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THE MYELOARCHITECTONICS OF THE DORSOMEDIAL THALAMIC NUCLEUS OF THE DOG

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The evolution of the dorsomedial nucleus is closely associated with that of the prefrontal cortex. In man and primates this nucleus attains its highest evolutionary level in connection with the strong expansion of the prefrontal cortical lobes. Many authors (Walker 1938, 1940, Waller 1940, Bonin 1948, Pribram, Chow and Semmes 1953, Krieg 1954, Scollo-Lovizzari and Akert 1963, Akert 1964, Brutkowski 1965), independently have confirmed the existence of three distinct systems of fibres which connect the particular parts of the dorsomedial nucleus with definite cortical regions and described them in detail. Walker (1936, 1938 and 1940) closely examined the cytoarchitectonics of the dorsomedial nucleus in the monkey. He demonstrated the existence of three parts of this nucleus, the magnocellular part, situated medially, the parvicellular part, situated in the central portion of the nucleus, and the paralamellar part, which lies on the lateral side. An analogous division of the dorsomedial nucleus was found in the brain of man by Freeman and Watts (1947). Using the method of retrograde degeneration following surgical lesions of the frontal cortex, these authors localized the cortical projection from the dorsomedial nucleus. Describing the cyto- and myeloarchitectonics of this nucleus in man, Dekaban (1953) ascertained the existence of only two parts, the magnocellular part and the parvicellular.

In carnivores the structure of the dorsomedial nucleus has not as yet been worked out in detail except for the studies carried out by Rioch (1929, 1931), who described the myeloarchitectonics of the whole diencephalon but paid only little attention to the dorsomedial nucleus. An investigation of the normal structure of his nucleus in the dog seems expedient, especially in the light of the recent data concerning the connections of the prefrontal cortex with the thalamus.

MATERIAL AND METHOD

Observations were made on five continuous series of sections from normal dog brains unoperated upon. Removed from the skull, the brains were fixed and embedded in celloidin. Next they were cut into continuous series of sections at 50 μ. Three of these series were cut frontally and stained by the methods of Weigert, Klüver-Barrera and Nissl, whereas two, a horizontal series and a sagittal, were stained by the Weigert method.

Continuous series of detailed drawings were made from each series of sections in each of the three planes, throwing the pictures of slides on a screen by means of a projector. The systems of fibres observed on the sections under a microscope and their course were next plotted on the drawings. The application of sectioning the brains in the three principal planes made it possible to check and reconstruct the course of the fibre systems.

RESULTS

Boundary and shape. The dorsomedial nucleus is a paired structure and the largest nucleus of the medial thalamic group. It is situated centrally and sharply delimited on the lateral and ventral sides by the fibres of the internal medullary lamina, inside which are the paracentral and laterocentral nuclei. The oral pole of the dorsomedial nucleus appears in the region of the posterior portion of the anteromedial nucleus. Dorsally it borders upon the parataenial nucleus (Miodoński 1968) and mediodorsally upon the paraventricular. These nuclei, together with the medullary stria, separate the dorsomedial nucleus from the wall of the third ventricle. Medially it touches the nuclei of the midline and caudally reaches the posterior area of the posteromedioventral nucleus and the place where the habenular nuclei become conspicuous in its dorsal side (Janklewicz 1967). The centrum medianum appears lateroventral to the dorsomedial nucleus.

The caudolateral border of the dorsomedial nucleus extends along the intermediate and posterior parts of the lateral nucleus.

The dorsomedial nucleus as a whole is an orocaudally oriented cylinder, regular in its anterior portion and somewhat lateromedially flattened posteriorly, especially where the parafascicular nucleus and centrum medianum expand (Sychowa 1961).

Cytoarchitectonics. The dorsomedial nucleus of the dog has been divided into two parts according to the size of nerve cells in Nissl sections. These are the magnocellular part, which occupies the medial portion of the nucleus, and the parvicellular part, situated in the lateral portion. However, different types of cells occur in both these areas. A certain number of small cells could thus be found in the magnocellular part and, on the contrary, the presence of large cells among the smaller ones in the other part. Different degrees of dispersion of the cells varying in size in these parts constitute the criterion for their distinction. Narkiewicz and Brutkowski (1967) presented a similar picture of the cytoarchitectonic structure of this nucleus.

