strength of these factors remain insufficient, the act of eating seems to sustain or initially even increase the level of alimentary excitation.

SUMMARY

The excitatory effect of the food reinforcement on the activation of the feeding system and performance of the alimentary instrumental reaction is discussed.

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THE CONTROL OF THE TERRITORY BY *LASIUS FULIGINOSUS* LATR

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Marking Ants. In the cases when an instantaneous observation of investigated individuals is required, it is quite enough to mark an ant with a dye according to the method, applied previously. Thus, for instance, when the functional and terrain groups were studied, different colors were used for marking particular groups of ants (Dobrzańska 1958); when individual observations were necessary, the color and shape of a mark of each individual were recorded (Dobrzańska 1959).

The dye stays on *Lasius fuliginosus* for a shorter period than on the species *Formica* and *Myrmica*, the reason for this being probably the fact that *Lasius*' abdomen is very smooth and much less hairy. Thus, in experiments during which even a brief delay of observation was required, it was necessary to invent another, more durable method of marking ants. Tying colored silk threads around the petiole turned out to be an effective method.

A thin silk thread should be tied in a single knot, leaving a loop with such dimensions which would allow the experimenter to slip it over an ant's abdomen. The knot slightly moistened and the loop held in the left hand, the ant should be taken with the right hand by its limbs or—very gently—by the head and, then, over the abdomen, the silken loop should be slipped in place around the petiole without, however, catching an animal's limbs in the loop. Hereafter, the loop is slightly tightened to such an extent as to freely encircle the petiole and, at the same time, not to slip off the abdomen. The second knot should then be tied in conformity with the position of the first and tightened by pulling at both ends of the thread. (The previous moistening of the first knot prevents it from further tightening which, otherwise, could be caused by the pressure of the second knot and the ant might be cut in half). After the double knot is thus tied, both ends of the thread are cut off with very thin scissors. Attention should be paid lest the limbs might be cut off.

Planting Strange Nests and Pupae. To investigate the manner of carrying the prey to the nest, at first, the entire nests of strange species were planted in the area, controlled by the colonies of *L. fuliginosus*. After marking a certain number of the pupa capturing workers, we tried to plant only the strange pupae. It turned out

that the individuals which robbed the strange nests took also the pupae and did not need an additional stimulus in the form of a strange nest as is the case in, for instance, *Polyergus rufescens* (Dobrzańska and Dobrzański 1960). Since, in these experiments, we were only interested in particular pupa capturing workers and in the manner of carrying the prey to the nest and not in the course of the assault and the struggle within the strange nest, it were only the pupae that we planted during further experiments. This allowed us to avoid the repeated destruction of ant nests.

The pupa capturing and carrying workers were individually marked and, subsequently, observed.

Uncovering the Tunnels. To investigate the behavior of *L. fuliginosus* in the tunnels and primarily their manner of carrying the prey to the nest, it was necessary to uncover the tunnels and to observe their inside. Lest the workers' normal behavior be disturbed in uncovered tunnels, we made use of the discovery of Lubbock (1888) who, investigating how ants do react to varicolored light, discovered their complete or almost complete indifference to yellow light. To cover the dug up tunnels, photograph plates were, therefore, used with their photosensitive layer infused with a yellow drawing ink. Thus prepared plates were sufficiently bright and transparent to allow for the observation of ants, moving in a shallow tunnel. On the other hand, their behavior in the tunnels indicated that they were sufficiently protected against the sunlight. This may be confirmed by the fact that some workers, leaving such a tunnel, behave in a similar manner as if they were leaving the nest, that is, at first, they frequently hesitate before getting out and crowd near the outlet (Goetsch 1953, Dobrzańska 1959).

RESULTS

Stations. L. fuliginosus is comparatively not very sensitive to the cold weather and does not stop its normal terrain rummage on a cold and rainy day. However, as every other *Lasius,* it is photophobic which makes its activities difficult in the forests having a poor underbrush and, therefore, brightly lit by the sun. In summer time, it is as early as at 9 or 10 a.m. that *L. fuliginosus* avoids all sunlit places. Even a far advanced plunder raid of *L. fuliginosus,* assaulting a strange nest, may be experimentally stopped. It is quite enough to remove the shadow and to light up the way to the attacked nest. Even the most frequented path of *L. fuliginosus* becomes instantly deserted when the sunlight is suddenly thrown on it in daytime. This is precisely the reason why a normal traffic of ants up and down the trunk is observed on the aphid infested trees even in noon hours. If such a tree is sunlit, all the traffic disappears at the foot of its trunk. The workers with their crops, filled with aphids' honeydew, descend the tree and disappear. Likewise, the ascending workers appear on the trunk but they are completely out of sight on the earth around the tree.

It has been revealed that a burrow, making up a shelter for the descending workers, may be always found, dug under the root of an aphid infested tree, frequented by *L. fuliginosus.* In prosperous colonies, some

of such burrows were lined inside with a carton pulp, resembling that of which the nests of this species are built.

For the reasons which I shall present in the discussion, I called these burrows s t a t i o n s, borrowing F o r e l's (1921-1923) term, used by him for the species *F. pratensis* and *L. niger*.

If the ways are lit, the *L. fuliginosus* workers wait at their stations till the hours of intensive insolation pass. However, it is also in other hours that a considerable number of ants are crowding the stations. This fact induced me to study their behavior.

Preliminary investigations showed that, regardless of the presence or absence of aphids on particular trees, stations are dug under almost each tree along the paths, frequented by *L. fuliginosus*. On the plan, shown in Fig. 1, stations were found under each tree marked with a letter. A considerable number of workers may be always found at all stations, located outside the range of tunnels (which will be discussed below). It is beyond any doubt that the stations are attractive to this species because they isolate the ants from external factors, primarily from the light. It results from this role of the stations that uncovering them for observation purposes would deprive them of their greatest attractivity and would disturb the normal mode of life of workers, sheltered in them. Covering them with yellow plates, applied to the exploration of tunnels, is impracticable in the case of stations since they are too deep and their inside could not be observed through the plates. For this reason, after a few stations were dug up to study their structure, I satisfied myself hereafter with either a partial opening, or—during subsequent investigations—a control of all outlet ways from the station. In looking for these outlets, other stations were also found with no paths, leading out of them, although a brisk traffic was observed both on the tree trunk and inside the station. It has been revealed by somewhat deeper digging that underground passages, or t u n n e l s were leading to these stations.

