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MID-LINE THALAMIC NUCLEI IN THE DOG

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Within the massa intermedia, which links the two halves of the thalamus dorsalis, lie several nuclei which have been given the name of mid-line thalamic nuclei. The area occupied by these nuclei is fairly large, and stretches from the parataenial nucleus level orally, as far as the plane which vertically cuts the n. interventralis caudally. Nuclei of this group are linked to nuclei of the same name of the anterior thalamic group: n. interanterodorsalis, n. interanteromedialis, n. parataenialis; both n. dorso-mediales, and beside this both laminae medullares interne. Dorsally and latero-dorsally this group of nuclei lie next to the third ventricle, the stria medullaris thalami and the n. parataenialis, and in the caudal section to the habenular nuclei. Laterally lie n. anteromedialis, n. reticularis and n. ventralis thalami, as well as pedunculus thalami inferior. Next, caudally, n. dorsalis medialis, n. paracentralis, n. submedius, n. ventralis thalami, and lamina medullaris externa. On the ventral side this group of nuclei is bordered by the hypothalamus and the third ventricle. The nuclei under discussion are arranged in a definite order which is found among the lower and higher mammals, and also in the dog (Fig. 1A). N. paraventricularis, lying directly under the ependymal layer of the third ventricle, is the most dorsally situated nucleus of this group. Moving downwards into the massa intermedia ventrally, we come successively to n. interparataenialis, n. interanterodorsalis, and n. interanteromedialis, which lies next to the ventrally and caudally situated n. centralis medialis and n. rhomboidalis. The most ventrally situated nucleus of this group is n. reuniens, which for the whole of its length borders on the dorsally lying n. centralis medialis, and on the ventral side with the hypothalamus.

N. interparataenialis, n. interanterodorsalis, n. interanteromedialis

and the pars dorsalis of the centro-medial nucleus (and partly n. rhomboidalis) are nuclei of the commissural type. This name is given to the concentration of the nerve-cells which accompany the commissural fibers linking identical structures in both halves of the dorsal thalamus. In addition, these nerve-cells are in contact with the fibers of the periventricular system, and are linked with the neighbouring thalamic nuclei.

The present study was undertaken for the myeloarchitectonics analysis of these nuclei in the dogs' brain.

MATERIAL AND METHODS

Three continuous series of preparations, sectioned in the frontal plane, and stained by the Weigert–Wolters, Klüver–Barrera, Nissl and Schultze methods were used. In addition, two continuous series of sections taken in the sagittal plane, stained by the Weigert–Wolters and Klüver–Barrera methods, and one continuous series sectioned in the horizontal plane and stained by Weigert–Wolters method were used. The sections were from 25–50 μ thick.

OBSERVATIONS

The massa intermedia thalami is a well-developed body which occurred in all the dogs' brains under investigation. It reaches about 6000—6500 μ in the oro-caudal dimension in the medium-sized dog's brain (averaging about 6200 μ) and about 6000 μ in the dorso-ventral dimension. The breadth of the massa intermedia is not uniform for the whole of its length. Its upper section, reaching the level of the lamina medullaris interna, is narrower (most markedly in the section lying between the two n. dorsomediales) compared with the section lying within the lamina medullaris interna and a little below it.

The free surface of the massa intermedia is covered by the ependymal layer, which passes into the ependymal layer of the wall of the third ventricle.

Using myeloarchitectonic criteria, two kinds of mid-line thalamic nuclei can be distinguished in the dog. They are single nuclei: n. interparataenialis, n. interanterodorsalis, n. interanteromedialis, n. centralis medialis, n. rhomboidalis, and double nuclei: n. reuniens and n. paraventricularis.

Many authors also include in this group of nuclei n. commissuralis interventralis, but having regard to the proximity of this nucleus to the ventral thalamus, it will not be considered in this paper.

The best developed nuclei of this group are n. centralis medialis, n. reuniens and n. paraventricularis, which is linked with area pretectalis

(embryologically originating from the same neuroblast material as the thalamus dorsalis — Kuhlenbeck 1954).

N. interparataenialis (Fig. 1AB)

This is a small nucleus, measuring about 300 μ along its oro-caudal axis, and lying in the oro-dorsal section of the massa intermedia. Laterally it passes into n. parataenialis, joining with its medio-ventral part.

