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SUBTHALAMUS IN DOG BRAIN

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The aim of this paper is to describe, on the basis of myelo-and cytoarchitectonics, the division, topography and structure of the subthalamic nuclei in the dog. The first author who described the subthalamus was Forel (1877). He proposed this term for the area lying orally to the mesencephalon including the subthalamic nucleus, zona incerta and fields H_1 and H_2. Some authors add to the subthalamus the entopeduncular nucleus (lying below the internal capsule), the tegmental field H of Forel or the red nucleus and substantia nigra. According to our observations, the subthalamus includes the subthalamic nucleus of Luys, the zona incerta, the nucleus of field of Forel, fasciculus thalamicus Foreli (H_1) and fasciculus lenticularis (H_2). The subthalamus in the dog is a small region lying in a ventrolateral part of the diencephalon squeezed between the thalamus (dorsally), the hypothalamus (medially, ventromedially) and internal capsule (ventrolaterally). Caudally it borders on the tegmentum.

MATERIAL AND METHOD

The study was carried out on a series of frontal sections of the dog brain stained by the Weigert–Wolters method (50 μ sections), as well as series of frontal sections, stained alternately by the Klüver–Barrera and the Schultze silver methods (20 μ sections). The results were compared with sagittal and horizontal sections of the dog brain, stained by the Weigert–Wolters, Klüver–Barrera and Schultze methods. A total of seven series were used for this study.

OBSERVATIONS

Subthalamic nucleus of Luys (Fig. 1 and 2, CL)

The subthalamic nucleus is the largest nucleus in the dog's subthalamus. It is situated above the internal capsule, and the posterior lateral hypothalamic nucleus. It the frontal and sagittal sections it is shaped like

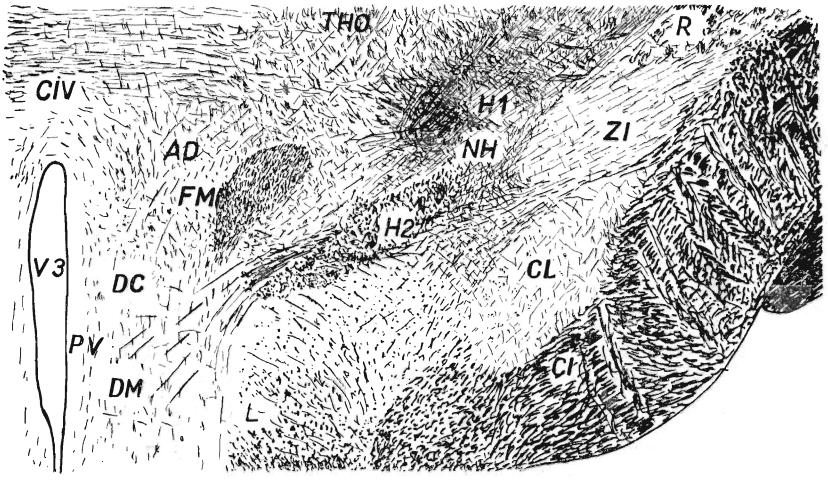

Fig. 1. Frontal section of the frontal area of the subthalamus of the dog. Weigert-Wolters stain.

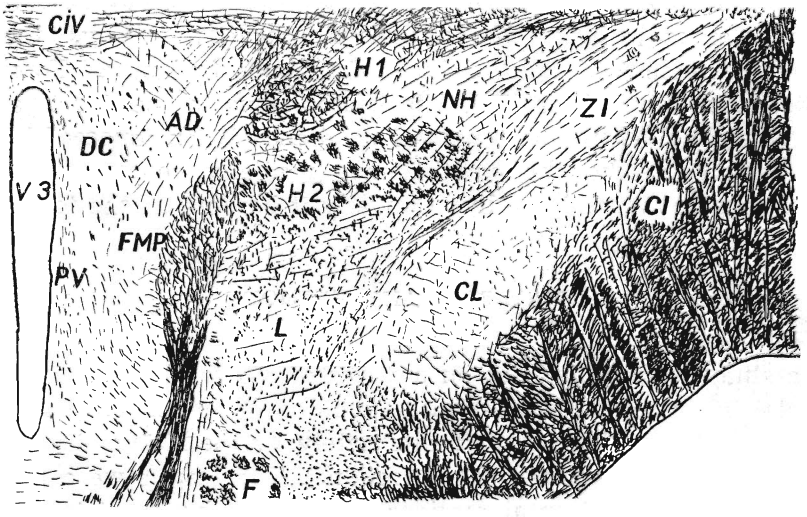

Fig. 2. Frontal section of the caudal area of the subthalamus of the dog. Weigert-Wolters stain.