Tunnels. In parts of the forest where earth is covered with the moss, such tunnels are located directly under the layer of the moss which, when removed, reveals them, Where there is no moss, tunnels are dug in the earth, their ceilings mostly situated at a depth of 3 to 4 cm, sometimes, even deeper. Some sections of tunnels run inside the empty birch roots (Fig. 2).

The best developed tunnels are in the neighborhood of the main nest, although some of them may be located near the daughter nests (which I shall discuss below). Most tunnels of an old, prosperous colony of *L. fuliginosus* are " asphalted " with a carton pulp, resembling the material of which the nests of this species are constructed. Originally, tunnels are probably built without " asphalt " and it is only in the course of their

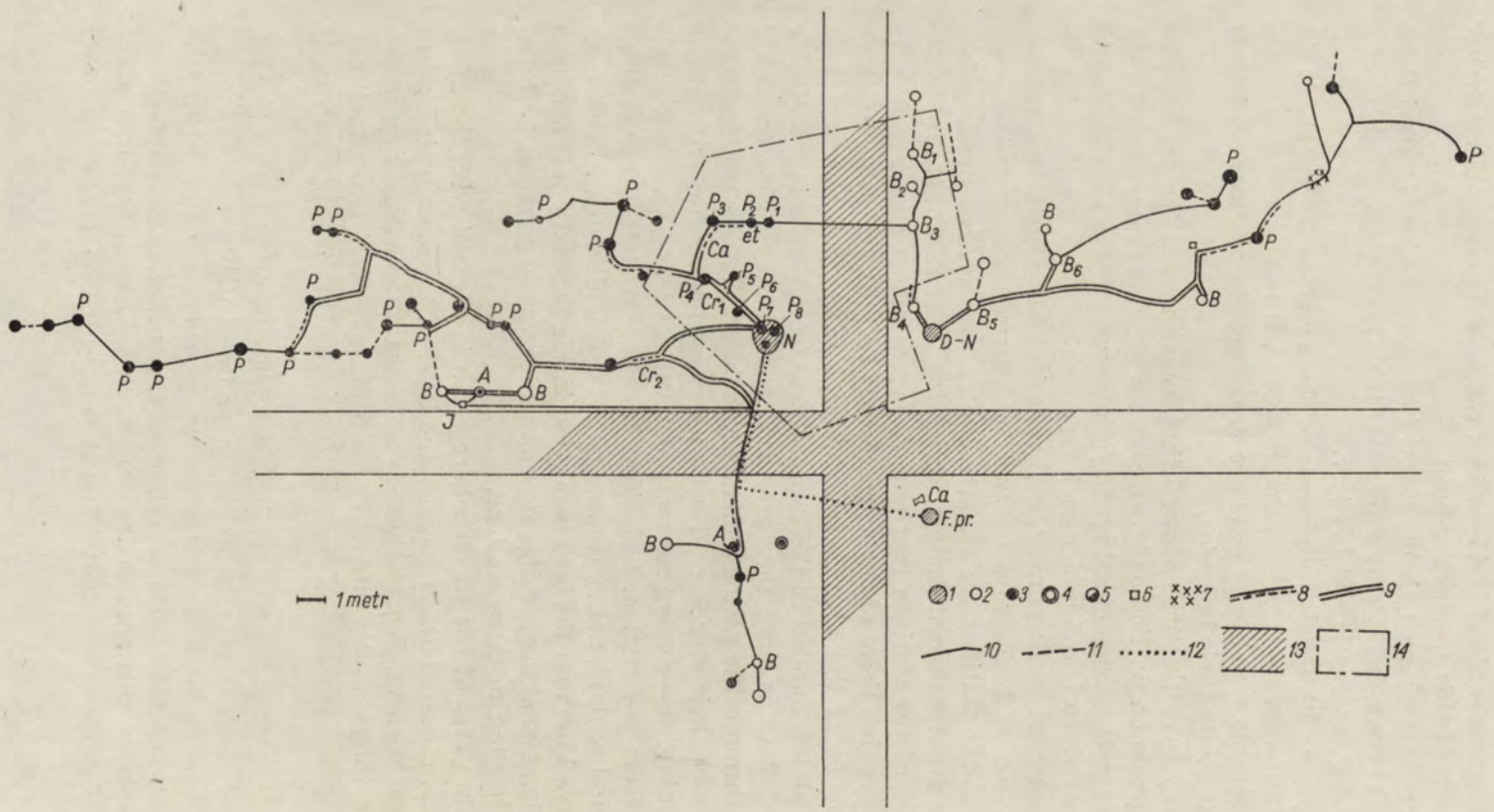

Fig. 1. Location plan. 1, nests ; 2, birches ; 3, pines ; 4, acacies ; 5, oaks ; 6, junipers ; 7, alderwood ; 8, tunnels ; 9, " asphalted " tunnels ; 10, frequented superficial paths ; 11, less frequented superficial paths ; 12, direction of attack to nest of *F. pratensis* ; 13, paths used by people ; 14, section visible in photo 3 ; N, main nest ; DN, daughter-nest ; F. pr., the attacked nest of *F. pratensis* ; B, birches with stations ; P, pines with stations ; A, acacies with stations ; O, oaks with stations ; J, junipers with stations ; Cr, tunnel crossroads with islands ; Ca, captured aphids

being used that they become lined with it. Such a conclusion may be drawn from the fact that the terminating parts of every tunnel are mostly " unasphalted ". As the distance from the nest increases, the unasphalted tunnels disappear, passing into superficial paths.