The mass of the nucleus is small, and similar in shape to a platelet bent into an arch in the ventral direction. It is of a commissural nature, and is composed of a few, delicate, poorly myelinated, loosely-arranged fibers. These fibers are grouped on the ventral and ventrolateral sides of n. paraventricularis. They run diagonally oro-medioventrad from the region of the pars medialis of n. parataenialis (Miodoński 1968b) and enter the area of n. interparataenialis, then run in the direction of the mid-sagittal plane of the thalamus. A short distance from it, they arrange themselves parahorizontally. Certain of these fibers intermingle in the mid-sagittal line with identical fibers coming from the contralateral n. parataenialis.

Laterally, in the parasagittal plane, fine, thin fibers of the periventricular system (running vertically) pass through the area of n. interparataenialis, and probably also enter into contact with the neurons of this nucleus. A little further laterally, strongly myelinated fibers of the stria medullaris thalami pass through the lateral part of this nucleus (the junction area in n. parataenialis pars medialis).

N. interanterodorsalis (Fig. 1AB)

This nucleus, like the previous one, lies in the oro-dorsal part of the massa intermedia, appearing slightly caudad and ventrad of the interparataenial nucleus. It is a body which in the brain of the dog is better developed than n. interparataenialis. In frontal section it reveals a gentle bow-form, a ventrally curved band which runs latero-dorsally and slightly underneath the parataenial nucleus. This section, running fairly diagonally, passes freely into n. anterodorsalis. The oro-caudal dimension of this nucleus is about 500 μ. Like the previously described nucleus, it is a nucleus of the commissural type.

From the myeloarchitectonic point of view, it is built of thin, delicate, comparatively strongly myelinated fibers. These are arranged in the form of a fairly compact band running oro-ventro-mediad and oro-mediad. Fairly numerous cells of the same type as the cells which appear in the area of n. anterodorsalis (Miodoński 1968a) appear between these fibers. In the area of n. interanterodorsalis these fibers run in the

direction of the mid-sagittal line, and pass through the strongly myelinated band of fibers of the stria medullaris thalami and the pedunculus thalami inferior which lie laterally. A short distance from the mid-sagittal plane, this band spreads out, forming a kind of fine fan. Some of the fibers (though not many) mingle with similar contralateral fibers. The remainder unite with the pedunculus thalami inferior and mix with (more medially than the former) the fibers of the periventricular system. Small, fine fibers run through the ventral surface of this nucleus and pass into the ventrally situated n. interanteromedialis, so that the boundary between the two is not well-defined. In Weigert preparations the area of the interanterodorsal nucleus is lighter than the more strongly myelinated n. interanteromedialis.

N. interanteromedialis (Fig. 1AB)

This is the largest of the three commissural nuclei of the anterior group of thalamic nuclei. It is the most ventrally-situated of them, and lies on the lamina medullaris interna and n. centralis medialis. Bundles of fibers of the mammillo-thalamic tract run through the lateral section of the nucleus, which has the form of fairly wide band, bent ventrally into an arch-type shape. These bundles run towards the nuclei of the anterior group. A little more mediad from the Vicq d'Azyr tract run numerous fibers which pass towards the radiatio thalamica anterior and the pedunculus thalami inferior (from the area of the nuclei of the anterior group). The nucleus measures about 1500 μ in the oro-caudal axis.

In Weigert materials the whole area of the n. interanteromedialis is occupied by a fine network composed of fine, fairly pale fibers. The main system here is fibers appearing from n. anteromedialis. Myeloarchitectonically, it is built of fine, thin, strongly and averagely-myelinated fibers. These run diagonally medio-ventro-orad and medio-ventrad (in horizontal plane they form an acute angle of not more than 20 or 30 degrees), and the majority of them, in the region where n. anteromedialis and n. interanteromedialis cross, they spread out in fan fashion. Further on, they are direct mainly medio-ventro-orad, and somewhat laterad, and join the system pedunculus thalami inferior descending on its medial side, and mixing somewhat with its fibers, through the lateral parts of the n. centralis medialis and n. reuniens (they reach the area of the medial forebrain bundle in the lateral hypothalamic nucleus). They cannot, further than this, be differentiated from other fibers which make up the pedunculus thalami inferior and run towards the ansa peduncularis (surrounding n. entopeduncularis, with which they partially enter into contact, medially and ventrally). Some of

them also run towards the regio medialis amygdalae (through the pars principalis of the substantiae innominatae — Miodoński 1967). About a third of the fibers appearing from the fan of fibers, described above as originating from the anteromedial nucleus, run, loosely grouped, medio-orad towards the mid-sagittal line. In this region, some of them mingle with similar contralateral fibers, the remainder deviate further ventrad and arranging themselves parasagittally mingle with the fibers of the periventricular system and reach the dorsal surface of the centro-medial nucleus. Through the whole area of this nucleus, practically, numerous fibers of the periventricular system run medially from the layer running vertically through the medial edge of the mammillo-thalamic tract, and mix with the fibers of the network.