a biconvex lens lying horizontally. The dimensions of this nucleus in the dog are 2.2 mm (orocaudally), 1.2 mm (dorsoventrally) and 2 mm (mediolaterally). Dorsally, the nucleus borders on the zona incerta, laterally, lateroventrally and oraly adjoins to internal capsule, and ventrally to the posterior lateral hypothalamic nucleus. Behind the nucleus (ventrocaudally) we can easily found the substantia nigra well visible on sagittal sections.

Weigert-Wolters sections show a set of well myelinized delicate fibers running in various directions in the subthalamic nucleus in the dog's brain. Only few long bundles of fibers may be seen among more numerous single fibers. Nine systems of connections have been distinguished, but their directions of conductions are not established.

The first system of fibers well visible in the sagittal sections consist of bundles of fibers running orocaudally across this nucleus. The diameters of the bundles are about 30 μ and they contain 7–10 thin nerve fibers each. These bundles leave the nucleus through the caudal boundary and while running dorsally they disperse in the tegmentum. The bundles situated on the ventral part of the nucleus concentrate together coming out as the subthalamotegmental tract (Singer 1962). This tract separates the subthalamic nucleus from the substantia nigra situated ventrocaudally.

The second system is made up of the fibers which enter subthalamic nucleus from the lenticular ansa. They penetrate through the lateral and ventral border after passing across the internal capsule. This system consists of a few thick fibers 4 μ in diameter. The fibers are thicker than in the first system and are stained stronger by the myelin method.

The third system is built of thin fibers 1–2 μ in diameter taking origin in the internal capsule. These fibers run out from among the bundles of the internal capsule and after penetrating through the oral or lateral border along the whole subthalamic nucleus they assume an oromedial course. This system disperses mainly within the lateral part of the nucleus, but some fibers also disperse in the medial part.

The fourth system includes the fibers extending dorsoventrally between the subthalamic nucleus and the internal capsule (Fig. 1). The fibers come from the nucleus, and after entering the internal capsule run paralelly to its fibers, so it is impossible to trace them.

The fifth system is composed of a few single fibers which penetrate the nucleus from its orocaudal side. They belong to the system of the medial forebrain bundle well visible in the horizontal sections.

There are also abundant connections between the subthalamic nucleus and the pallidum. In the horizontal sections we can see the system of orocaudal fibers penetrating into the nucleus. They converge in the

caudal area of the nucleus and form a loose wide tract which runs outside, dorsolaterally above the internal capsule. Afterwards the fibers turn anteroventrally and scatter the pallidum.

The subthalamic nucleus is also connected with the posterior lateral hypothalamic nucleus. The connection is made up of thin fibers (1–2 μ in diameter) slightly myelinated. They leave the nucleus through its ventral and ventromedial border (Fig. 1).

The next system of fibers leaves the nucleus throughout the medial and mediodorsal border. After passing through the H_1 field of Forel (Fig. 1) they enter the dorsal hypothalamic nucleus, but some fibers running more caudally sink into the dorsal supramammillary commissure.

The last connection is built of the fibers disorderly dispersed between the H_2 field of Forel and the subthalamic nucleus.

Only few fibers enter the nucleus from the dorsal supraoptic commissure. They penetrate in the anterior area of the nucleus from its ventromedial side. The fibers run singly and are strongly stained in Weigert sections.

Inside the subthalamic nucleus of Luys of the dog the nerve cells are intensely stained. They are oval in shape and their diameters in paraffin sections are about 20–25 μ.