Fig. 2. A section of an empty birch root with a tunnel inside it

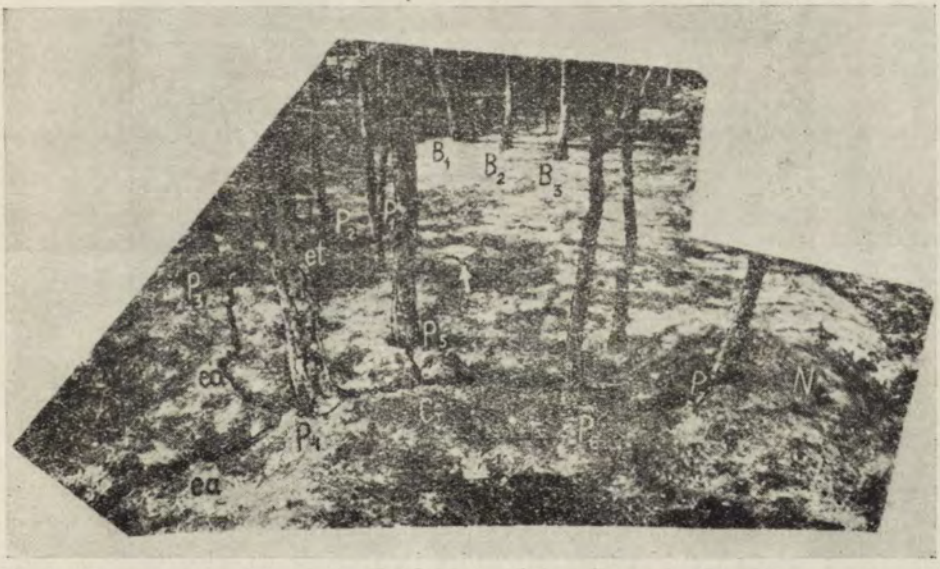

Fig. 3. General view of tunnels, getting out of the main nest. Tunnels are uncovered for taking photographs. A school copybook and a pen are visible in the middle. For explanation of signs, cf. Fig. 1 and the text

The part of the tunnels near the main nest is shown in the photograph (Fig. 3). To take the photographs, the tunnels were uncovered over their entire length. The points, marked " ea ", denote the places where the

" asphalt " ends and those with " et " letters—the places where tunnels terminate and superficial paths begin. The crossroad which, in (Fig. 4), is shown magnified, is marked by letters " Cr ". In this photograph, it is seen that the bends of these tunnels are taken by short cuts and, consequently, islands of ground are left in the middle of the crossroad. It may be seen from the plan (Fig. 1) that the total length of the tunnels in the nest examined amounts to 35 m.

In the paragraph in which stations were discussed, I have mentioned that their role is much less important in the places through which underground tunnels run. There are stations (burrows), that is true, but their traffic is rather insignificant since workers mostly do not stop, passing directly through the tunnels. In my opinion, this shows the protective role of stations which were built first, when there were no tunnels and when workers, running along open ways, sought shelter at them. After the tunnel is built, the entire road becomes a safe shelter. Consequently, the original role of the station loses its importance and the previously brisk traffic disappears.

Fig. 4. Crossroads, marked in Fig. 1 by letters Cr_1, magnified

L. fuliginosus does not, however, construct the tunnels in all places where its safety would seem to require it. During a period of two years, I observed, for instance, a superficial way of this species, running across a narrow path (at most, 1 m wide), used by many people. Since this path was very firm and had a hard surface, several hundreds of ants perished every day, crushed by passers-by. However, over two years of my observations nothing was changed on this path, no tunnel was constructed and hundreds of workers were continuously killed there every day.

Daughter-nests. At a certain distance from the main nest of the colony smaller nests are frequently situated, also built of the carton pulp. Once more using Forel's expression, I call them daughter-nests. In the colony described, only one such daughter-nest (in Fig. 1, marked by letters DN) has been found 3 m from the main nest the entrance to which has been marked by letter N. Around the daughter-nest, tunnels are also built but they are shorter.

During a two-year investigation period in this *L. fuliginosus* colony great efforts were made to discover the ways and manners in which a contact occurs between the main nest (N) and the daughter-nest (DN). However, neither tunnels, nor superficial, directly connecting ways, have been revealed between them. On the area which directly divided N from DN, there were only single workers that appeared now and again and no permanent, much frequented path was formed across that area. These two parts of the colony were connected with each other only indirectly, that is, by the path, marked P_1-B_3. The latter was always frequented but this was a traffic between the feeding ground and the nest or, probably, the daughter-nest. We have never succeeded in finding if any worker went this way directly from N to DN or in opposite direction.

On the basis of two years of experiments and observations (during various periods, depending on the functions carried out and on the feeding ground, a total of over 3,000 individuals were marked in that colony) it may be concluded that there is no permanent contact and no direct communication between these two main centers of the colony, that is, the main and the daughter-nest. Each of them exists separately and, in fact, has its own permanent team of workers. This is not only an individual, but also a territorial division. It was very seldom that the prey, found in the neighborhood of DN (cf. the plan, birch trees, marked B_1-B_6), was carried to N and, even when this happened, it came only from the B_1-B_3 area. On the other hand, the prey, acquired on the N side (pines P_1-P_8), was never carried to DN. The prey, experimentally placed on the road P_1-B_3, was divided by the ants. A part of it was carried by the workers towards B_3 from where it was conveyed further to DN and, another part, was carried through S_1 to N. The ratio of this division depended on a place where the prey was planted on the ants' way. We succeeded in finding a certain point of balance from which more or less a half of the prey was carried to one side and a half to the other. This was correlated with some fixed boundary between the area, rummaged by the team of workers, belonging to N and the area which was a feeding ground of those from DN.

Despite this division, N and DN could not, however, be considered to be separate colonies. Several times, workers from DN were observed as they entered the N nest and, once, it was the other way round. Two times,

an individual was observed which supplied the DN and, hereafter, carried its prey to the N. Thus, the division was not complete, although, a considerable extent of separation was undoubtedly recorded in this colony. This is the more difficult to elucidate as, in DN, we never succeeded in discovering the presence of the progeniture and over these three years, not a single nuptial flight was observed either. It seems, therefore, that the daughter-nest had not its own female.

Investigating the Behavior of Aphid Milking Workers. During a period of 8 years, these investigations have been carried out in strongly variable types of terrain (at Michałówka near Puławy, at Mikołajki, at Suchawa in the vicinity of Spała, at Zdworze near Łąck). They were stretched over such a long period because there were several difficulties to overcome, such as, the lack of durable methods of marking ants, the completely different behavior of the aphid milking *L. fuliginosus* individuals from that of previously studied species and the existence of stations and tunnels which was discovered only in the course of these investigations.