Myeloarchitectonics. The bundles of myelinated fibres passing through the dorsomedial nucleus are systems which come from three thalamic radiations: the anterior and intermediate thalamic radiations and the inferior thalamic peduncle.

The anterior thalamic radiation is an assemblage of numerous systems of fibres which connect the frontal cortical region with the anterior and medial groups of the thalamic nuclei. They arise from the white

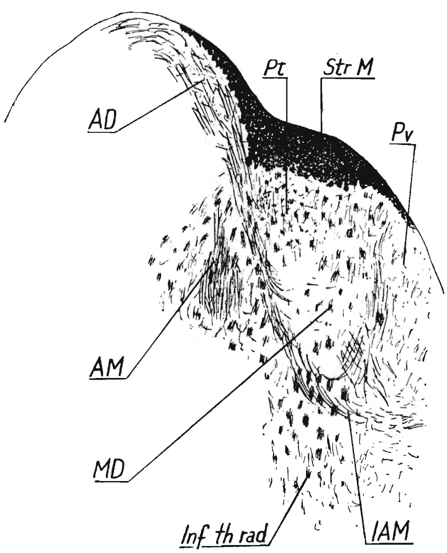

Fig. 1. Myeloarchitectonic picture of the dorsomedial nucleus on the basis of frontal sections, starting from the oral pole towards the caudal (standard series stained by the Weigert metod). Section no. 171b

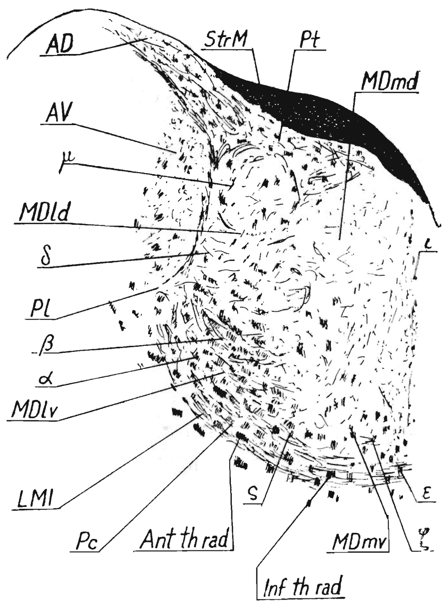

Fig. 2. Section no. 179b (other explanations as in Fig. 1)

matter of the frontal lobes, enter the anterior branch of the internal capsule, in which they go round the caudate nucleus, and reach the oral pole of the thalamus (Fig. 1—3, 6 and 7, Ant th rad). Here the bundles begin to scatter among the anterior nuclei and into the area of the internal medullary lamina, from which they penetrate into the dorsomedial nucleus.

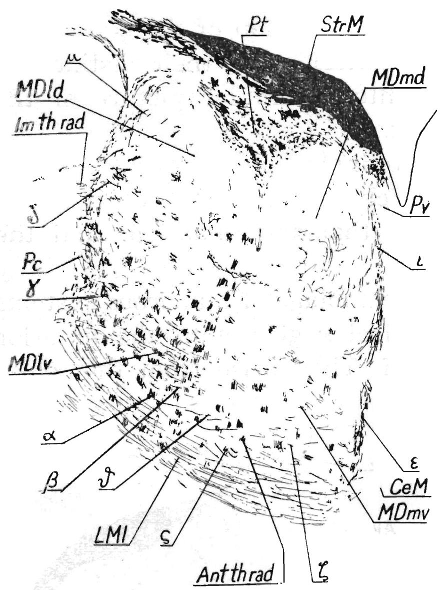

Fig. 3. Section no. 185b (other explanations as in Fig. 1)

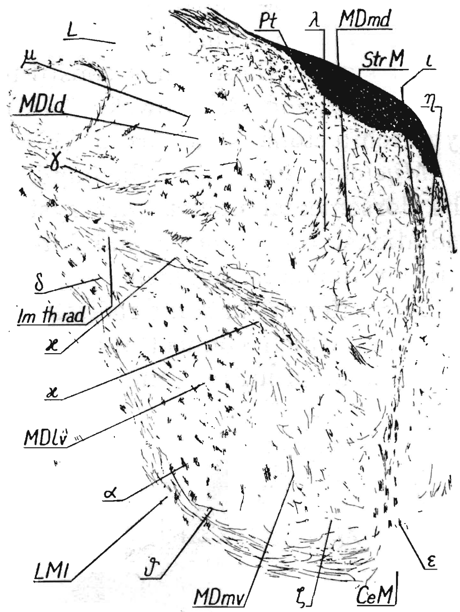

Fig. 4. Section no. 197b (other explanations as in Fig. 1)