In addition, the interanteromedial nucleus is linked by short fine fibers with varying directions, with the n. interanterodorsalis, lying dorsally, and more strongly with n. centralis medialis, lying ventrally. Fairly numerous fine interconnectional fibers run through the lamina medullaris interna, which is fairly thin in this section, and then between the lateral part of n. interanteromedialis and n. ventralis. Besides the connections described above, fine, fairly strongly myelinized fibers originating from the dorsal surface of the lamina medullaris interna penetrate the ventro-oral region of this nucleus. Further caudally slightly less myelinated fibers running between n. interanteromedialis and n. dorsomedialis are visible. From the cytoarchitectonic point of view the region of the interanteromedial nucleus does not differ from n. antero-medialis (Miodoński 1968a).

N. rhomboidalis (Fig. 1BCD, 2)

This is a single nucleus, lying between n. interanterodorsalis and n. centralis medialis, and further caudally, between both n. dorso-mediales. N. paraventricularis is forced into the (fairly narrow) dorsal surface of the rhomboidal nucleus, slightly furrowing it in the mid-sagittal line (a similar relation is described in pigs by Welento 1964). The oro-caudal dimension of the rhomboidal nucleus is about 2000 μ. In shape it is similar in cross-section to a rhomb, hence its name. It rests on the dorsal surface of the centro-medial nucleus, and comes into contact with the lamina medullaris interna. The surface fibers of this lamina divert medio-dorsad, and pass onto the dorso-lateral surface of the rhomboidal nucleus, indicating at the same time the fine boundary with the dorso-medial nucleus. Slightly laterally from them run bundles of fibers of the medial olfacto-habenular tract.

In n. rhomboidalis a fine network built up of very thin, poorly myelinated small fibers running in different directions is visible.