Fig. 5. Aphid milking *L. fuliginosus* workers. Two "full" workers (fw's) visible

The aphid milking *L. fuliginosus* workers fill their crops with aphids' honeydew in a similar manner as other species of ants (Fig. 5). However, their further behavior pattern, is quite different. Walking along the trunks of aphid infested trees, the *L. fuliginosus* workers move chaotically, stopping, turning back and, in their general behavior, resembling the terrain reconnoitering ants. Even if a worker happens to move along a straight line and in a definite direction, it is quite enough to observe it for a few minutes to discover that such movement is short-lived and that, soon, it resumes its usual chaotic activity. This type of behavior is observed even in workers with swollen, filled crops which is never met with in the *For-*

mica species. Such a " full " worker (fw), descending the tree with a visible effort, all of a sudden, turns back without any evident reason, for some time, ascends the tree once more and then, again turns downwards and starts to descend. There were cases when fw's walked to and fro over the entire tree trunk as long as 40 to 60 minutes, doing a vast and apparently absolutely unproductive work before they reached the station at the foot of this tree.

The workers stay at the station for quite a long time, sometimes, even a few hours. In the meantime, similarly as in other species of ants, the fw offers the aphid honey to its fellows met on its way. If, however, after relatively long walking, it does not get rid of the content of its crop, then—as an ultimate result of its chaotic and slow movement with several long stops at each station, met on its way—it walks in a general direction of the main or the daughter-nest. In fact, all fw's which, sometimes, after many hours, reach at last the nest, are the same individuals which took in the aphid honey. Other workers, which, on the way, are treated by the latter with the honeydew, do not fill their crop to carry further their contents but they take in only a drop of the honey for their own use (similarly as, under analogous conditions, is the case in other species).

The workers, descending the tree with " empty " abdomen, were investigated separately. To find out what is it that such workers are occupied with and if, in *L. fuliginosus*, they make up a separate functional group, they were stained with a different color. A total of 412 such " empty " workers (ew's) and 2,627 fw's were marked. It has been shown by further observations that the workers which, in one case, descend the tree with empty crops, in other case may have it filled and in still other cases, they perform a fully different duty. The experiments in which insects were put on the trunk of an aphid infested tree, have revealed that these workers are also interested in other types of the prey. Among the insect dragging ants, there were even the " full " workers (Fig. 6) which was never observed in the species of *Formica*. Several times, such workers carried an insect, and one of them even carried a small stick but, in general, it happens very rarely. On the other hand, it is a fairly frequent phenomenon that the prey are carried by " empty " workers which have previously been marked as " full " ones.

As a result of subsequent studies on carrying the prey to the nest, it turned out that the ants, previously marked as the aphid milking workers, may be also found among those which robbed strange nests and carried pupae. It sufficed to plant a strange nest or some pupae in the neighborhood of the area, frequented by the aphid milking workers and they changed their route, turned and went for the pupae. Even the workers

Fig. 6. Fw attacking a caterpillar

which, at present, were fw's might be met with near the pupae. However, it should be mentioned that they never or almost never carried them and, even if it happened, these were pupae with rather less swollen abdomens. It seems therefore, that a pupa is too heavy a load for an ant whose own crop is filled with secretions. On the other hand, pupae were often captured by workers which once were marked as "full" and which, subsequently, might be met with as they milked aphids.

Investigating the Behavior of Prey Carrying Workers.

A total of 10 spontaneous robbing raids on strange nests were observed and, in 7 cases, such assaults were provoked artificially by planting the entire nests of other species at different distances from the ant paths. In later experiments, only strange pupae were planted (cf. Introduction). In these cases, the pupa capturing *L. fuliginosus* workers were marked individually in a total number of 213 ants. (Fig. 7 represent a marked pupa carrying worker).

In the first experiment, the prey was placed near the B_1-B_2 road. The tunnels were covered with yellow plates (cf. Introduction) and the approaches to the daughter- and to the main-nest were observed. After 40 to 50 minutes, great number of pupa carrying workers started to appear in the tunnel, leading to the daughter-nest but there was not a single one of those which were marked in the course of capturing the pupae. During the

entire observation period, only two pupae reached the main nest and they were also carried by unmarked workers.

Moving backwards along the path from the daughter-nest to the place where pupae were captured, it was only behind birch B_2 that we once more discovered the presence of marked workers, many of them carrying no pupae at all. The observation method was, therefore, altered and, during further investigations, individual workers, marked in the course of pupa capturing, were observed. They were followed by the observers who kept a detailed record of their behavior.

A very interesting manner of supplying the prey to the main and the daughter-nests was revealed in the course of repeated experiments of this

Fig. 7. *L. fuliginosus* worker, stained with dye, carrying the pupae

type. At this opportunity, a few different types of behavior patterns were observed, depending on the place where the prey was found and on a kind of roads that were leading to this place from the nest.

(1) Pupae were placed in the vicinity of the B_1-B_2 road and all workers which took them were marked. At this opportunity, it turned out that the number of the pupa capturing workers is, when pupae are loosely scattered, very limited, mostly not exceeding a dozen individuals. After they were marked, no more new workers were recorded, but always the same, previously marked, individuals appeared again and again and took the remaining pupae.

Most pupa carrying workers disappeared at station B_2 (under the B_2 birch). The first workers, dragging pupae, did not appear behind that tree until 30 to 40 minutes afterwards but not a single one of them was marked. Although, occasionally, the marked workers might be seen between

trees B_2 and B_3, they were always without any load and, after a brief period, they returned to their section of the way before B_2 and, for the most part, as far as the place where pupae were placed.