The intermediate thalamic radiation enters the thalamus mainly at its lateral wall and it is made up of a large mass of fibres. The direction of radiation is, as a rule, towards the ventral and lateral thalamic nuclei, but a small part of the bundles of this group passes through the internal medullary lamina more medially and sink into the dorsomedial nucleus (Fig. 3—7, Im th rad).

The bundles of the inferior thalamic peduncle come from the olfactory and orbital regions and from the areas situated ventrally to the corpus striatum (among other areas, from the amygdaloid complex). This system becomes distinguishable in the anterior portion of the thalamus, medially to the internal capsule (Fig. 1, 2, and 6, Inf th rad); having crossed the fibres of the internal capsule, it turns dorsally towards the thalamus. Here it meets the bundles of the anterior thalamic radiation and tends to the oral pole of the thalamus, to the anterior and medial nuclei and the anterior portion of the ventral nucleus.

The dorsomedial nucleus does not show a uniform myeloarchitectonic picture all over its area. There is a clear-cut division into two parts, a lateral and a medial, and these may in turn be divided into dorsal and ventral portions. Thick bundles of fibres coming from the inferior thalamic peduncle and anterior thalamic radiation enter the ventral portion of the dorsomedial nucleus. Owing to them, the texture of fibres in this portion is more compact than in the dorsal portion, where there occur thin bundles of fibres and numerous single fibres.

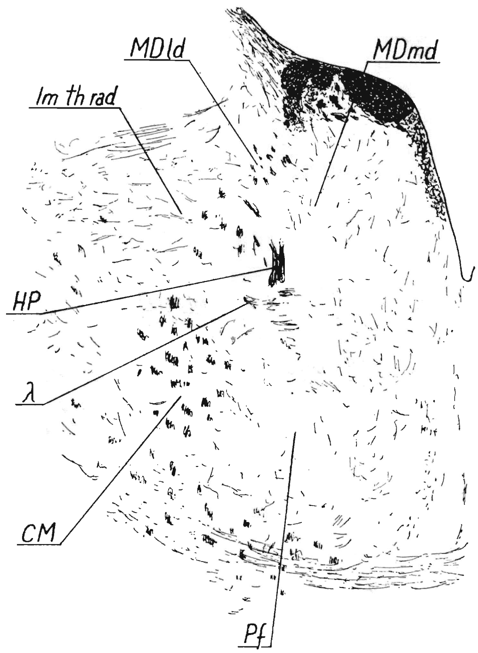

Fig. 5. Section no. 205c (other explanations as in Fig. 1)

In the two above-mentioned portions of the dorsomedial nucleus the lateral part stretches farther to the rear than the medial part and posteriorly they are, besides, separated by the habenulointerpeduncular tract (Fig. 5 and 6, HP). The medial part is overlapped by the parafascicular nucleus, which has connections with the dorsal portion of this part. The centrum medianum expands over the lateral part from the ventral side (Fig. 5, CM).

The lateral part of the dorsomedial nucleus appears as far orally as its pole and extends up to the caudal end of the nucleus. The main system of this part, giving it its characteristic myeloarchitectonic appearance, is composed of bundles which run obliquely from the oroventral side to the caudodorsal and divide this part into two portions, a dorsal and a ventral. In the oroventral region these bundles form fairly compact layers, situated one over another for a third of the height of this part (Fig. 2—4, α). Above these layers, in the dorsal portion, the bundles become looser, split into smaller ones, which in turn break up into single fibres. Without changing their principal caudodorsal direction, they scatter deeper and farther medially to penetrate into the dorsomedial portion of the dorsomedial nucleus, only slightly turning towards it. Here they divide into single fibres.