In the dog's subthalamic nucleus of Luys is the largest nucleus in the subthalamic area. It is homogenous, whereas in the Primates (Whittier and Mettler 1949, Carpenter et al. 1968) the subthalamic nucleus is distinctly divided into two parts: medial and lateral. Both parts are different in cytoarchitectonics and have different connections with the globus pallidus.

The observed connections of subthalamic nucleus with the fibers running from the internal capsule may correspond to the connection described by Carpenter et al. (1968) in monkey brain, which pass from the globus pallidus and may also concern the connection with the putamen and caudate nucleus mentioned by Bochenek and Reicher (1963). These authors mention another connection with the frontal cortex (area 6) which was found in our material.

Nucleus of field of Forel (Fig. 1 and 2, NH)

Nucleus of field of Forel is the second structure in the dog's subthalamus. It is situated between the H_1 and H_2 fields of Forel. The zona incerta and subthalamic nucleus mark out the lateral boundary of the nucleus. Medially in the oral portion it touches the dorsal hypothalamic nucleus.

Nucleus of field of Forel lies in a frontal part of subthalamic area.

The end of the nucleus is situated in region where the H_1 and H_2 fields of Forel unite together.

Nucleus of field of Forel has a connection with the thalamic external medullary lamina. This connection is represented by the bundle of fibers extending laterally from the nucleus to the zona incerta (Fig. 1 and 2). Some fibers sink into the nucleus of field of Forel but the rest of them comes down to the area H_2 of Forel lying below. This fascicle shows a ventromedial course and lies in the frontal plane. Its fibers penetrate the whole area of nucleus.

The next connections of the nucleus of field of Forel is made up of delicate fibers coming from the ventral portion of the thalamus. They enter the nucleus through the area H_1 of Forel. The fibers of this system scatter inside the whole nucleus, but they are less abundant than the first system.

The anterior portion of the nucleus receives the fibers laterally from the zona incerta (Fig. 1). In the nucleus the fibers turn medially and ventromedially. Most of them disperse in it, but some fibers passing through the medial border of the nucleus enter the dorsal hypothalamic nucleus.

The ansa lenticular fibers sink into nucleus of field of Forel ventrocaudally after penetrating among the fibers of the internal capsule. They are thick (4 μ) and strongly stained in the Weigert method. Most of them disappear in the nucleus, but some penetrate dorsally, and after passing through the H_1 field of Forel they turn orally terminating in the region of ventral thalamic nuclei.

Inside the nucleus of field of Forel there are oval cells (12×20 μ), triangular cells (15×25 μ) and circular cells (20 μ), well stained by the Nissl method.

The nucleus of field of Forel occupies the center of the dog's subthalamic area, between the fibers of both fields of Forel.

Some authors do not distinguish this nucleus as a separate part of the subthalamus. Rioch (1929) described it together with the zona incerta. We can not agree with the Rioch's opinion because in the dog, zona incerta and nucleus of field of Forel are different; therefore in this paper they have been described separately.

Zona incerta (Fig. 1 and 2, ZI)

Zona incerta is the most dorsally situated nucleus in the dog's subthalamus. It lies above the capsula interna and the subthalamic nucleus. In the frontal sections this zona is shaped as a horizontally lying rhomb with easily traceable borders.

Laterally, zona incerta borders on the thalamic reticular nucleus, ventrally on the nucleus of field of Forel, and dorsally it separated from the thalamus by the fibers of thalamic external medullary lamina. Dorsomedially in the anterior subthalamic region the zona incerta comes into contact with Forel's H_1 field. Because of a nearly complete lack of orocaudal fibers, it is easy to distinguish the zona incerta from the Forel's H fields.

In frontal sections the zona incerta is composed of a regular set of thin fibers extended slantingly medioventrally, loosely penetrating through the whole nucleus. This is the main system of fibers in this nucleus. In the lateral side it sinks into the thalamic reticular nucleus, and medial part of its fibers enters the nucleus field of Forel and field H_2 of Forel. In myelin sections the fibers of this system are poorly stainable.