All workers which carried the pupae behind the B_2 birch (along the section B_2-B_3) were marked with a new, different color. It was not until 45 to 60 minutes after the beginning of the robbery that a greater number of pupa carrying ants started to appear in this place. It has been shown by the further observation of these ants that an analogous process took place under the B_3 birch, that is, the marked workers with pupae disappeared at station B_3 and, after some time, pupae were carried to the other side of the tree but, this time, once more by other, unmarked workers which we stained with the third color. It was also behind the B_4 tree that the necessity occurred of marking (with the fourth color) a new group of workers, carrying pupae. It were only the latter workers that supplied the prey to the daughter-nest. At each of the three stations, located along the way to the daughter-nest, a change of carriers took place as a rule. Each of the workers marked, in general, circulated only between two adjoining stations, taking the prey from one to the other. Each group of workers, marked with a different color, has, therefore, negotiated only a comparatively short, limited section of the way, carrying the pupae from one to the other station. Some single individuals of these groups happened sometimes, but rather rarely, to exceed " their " section of the way but it always occurred when they were walking without the load.

Most pupae, carried by the workers, were handed over by one party of workers to another inside the station. There were cases, however, when single individuals, not reaching the station, delivered their load on the surface. Such workers should be divided into a few types of a different behavior. Some of them actually fought for a pupa against their very active fellows who, leaving the successive station, went out to meet the carriers ; others, readily delivering their burden to such fellows, instantly sped for a new load and, finally, still others threw their pupae on the ground near the stations and, neither waiting for their relief, nor even stopping for a brief moment, ran back to bring a new prey. The latter two types are workers whose entire attention is focused on the operation carried out, that is, at a given moment, on the capture of pupae. They were less interested in the further fate of the prey. A similar, although not so distinct division into types of behavior might be observed inside the stations which, in part, were uncovered to investigate the course of the prey conveying. In this case, there were also different individuals which more or less readily delivered their load, however, none of them left the station, carrying the pupae. It is quite likely, that a station, being a sort

of a substitute for the nest disposes the ants to leave the prey inside it. This may be supported by the observation that a great number of workers never return to the nest or to its daughter-nest but permanently stays at a given station.

It must be emphasized that these considerable differences in the behavior pattern of prey carrying workers occurred primarily among the individuals which were directly capturing the prey, that is, foraging all over the feeding grounds. In further stages, when pupae were only carried from one to another station, these differences in behavior were distinctly decreasing. In these stages, the more impulsive individuals differed only in their going out of the station to meet the carriers and to take over the pupa as soon as possible.

Thus, the workers, rummaging the feeding grounds, display much greater excitation and individual variability than those, walking along permanent roads and staying at the stations. This agrees with the division into types of behavior patterns I introduced for the previously investigated species of ants (Dobrzańska 1959).

(2) When the prey was being carried to the nest along the road which, apart from the P_1-P_2 section, ran exclusively by tunnels, the behavior of workers changed. As it has already been mentioned above, the number of pupae, carried to the main nest, depended on the place where the prey was placed on the P_1-B_3 road, that is, it increased the nearer it was the P_1 point. The workers, carrying the prey towards the main nest, attempted to carry it as far as possible and changing the carriers did not take place in such a strict manner as it occurred on the way to the daughter-nest. There were workers which handed over their prey close to P_1 and, sometimes, they even placed it on the ground and departed without waiting for their fellows to take over the load. However such instances were rather exceptional. Most ants tried to carry the prey as far as possible, avoiding the stations at which the traffic was slight. Some more skillful individuals succeeded in carrying the prey as far as the long P_3-P_4 section and it was only in this place where they allowed other ants to take away their load. The fights for pupae were very stubborn and, sometimes, the combatant ants could not be dispersed by hand. There were single workers which adroitly avoided all attacks and carried the prey even further. This was undoubtedly an individual skill and obstinacy since a few workers were observed which, with their prey, always reached further points than the other ones. Sometimes, they even happened to carry the pupa to the very nest. There were cases when such an obstinate worker, after turning over the pupa, " thought better of it " and, after a moment, overtook its adversary and snatched away the prey.

(3) Finally, the third type of carrying the prey has been recorded, that is, carrying it over a quite new area.

Natural attacks of *L. fuliginosus* on strange nests were observed more than once. Sometimes, it took place far from the intruders' colonies. It was always observed that the prey was carried to the nearest permanent road of *L. fuliginosus* by the individuals which directly took part in the robbery. This was most distinctly seen in the case when the attacked nest was situated in an area so far little frequented by *L. fuliginosus* and at a considerable distance from its own nest. Here is the description of one of such attacks on a small nest of *F. pratensis* (F. pr. in Fig. 1).

It was situated, in a straight line, 8 m from the *L. fuliginosus* nest but, since the approach to the assaulted nest required a certain detour (cf. Fig. 1), the total distance covered by the robbers during their raid amounted to about 11 m. The intruders' path led across two carriage roads, one of them wide and much frequented. The attack took place after two days of rains which momentarily revived the forest, parched by a fortnight of heat and draught (summer, 1963).

It is of much interest that, although the distance from the attacked nest to the daughter-nest of *L. fuliginosus* was almost three times shorter (cf. Fig. 1), not a single captured pupa was taken to this daughter-nest, all of them were carried to the main nest. This undoubtedly results from the fact (depicted in the location plan) that the assaulted nest of *F. pratensis* was found and attacked by the workers, belonging to the community of the main nest.

Marking 140 robbers allowed us to discover that all pupae were carried, without any change of carriers, all the distance of 11 m which divided the robbed from the robbers' nest. Not a single case was observed of snatching away the prey by one worker from another.

It is worthwhile emphasizing that it was as early as during the robbery and the battle that a great number of the *L. fuliginosus* workers milked the aphids, just captured from *F. pratensis* and this took place hard by the invaded nest (" Ca " in Fig. 1).

DISCUSSION AND CONCLUSIONS

Lasius fuliginosus is one of the most frequently and commonly met with species of ants, occurring in our forests and extensively described by the biological literature, but our knowledge of its ethology is rather limited. The most part of information on this species concerns the structure and the building materials of its original nests and the secretions, related with the production of the carton pulp and with the growth of fungi. Much has also been written about the foundation of nests and a possible

parasitism of this species but there is the difference of opinions on this subject and these problems are still under dispute.