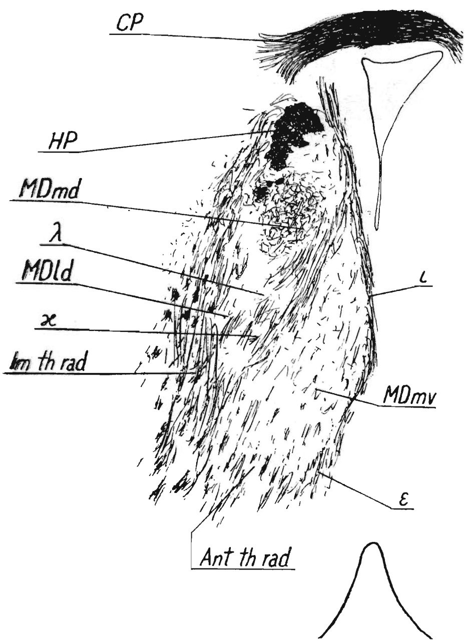

Fig. 6. Myeloarchitectonic picture of the dorsomedial nucleus on the basis of horizontal sections (Weigert). Section no. 183a, laid dorsally

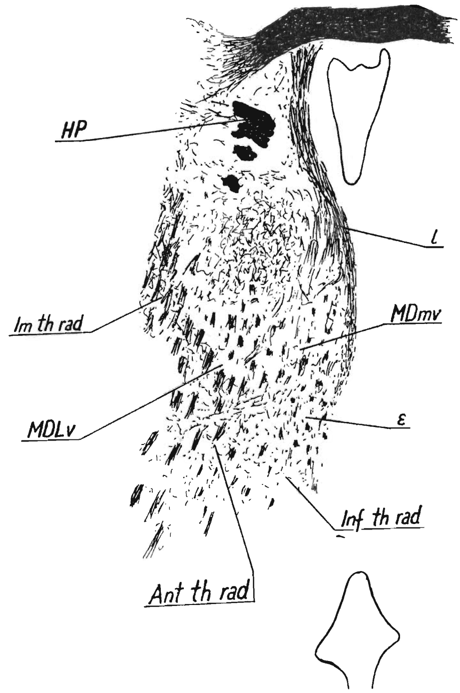

Fig. 7. Section no. 191a, laid ventrally (other explanations as in Fig. 6)

In addition to this large system, one can distinguish several smaller ones, which vary in their courses.

In the ventral portion of the lateral part of the dorsomedial nucleus there occur long single fibres which separate the layers of the compact bundles. The system of these fibres extends in a subhorizontal plane (Fig. 2 and 3, β) and can be traced successively in the ventral nucleus, the internal medullary lamina, and the dorsal portion of the medial part of the dorsomedial nucleus. It seems to be an association system.

Dorsal portion of the lateral part of the dorsomedial nucleus. In the frontal sections the texture of fibres at half the height of the lateral part is somewhat different from that in its ventral portion. Neither are the bundles of fibres in the dorsal portion of the lateral part packed up so closely as in the ventral portion, and they show various directions of their course. For the most part, they are derived from the intermediate thalamic radiation and form an irregular and loose pattern of texture of fibres which run from the lateral side towards the medial. Coming from the orolateral side, part of the fibres take a medial direction (Fig. 3 and 4, γ), whereas others which also extend medially come from the dorsolateral side (Fig. 2—4, δ). Some bundles become looser, breaking up into thinner bundles (of several fibres each), and somewhat more medially, into particular fibres.

Small bundles, of several fibres each, come from the intermediate thalamic radiation through the ventral nucleus and internal medullary lamina and enter the dorsomedial nucleus at its lateral wall (Fig. 2—4, μ). They have a dorsocaudal direction and scatter in the dorsal portion of this nucleus.

Within the bounds of the internal medullary lamina a large number of fibres have a very thin myelin sheath. They pass ventromedially along the border of the dorsomedial nucleus and tend to the mediocentral nucleus. Part of these fibres pass also to the other side and a few of them sink into the lateral and ventral portions of the dorsomedial nucleus (Fig. 3 and 4, ϑ).