The other systems in the zona incerta are less developed. There are a few fibers of the lenticular ansa penetrating ventrally into the anterior region of the zona incerta after passing through the internal capsule. This fibers are thicker (3–4 μ in diameter) and show a stronger staining than the fibers if the first system.

Inside the zona incerta there are also a few bundles of fibers from the ventral portion of the thalamus. The diameters of these bundles are 75 μ, while their lenghts are about 170 μ in the 50 μ sections. These fibers extend ventrocaudally, and they do not leave the borders of the nucleus.

The connection between the zona incerta and the posterior lateral hypothalamic nucleus has also been investigated. These connections are formed by the tract which runs ventromedially outside the zona incerta. After leaving the zona incerta the tract comes along the dorsal surface of the subthalamic nucleus and then reaches the laterodorsal margin of the posterior hypothalamic nucleus (Fig. 2).

The zona incerta lies in the dorsolateral region of the dog's subthalamus surrounded by the thalamus, internal capsule and subthalamic nucleus and has connections with them. According to Gurdjian (1927) the zona incerta in the rat brain receives cortical fibers through the internal capsule and sends the fibers to the tectum, tegmentum and supramammillary commissure. These connections have not been anatomically found in this study.

Zyo et al. (1963) found a bilateral connections of the zona incerta through the dorsal supramammillary commissure. This agrees with our observations.

Rioch (1929) divided the zona incerta in the dog into two parts: zona

incerta proper and caudalis. In our material the zona incerta shows a homogenous structure which does not agree with Rioch's division.

Fields of Forel H_1 and H_2 (Fig. 1 and 2, H_1 H_2)

The fields of Forel are two concentration of nerve fibers. They fuse together at the back of subthalamus, forming the single tegmental H field of Forel situated as far as the mesencephalon (not studied in this paper). Between the fibers of Forel's H_1 and H_2 fields there are small numbers of nerve cells stained intensely in Nissl method.

1. H_1 field of Forel occupies the dorsal area of the subthalamus between the thalamus (dorsally), and the nucleus of field of Forel (ventrally). It forms the medial prolongation of the thalamic external medullary lamina. Medially the H_1 field of Forel touches the dorsal hypothalamic area, caudally the H field of Forel (tegmental), and laterally the zona incerta. In the anterior region the H_1 field shows an oval shape (lying horizontally) while caudally it becomes irregular.

The H_1 field of Forel is made up of well myelinated nerve fibers directed orocaudally. They run caudally to the tegmentum. This system is composed of fibers coming from the medial portion of the thalamic external medullary lamina as well as from the ventral thalamic nuclei.

The fibers from the thalamus sink into the H_1 field singly or forming bundles directed lateroventrally or laterocaudally. Some of them penetrate into the zona incerta (laterally) or to the nucleus of field of Forel (ventrally). Remaining fibers run caudally to the tegmentum. The thalamic fibers are poorly stainable in the Weigert–Wolters method.

The lateral border of the H_1 field is crossed by the fibers from the main system of the zona incerta. They disperse among the other fibers of this field.

In the caudal area of the subthalamus, the H_1 fields are connected bilaterally by means of the commissural fibers which pass by the ventral portion of the adhesio interthalamica area (in the ventral part of commissura interventralis), (Rioch 1929).

2. H_2 field of Forel is a region of many neuronal connections. Rostrally it border on the inferior thalamic peduncle and posterior lateral hypothalamic nucleus. Ventrally it neighbours on the lateral hypothalamic nucleus and the subthalamic nucleus, medially on the dorsal hypothalamic nucleus and fasciculus mammillaris princeps. Laterally it comes into contact with the zona incerta, dorsolaterally with the nucleus of field of Forel and caudally with H_1 field.

The H_2 field is characterized by orocaudal and caudodorsal sets of fibers running singly or more frequently forming bundles which fill up compactly the whole area of the field.

The diameter of these bundles amounts to 70 μ while the diameter of the single fibers amounts to about 4–5 μ. In the caudal region of the field the bundles are much more numerous and they sink into the tegmental area.