As a matter of fact, there are contradictory opinions on many problems of the *L. fuliginosus* biology. There are different views on the composition of mechanical particles, used to make the carton pulp. The fact that the *L. fuliginosus* nest walls are built of vegetal particles stuck together by means of secretions, coming from workers' glands was discovered by Meinert (1860). Lagerheim (1900), who was first to describe the nests in detail, found that these particles need not necessarily be of a vegetal origin and that the carton may be also built of earth or sand which was confirmed by Lannoy (1908) but contradicted by Raignier (1952) who maintains that only vegetal particles are used by these ants to construct their nests.

The original opinion that carton nests are always built in a tree or in its roots, has also been undermined. Ruzskii (1905) describes the nests of *L. fuliginosus*, found in the soil under stones, while Forel (1874), Brun (1913), Stitz (1939), Gösswald (1932) and Wilson (1955) — those dug directly in the soil. Donisthorpe (1927) and Wilson (1955) consider all the types of nests, mentioned above, to be typical.

Rich materials have been collected with regard to the trees, chosen by these ants to found their nests in them. According to Lagerheim, the oak is a favorite tree of *L. fuliginosus*. Ruzskii agrees with this view but notes that there are also nests, built in the trunks of lindens, elms and birches. Lannoy mentions the willow, Forel — the walnut, Stitz — the willow and the poplar.

Completely contradictory are the views on the nature of the settlement places, chosen by this species. Nasonov (1889) maintains that this species settled in woods and shaded places. Stitz is of the opinion that *L. fuliginosus* likes dry sites but he notes, at the same time, that this species also settles on soaked grounds. The same was noticed by Donisthorpe when he described the nests, founded in the soaked sandy ground near the sea.

As to my observations, I met *L. fuliginosus* in dry, young woods, well lit by the sun (Zdwórz), on a pond, situated in an old, wet, strongly shaded park at Puławy and on open shores of Masurian Lakes, devoid of vegetal cover.

In my opinion, all these contradictions may be explained if we assume that the species of ants under study has the capability of adaptation to considerably variable climatic and biocenotic conditions. Attention should here be paid to the unusually widespread settlement of this species. Stitz

(1939) maintains that it is met with all over " its " area, that is, from the Scandinavia to the Mediterranean islands and from Portugal to Japan. Ruzskii presents the boundaries of the *L. fuliginosus* settlement, expressing the view that this species lives in all places where leafy woods occur.

The contradictory opinions of many authors are probably caused by the fact that their observations were collected at many varying sites. According to my findings, *L. fuliginosus* shows a marked plasticity, depending on biocenotic conditions. On wet territories, it builds its nests in the tree trunks, while in dry places, it digs them in the earth. I have not made investigations from this point of view but it is quite possible that the composition of the building material also depends on the degree of moisture at a given site.

Tunnels and stations are also elements of the adaptation to definite conditions. As I have mentioned in the experimental part of this paper, the tunnels were, in general, built in places where the foraging of this photophobic species might be disturbed by the excess of light.

The extensive network of tunnels is undoubtedly favorable to the domination and reconnaissance of terrain by this species. In the case under study, this network covers an area of at least 280 sq m (35×8). Over this entire area, unlimited number of reinforcements may be summoned at any time and for any purpose (finding prey, encountering danger, etc.). The fact that in the literature there is very little on tunnels, built by *L. fuliginosus* is beyond my grasp, the more so as many authors describe the roads used by this species. Thus, for instance, flat roads, free of any vegetation and distinctly seen between particular nests of the *L. fuliginosus* colonies, are described by Scheiderer (1913). They are mentioned by Forel (1921–1923) who ascertains that they are less distinct than the roads, built by *F. pratensis.* Brun (1924) describes carefully smoothed roads, with all obstacles removed, stretching for some scores of meters, belonging to *F. rufa* and *F. pratensis* ; in his opinion, *L. fuliginosus* has similar roads. Worn paths, leading to places where aphids are in abundance or used as " streets " between related nests of *L. fuliginosus* are also discussed by Stitz. The formation process of such roads is, even in detail, described by Goetsch (1953).

It is a surprising fact that, among all these descriptions of roads of this species, it is only a few and rather inexplicit mentions, concerning the tunnels. I met with the first mention of this type in Lannoy (1908) who hints that *L. fuliginosus* builds tunnels through obstacles ; unfortunately, the author lets it go at that and does not enter into any details. Donisthorpe (1927) refers to Rothney (1893) who described two oak trees which, growing on opposite sides of a gravel path, were con-

nected with each other by *L. fuliginosus* by means of a tunnel. And finally, Donisthorpe himself, describing a certain road of this species, admits that he could not discover the beginning of this road and, referring to Rothney's data, considers it to be possible that an underground tunnel might be hidden underneath. That is all on *L. fuliginosus*' tunnels which I have succeeded to find in literature.

My own firm belief is that in the case, described by Donisthorpe, he indeed had to do with a tunnel. On the other hand, I never met with such a case as that, described by Rothney, that is, of a tunnel, dug below the path used by man. I want it to be clearly understood that, speaking about the adaptive capabilities of *L. fuliginosus*, I mean, mostly and primarily, its permanent adaptation to the variable climatic and biocenotic conditions. As to the plasticity and adaptation to definite variable situations, I must admit that on the basis of my own observations of the tunnels I am rather skeptically disposed in this respect. I have never succeeded in watching a tunnel, built in some dangerous place, as a protection against any nonclimatic factors. The superficial road I described which was leading across the beaten path, frequented by human beings, seems to be the best example. The question remains unexplained if the rare cases of building tunnels below man's paths come from the lack of adaptation to definite conditions or are caused by the hard beaten ground, forming the surface of these paths. At any rate, Rathney's description may be reckoned among rare cases.

The colonies of L. fuliginosus are polycalycine in character, that is, with the lapse of time next to the main nest smaller nests branch off, which connect into a common colony (Donisthorpe 1911, Scheiderer 1913, Stitz 1939). These new, branched-off nests are called by Forel (1921/23) daughter-nests (succursale). At the same time, however, he emphasizes that, using this expression, he means small, separate nests, situated at a certain distance from each other, which, in time, may become complete nests of the polycalycine colony.