The medial part of the dorsomedial nucleus stretches along the lateral part and appears somewhat caudally to the oral pole of the nucleus to end somewhat in front of its caudal pole. Two regions, a dorsal and a ventral, can be distinguished also in this part. In the anterior part of the dorsomedial nucleus the ventral portion is characterized by the presence of a large number of compact bundles composed of more than ten intensely stained fibres each. The bundles of this system, which enter the ventral portion of the dorsomedial nucleus, come from two regions situated ventrally to this nucleus, a medial region (Fig. 2 and 3, ε), extending from the hypothalamus, and a more lateral one (Fig. 2 and 3, ς). The fibres from this last area pass through the subthalamic structures and internal capsule to the region of the entopeduncular nucleus. The course of these bundles is from the oroventral end to the dorsocaudal. All in all, they form a system which comes from the inferior thalamic peduncle (Fig. 2 and 3, ε) and the anterior thalamic radiation (Fig. 2 and 3, ς).

The ventral portion of the medial part receives, in addition, very numerous poorly myelinated single thin fibres which extend from one side of the dorsomedial nucleus to the other, through the nuclei of the midline. Here they form a thin but fairly densely woven structure.

These fibres normally run horizontally, from the oral region on one side obliquely to the caudal region on the other side (Fig. 2 and 3, ζ). In the field of the midline nuclei the fibres coming from the contralateral sides cross at acute angles and form a network. Inside the dorsomedial nucleus this system occurs in the form of thin subparallel bundles between the compact bundles of the systems from the anterior thalamic radiation and inferior thalamic peduncle.

The single thin fibres, present in the field of the midline nuclei, penetrate into the dorsomedial nucleus, connecting the anterior paraventricular nucleus and periventricular nucleus with it (Fig. 4, η).

The dorsal portion of the medial part of the dorsomedial nucleus is filled with single fibres, which become denser in the middle region. These fibres run in various directions and it is difficult to distinguish regular systems among them. Only in the mediocaudal portion a system leaving this part can be seen. It consists of thin loose bundles, there being occasional single fibres which also tend in the orolateral direction. This system next passes through the lateral part of the dorsomedial nucleus and its bundles mingle with the bundles of the intermediate thalamic radiation (Fig. 4—6, λ).

Apart from this system there occurs a distinct system of single fibres coming from all over the medial part towards the lateral side with a slight deviation to the front (Fig. 4 and 6, ϰ). At the lateral border of the dorsomedial nucleus these fibres form loose and thin bundles which disappear in the fascicles of the intermediate thalamic radiation.

A system of thin fibres, which run singly or form slender bundles, composed of a few fibres each, occur in the dorsal portion of the dorsomedial nucleus in horizontal sections. They run on a slant from the front to the rear, on the medial side of the dorsomedial nucleus. In the posterior part of the nucleus this system expands to form a broad bundle which goes caudoventrally under the posterior commissure towards the tegmentum (Fig. 6 and 7, ι). This system is also well seen in frontal sections, in which it has the form of a stream of bundles running on a slant along the mediodorsal border of this part (Fig. 2—4, ι).

DISCUSSION

The myeloarchitectonics of the dorsomedial nucleus has not hitherto been worked out in detail. The authors usually confined themselves to mentioning a few most noticeable large systems of fibres running through this nucleus. In order to acquire more information about the structure of the dorsomedial nucleus, it therefore became necessary to examine the courses of all the systems open to microscopic observation and to make an attempt at defining their function in the connection of particular centres.

The foregoing observations show that the dorsomedial nucleus contains great masses of fibres which run through the anterior and intermediate thalamic radiations and inferior thalamic peduncle. The fibres from these three large groups scatter in the ventral portion of the lateral and medial parts of the dorsomedial nucleus. The ventral portion of this nucleus has a characteristic dense texture of fibres. Another feature of this mass of fibres is the typical dorsomediocaudal direction of their course. The density of fibres and the general direction of their course allow the distinction of two large parts, a medial and a lateral, in the dorsomedial nucleus. In general, they correspond topographically to the position of two out of the three component masses found in the dorsomedial nucleus of the monkey brain by Walker (1938), i.e. to the magno- and parvicellular parts, respectively. This conformity is not only topographical, since in the dog I managed to find the occurrence of larger cells in the part corresponding to the magnocellular region, and smaller cells in the part which corresponds to the parvicellular region in the monkey. The third component mass of the dorsomedial nucleus distinguished by Walker, i.e. the paralamellar region, which lies farthest to the lateral side in the monkey, has no morphological homologue in the dog. A study by Warren et al. (1962) shows a similar bipartite scheme of division of the dorsomedial nucleus into a lateral and a medial part in the cat.