The fibers from the lenticular ansa enter the H_2 field on its oral side. After passing between the fibers of the internal capsule or posterior lateral hypothalamic nucleus they reach the lateroventral margin of the H_2 field and dwindle away inside it.

The H_2 field receives a distinct set of fibers from the internal capsule. The fibers of this system separate from the capsula interna in the region between the subthalamic nucleus and the zona incerta. Then they lie along the border of these two structures (Fig. 1 and 2), and partly in the ventral part of the zona incerta. These fibers from the tract which contains the poorly stainable elongated nerve fibers running medially in the frontal plane. They enter the field through its lateral boundary.

The fibers from the zona incerta enter the H_2 field on its lateral border, dorsally to the system from the internal capsule. The fibers of this system run ventromedially and penetrate the whole H_2 field of Forel with no change of direction.

There is a abundant connection between the H_2 field of Forel and posterior lateral hypothalamic nucleus lying ventrally to it. This connection is made up of numerous thin fibers penetrating the border between these two structures. The fibers are not ordered, but run in various directions through the border region, and mingle with the fibers of other systems of the field.

In the medial direction the H_2 field sends off a tract of thick, well myelinated fibers. After passing above the fornix, it turns ventrally and medially. The ventral fibers from the connection of H_2 field with the nuclei of the pars intermedia hypothalami (ventromedial, dorsomedial and posterior lateral hypothalamic nucleus), and the medial fibers from the connection between the H_2 field and the dorsal hypothalamic nucleus.

In the caudal region of the subthalamus there is a bilateral connection of both Forel H_2 fields through the medium of the dorsal supramammillary commissure fibers. They sink medioventrally into the H_2 field and join medially the hypothalamotegmental tract, which runs caudally together with the fibers of the H_2 fields and soon scatters in the tegmentum.

The H_1 and H_2 fields of Forel form two concentration of nervous fibers in the subthalamus. In the literature the H field of Forel is also distinguished (Singer 1962), but this field lies already in the tegmentum,

and in the dog it is composed of fibers passing caudally from the subthalamus to mesencephalon.

According to Bochenek and Reicher (1963), the H_1 field sends off fibers to the thalamus, and Rioch (1929) considers that the H_1 fields is crossed by the rubrothalamic tract.

The H_2 field of Forel occupies a bigger area than H_1 field and contains more fibers, mainly orocaudal. The H_2 field remains in relation with the extrapiramidal system, and has strong connections with the globus pallidus (Carpenter et al. 1968). According to Everret (1966) this field conducts impulses to the red nucleus and medial longitudinal fascicle. The H_2 field in the dog's brain is also connected with the tuberal portion of the hypothalamus and lateral hypothalamic nucleus, but its influence upon vegetative functions has not ben described in the accessible papers.

SUMMARY

The term "subthalamus" is here used for the region situated between the thalamus, the hypothalamus and the internal capsule. The paper is based on a seven complete series from the dog brains sectioned in three principal planes and stained by Weigert–Wolters, Klüver–Barrera and Schultze methods.

The following parts have ben differentiated in the subthalamus of the dog: the subthalamic nucleus of Luys (crossed by a nine fibers systems), the zona incerta (composed of a four systems of thin fibers), the nucleus of field of Forel (between the fibers of the H_1 and H_2 fields of Forel, includes a four systems of fibers), fasciculus thalamicus Foreli (H_1) (four systems of connections), and the fasciculus lenticularis (H_2) (seven systems of connections).

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Abbreviations

AD	Dorsal hypothalamic nucleus	H_1	H_1 field of Forel
CL	Subthalmic nucleus of Luys	H_2	H_2 field of Forel
CI	Internal capsule	NH	Posterior lateral hypothalamic nucleus
CIV	Thalamic interventral commissure	L	Nucleus of field of Forel
DC	Dorsocaudal hypothalamic nucleus	PV	Periventricular area
DM	Dorsomedial hypothalamic nucleus	R	Reticular thalamic nucleus
F	Fornix	THO	Thalamus
FM	Mammillothalamic tract	V3	Third ventricle
FMP	Fasciculus mammiliaris princeps	ZI	Zona incerta

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