I would like to emphasize that, according to Forel's definitions, the daughter-nest will only in future become a complete nest but, at present, it is not. This author does not, however, explain what is precisely this difference, which are the characteristic features of the daughter-nest in contradistinction to the complete nest. Now, on the basis of my own observations, I would attempt to define this difference : it seems that such a new nest should be called a daughter-nest as long as it has not its own female and its own progeniture (as is the case of the colony I described).

Finally, Forel uses another name, a station which I have borrowed. He applies this name to shelters, dug in the earth which are supposed to play the role of a hiding place in the night or as a protection against the

rain and cold. The author terms them as "very small, partial nests". Although he does not mention *L. fuliginosus* as one of the species which have the stations (instead, he names *F. pratensis* and *L. niger*), his definition of these stations as temporary shelters is in full conformity with what I showed for *L. fuliginosus*. It should be added that, for *L. fuliginosus*, they also serve as a protection against the light.

It is an open question whether or not the stations become in time the daughter-nests. For my part, I consider it quite possible.

The division of territory and work is a separate problem. In all aphid breeding species of ants, the workers with social stomachs, filled with honey (fw's), travel from aphids to the nests. The abdomens of such workers are markedly swollen. In all species of *Formica*, I investigated, such workers rapidly move towards their nest, using as short a way as possible. Sometimes, they may stop to give a drop of honeydew to a starved fellow ant and then, immediately set out again. When they return from the nest to the aphids, these workers (now, with empty crops) cover their non-stop way at a considerable speed. The workers make up a separate functional group (Ökland 1931, Kiil 1934, Dobrzańska 1959) which, with regard to its composition, belongs to one of the most stable ones. Another group is formed by workers, staying on aphid infested trees but descending them with "empty" abdomens (ew's) and chaotically walking to and fro all over the tree trunk. It has been shown by investigations (Dobrzańska 1959) that these individuals do not visit aphids; probably, they use the tree trunk as their feeding ground. In the present paper, it is being shown that these conditions in *L. fuliginosus* are different. The two groups of workers (fw's and ew's) do not make up separate functional groups and, on the other hand, together they also do not constitute any separate group. They may easily pass to other functions in which they have nothing to do either with aphids, or with a given tree. They are united only by staying in a given area.

On the basis of the material I collected over several years of studies, I conclude that, in *L. fuliginosus*, the organization of work is not based on the division of functions as is the case of the *Formica* species. The division of territory is the basis for this organization. A permanent stay of a considerable number of idle workers at the stations resembles the organization of a beehive where idle workers await the summons of scouts. In *L. fuliginosus*, one may discover an even higher efficiency since the reserves need not be looked for as far as in the nest. They are always available, waiting at the stations and even walking about the roads. Accordingly, one may expect this species to have an efficient system of mutual information.

Such an organization of work exacts from workers the capability of switching over from one to another operation. The fact, described above, of some workers which were plundering the strange nest and, in some moment, when the battle was still fought, switched over to milking aphids may be the best example of such capability. It is worth mentioning that that robbery took place far from the robbers' nest and, therefore, the active, militant and excitable workers took part in it, quite different in character than the aphid milking workers in *Formica* (Dobrzańska 1959).

On the other hand, the chain transport I discovered in this species, makes up a proof for the division of territory. Each section of the area, controlled by a colony of *L. fuliginosus*, has its own group of workers, conversant with all features of this territory and, if necessary, moving over it efficiently and faultlessly.

Using a name, a chain transport, to denote the conveyance of the prey by the *L. fuliginosus* workers, I must emphasize that this phenomenon is different from that, described by Stäger for *F. rufa* (1924—1925, 1935). The exchange of the load carrying workers, described by this author, is caused by the inefficiency in coördinating the coöperation of a few workers, carrying the same load and by the fact that they do not know the area (the author mentions that this process becomes intensified if the obstacles on their way are negotiated in an awkward manner). Thus, the "chain transport", described by Stäger is a negative phenomenon and it does not speed up the transportation of the prey to the nest but, on the contrary, according to the author, slows it down several times.

The chain transport in *L. fuliginosus* results from a considerable degree of the territory specialization, that is, from the training of particular individuals in crossing separate sections of an area. Such a phenomenon is undoubtedly adaptive in character and it speeds up the transportation of the prey. Moreover, the name, "chain transport" seems to imply a wellorganized conveyance of the load carried and may be better applied to *L. fuliginosus*.

A different behavior of the prey carrying workers near the nest may be justified by the presence of tunnels, dug in this place. Tunnels are, to a much greater extent than the superficial roads of the *Formica* species, as if part of the nest and its prolongation. In the tunnels, there are the same isolation from external factors and the same smells. This is the reason why the original role of the stations which, on superficial roads, are a resting place from the influence of the external factors, disappears in the part of the area with tunnels and, therefore, the stations become, of necessity, "reloading stops", because a resting worker, tired by external stimuli and needing such a rest after its action, may easily hand

over its load to its already rested fellow worker. It may well be that a strict division of territory took place precisely in this manner : a worker, deprived of its prey at the station, after some time of rest, of necessity sets out and returns for a new prey.

In the tunnel, there is a quite different situation. It is the stay in it that is the rest itself. The rest inside of a tunnel does not require making stops and interrupting the operation of carrying the load. On the other hand, all possible " specialists ", active only on a given stretch of the road or tunnel, are, of necessity, rather passive and little excitable as all workers, permanently isolated from external factors and, therefore, they are not enough predestinated to take over the prey from the individuals which came with this load, that is, those feeding in the field, active, excitable and militant.

The lack of the chain transport in a new, unknown area may be easily explained. In such a territory, there are no " specialists ", conversant with its characteristic features and there are no " reloading stations." On the other hand, such a raid is undertaken by the most aggressive and active workers which are reluctant to give up their prey.

Bringing to the nest such specific kind of the load as the liquid honey of the aphids is marked by different aspects. This load neither may be abandoned and left to be transported further by other workers, nor snatched away by one worker from another. This is the reason why " full " workers which did not, on their way, fed the fellow ants with the contents of their crop, must carry their load to the nest or to the daughter-nest regardless of the distance they have to cover.