The results of experiments carried out by the authors (Clark and Boggon 1933, Walker 1940, Clark and Mayer 1950; Guiliery 1959, Narkiewicz and Nauta 1960, 1964, Warren et al. 1962, Brutkowski 1967, Rinvik 1968, Sychowa et al. 1968) who used the method of retrograde degeneration indicate the existence of connections of the dorsal and lateral frontal cortex with the lateral part of the dorsomedial nucleus and those of the ventral and medial frontal cortex with its medial part in the cat. In the dog the relations between the frontal cortex and the dorsomedial nucleus are, as a rule, similar but the lobe of the frontal cortex of the dog is better developed than that in the cat. In consequence, the projection to the dorsomedial nucleus seems more abundant in the dog, which in the present myeloarchitectonic observations finds expression in the existence of compact layers of fibres which enter the dorsomedial nucleus. Studies of degeneration following injury to the frontal cortex (Narkiewicz and Brutkowski 1967, Sychowa et al. 1968) suggest that the area of projections from these regions is somewhat shifted in the dorsomedial nucleus of the dog as compared with the corresponding system in the cat.

SUMMARY

Five continuous celloidin series of frontal, horizontal and sagittal sections from normal dog brains unoperated upon were used to investigate the myeloarchitectonic structure of the dorsomedial nucleus in thalamus. The methods of Weigert, Klüver-Barrea and Nissl were applied to stain the sections.

The dorsomedial nucleus consists of two parts, a lateral and a medial, and these may in turn be divided into dorsal and ventral portions. In the lateral part of the dorsomedial nucleus compact bundles coming from the anterior thalamic radiation, and single fibres connected with the internal medullary lamina were found. The medial part of the dorsomedial nucleus is characterized by the presence of a large number of compact bundles from inferior thalamic peduncle, from the ventral portion of the striatum, and from bundles from the medial part of hypothalamus. This part of the dorsomedial nucleus receives, in addition, very numerous single fibres which run from the commissural system, the intermediate thalamic radiation and from tegmentum and paraventricular nucleus.

Abbreviations

AD, nucleus anterior dorsalis
AM, nucleus anterior medialis
Ant th rad, anterior thalamic radiation
AV, nucleus anterior ventralis
CeM, nucleus centralis medialis thalami
Cl, nucleus centralis lateralis
CM, centrum medianum
CP, commissura posterior
HP, tractus habenulointerpeduncularis
IAM, nucleus interanteromedialis
Im th rad, intermediate thalamic radiation
Inf th rad, inferior thalamic peduncle
L, nucleus lateralis
LMI, lamina medullaris interna
MDld, nucleus medialis dorsalis pars lateralis portio dorsalis
MDlv, nucleus medialis dorsalis pars lateralis portio ventralis
MDmd, nucleus medialis dorsalis pars medialis portio dorsalis
MDmv, nucleus medialis dorsalis pars medialis portio ventralis
Pc, nucleus paracentralis thalami
Pf, nucleus parafascicularis
Pl, nucleus paracentralis lateralis thalami
Pt, nucleus paratenialis
Pv, nucleus paraventricularis
Str M, stria medullaris

Symbols for systems

Nucleus medialis dorsalis pars lateralis portio ventralis
- α, compact bundles comming from the anterior thalamic radiation
- β, single fibres between compact bundles
- ϑ, connections with the internal medullary lamina
- ϰ, fibres running from the medial part to the intermediate thalamic projection

Nucleus medialis dorsalis pars lateralis portio dorsalis
- γ, thin bundles extending orolaterally from the intermediate thalamic radiation

δ, thin bundles extending dorsolaterally from the intermediate thalamic radiation
κ, single fibres running from the medial part of the dorsomedial nucleus towards the intermediate thalamic radiation
μ, single fibres running from the dorsocaudal portion of the dorsomedial nucleus towards the intermediate thalamic radiation

Nucleus medialis dorsalis pars medialis portio ventralis
ς, bundles from the inferior thalamic peduncle, from the ventral portion of the striatum
ε, bundles from the medial part of the hypothalamus
ζ, commissural system
κ, fibres tending to the intermediate thalamic radiation

Nucleus dorsalis medialis pars medialis portio dorsalis
λ, system extending towards the intermediate thalamic radiation
ι, system going to the tegmentum
η, fibres from the paraventricular nucleus

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