On the basis of the facts described and of the entire reasoning I conclude that : (1) in *L. fuliginosus*, there is no division of work as concerns external functions (outside the nest) ; (2) the ants of this species foraging their feeding ground according to the principle of the division of this area between particular, permanent groups of workers ; (3) this reconnaissance is considerably facilitated by the network of underground tunnels ; (4) the lack of the division of work in this species implies the existence of a very accurate system of conveying information, similar to that, observed in bees.

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Book reviews

Progress in Biophysics and Molecular Biology. Vol. 14. Edited by J. A. V. BUTLER and H. G. HUXLEY. Published by Pergamon Press, Oxford-London-Edinburgh-New York-Paris-Frankfurt, 1964, pp. 348.

Progress in Biophysics and Molecular Biology publishes articles on the current topics written by known specialists. Volume 14 now presented contains six articles concerning photosynthesis, lysosome enzymes, active transport across the cell membrane, muscle relaxing factor, mechanism of action and the active centre of alkohol dehydrogenases, and physical chemistry of phospholipids.

1. L. N. M. Duysens from the Biophysics Laboratory of the University of Leiden is concerned with "Photosynthesis". The author describes methods and techniques suitable for the study of photosynthesis. Some of them may be useful for other investigations as well. In the chapter on over all reactions of photosynthesis, the author summarizes some results and concepts based on measurements of the rate of gas exchange during photosynthesis, and the quantum requirement. In next chapters, he discusses the pathway of the light energy from the photosynthetic pigment molecules via chlorophyll A or bacteriochlorophyl to the reaction centers, and the experimental evidence for the existence and function of the reaction centers. Finally the "dark" redox and phosphorylation reactions, the reactions leading to the reduction of carbon as well as the hydrogen and electron transport in photosynthetic organism and some interesting speculations about the evolution of photosynthesizing cells are presented.

2. In the article on "The subcellular localization of the lysosome enzyme and its biological significanse" G. A. Levvy and J. Conchie from the Rowett Research Institute, Bucksburn, Aberdeen, discuss critically "the biochemical evidence on which the lysosomal theory was founded, and upon which it stil rests.

This theory deals with certain hydrolytic enzymes associated with the cytoplasmic granules, within which their activity is restricted by enveloping membrane. The original theory was based almost entirely on results obtained with β-glucuronidase in mouse liver and with acid phosphatase in rat liver. However, a large number of the hydrolytic enzymes in the mammalian cells are not associated with the cytoplasmic granules. Sometimes an enzyme could be essentially "cytoplasmic" in one tissue and particle-bound in another. It is difficult to see how to differentiate between the "lysosomal" enzymes and the other hydrolytic enzymes which are not particle-bound or not latent. Moreover, the lysosomal particles are so heterogenous that they overlap both mitochondria and microsomes hence their identity with these granules is still under discussion.

3. J. C. Skou from Physiological Institute of University of Aarhus, Denmark, reviews the very interesting and controversial problem of "Enzymatic aspects of active linked transport of Na^+ and K^+ through the cell membrane". The ($Na^+ + K^+$)-activated enzyme system which hydrolyzes ATP has been isolated from a large number of tissues, its asymetry in affinity to Na^+ and K^+ indicates that the site

of the inhibitory effect of K^+ is identical with that of activating Na^+, having several times greater affinity for Na^+ than for K^+. This system is located in the cell membranes and probably being also present in other parts of the cell. The inhibitory effect of cardiac glycosides on the activity of the system due to Na^+ and K^+ shows close correlation to its effect on the active transport or cations across the cell membrane. This finding leads the author to a conclusion that the enzyme system is either the transport system or a part of it. At the end of his article J. C. Skou gives an elegant proposal about the possible mechanism of the active transport of Na^+ and K^+ across the cell membrane as liked with ATPase activity.

4. Wilhelm Hasselbach from Institute for Physiology in the Max Planck Institute for Medical Research, Heidelberg, gives a systematic review on "Relaxing Factor and the Relaxation of Muscle". The aim of this article is to discuss the present knowledge concerning the efforts of identification of physiological relaxing factor as well as the understanding of the mechanism of its action. The autor presents the studies on the inhibitory effect of muscle vesicles (fragments of sarcoplasmic reticulum) on the interaction of L-myosin and F-actin, based on the removal of free calcium from the medium. On the basis of the present evidence it is postulated that *in vivo* the calcium pump of the sarcoplasmic reticulum takes an essential part in the intracellular regulation of muscular activity by changing the concentration of free calcium ions in the muscle.

5. "The Mechanism of Action and the Active Centre of the Alcohol Dehydrogenases" is reviewed by J. S. McKinley-McKee from Medical Research Council and Postgraduate Medical School, London. On the basis of the numerous experimental data obtained by the physicochemical methods of studying enzyme-coenzyme complex, and enzyme stereospecificity to both substrate and coenzyme, the author discusses the probable structure of the enzyme-substrate and/or coenzyme complexes and the current theories of the active centres of the alcohol dehydrogenase. It is interesting that there is evidence for the existence of four subunit of YADH, each with one active site. In contrast, LADH contains two active sites and has approximately half the molecular weight of YADH. Therefore two single active site sub-units in LADH molecules are likely to exist.

6. D. G. Dervichian from the Department of Biophysics in the L. Pasteur Institute, Paris, is concerned with "The Physical Chemistry of Phospholipids". D. G. Dervichian discusses "The physical chemistry of phospholipids". The unique physico-chemical properties of phospholipids are the result of the double nature, amphiphilic and amphoteric, of their molecules. Marked independence of the paraffin chains and the polar groups, bound-up in the same molecule, results in that they can react in an autonomous way with the neighbouring molecules, including water. A variety of consequences follow these special characteristics which are of utmost importance for the structure and function of the living cell. The knowledge of the physico-chemical behaviour of phospholipids in biological systems is essential for understanding of the ultrastructure of the biomembranes, as well as of several processes underlying the function of cell and subcellular structures. The excellent article by Dervichian covers a great range of problems, related to the physical and chemical properties of this important group of compounds.

This book may be of great interest not only to biochemists and biophysicists *sensu stricto* but also to many scientists working in various fields of biology.

Zofia Zielińska, Warsaw, Poland

Cena zł 27.—

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