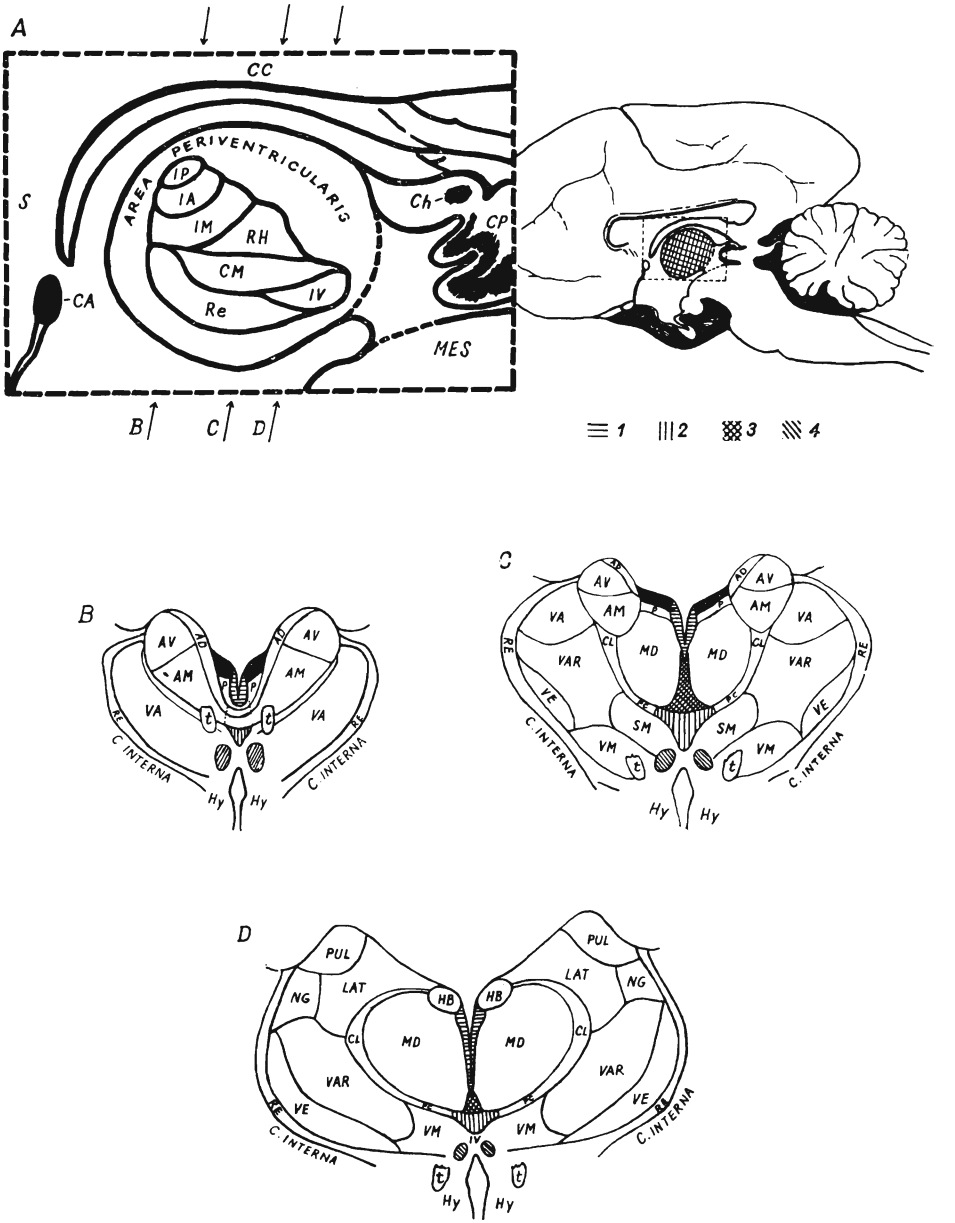

Fig. 1. Diagram of the topographical relations, of the mid-line thalamic nuclei. A, Sagittal section; B, Frontal section on the level of the anterior thalamic nuclei; C, Frontal section on the level of the submedius nucleus; D, Frontal section on the level of the habenular complex. 1, periventricular area and paraventricular nucleus; 2, centromedial nucleus; 3, rhomboidal nucleus; 4, reuniens nucleus

In the basal part of the rhomboidal nucleus, which rests on the dorsal surface of the centro-medial nucleus, occur fine, thin fibers which link both nuclei together. Numerous thin, fine fibers from n. dorso-medialis also run to the basal part of the rhomboidal nucleus. Some of these fibers run diagonally medio-ventrad and slightly orad, coming from the central area of the dorso-medial nucleus. They are grouped more numerously in the narrower part of the rhomboidal nucleus, the part which lies between the two dorso-medial nuclei. The remaining fibers coming from the lateral part of the dorso-medial nucleus reach the basal part of n. rhomboidalis and arrange themselves almost horizontally (in a direction similar to the direction of the fibers in the lamina medullaris interna). Both of these types of fibers, occurring mainly in the caudal section of the nucleus under discussion, cross each other in the mid-sagittal line or, turning ventrad, join the periventricular system which passes across n. rhomboidalis. Fine, thin fibers which run oro-ventro-laterad can be seen coming from this nucleus and mixing with very similar fibers from n. centralis medialis, and then entering the pedunculus thalami inferior (medial side). In addition, fairly numerous fibers of the periventricular system run across the rhomboidal nucleus and pass dorsally to the paraventricular nucleus, then ventrally to the centro-medial nucleus and n. reuniens (vertical fibers diverting oro-ventrad), and numerous fibers of the same system coming from the hypothalamus and running dorsad to n. paraventricularis also appear here (vertical fibers diverting oro-dorsad).

N. centralis medialis (Fig. 1ABCD, 2)

This is a single nucleus lying in the mid-sagittal line of the thalamus. It is counted, mainly its dorsal part that is, as one of the commissural nuclei. It lies practically wholly — with the exception of the oral pole — within the U-shaped lamina medullaris interna. This lamina is directed in a shallow arch medio-ventrad towards the mid-sagittal line, and divides around both sides of the centro-medial nucleus, surrounding it with its fibers both from the dorsal and ventral sides. The main mass of this nucleus, which is composed of the pars dorsalis of the centro-medial nucleus, "lies" in the extremely compact dorsal part of the lamina medullaris interna. The pars ventralis of this nucleus, descending ventrad in the mid-line (between both n. reunientes), "lies" between the loosely arranged fibers of the ventral part of the lamina medullaris interna. The ventral part of this nucleus does not reach the free edge of the massa intermedia, the aperture of the third ventricle, from which it is divided by periventricular system. The oral pole of the centro-medial nucleus lies in the layer slightly to the front of the oral pole

of the dorso-medial nucleus. The n. centralis medialis stretches in the oro-caudal dimension along almost the whole length of the massa intermedia, disappearing slightly orad from the caudal end of n. commissuralis interventralis.

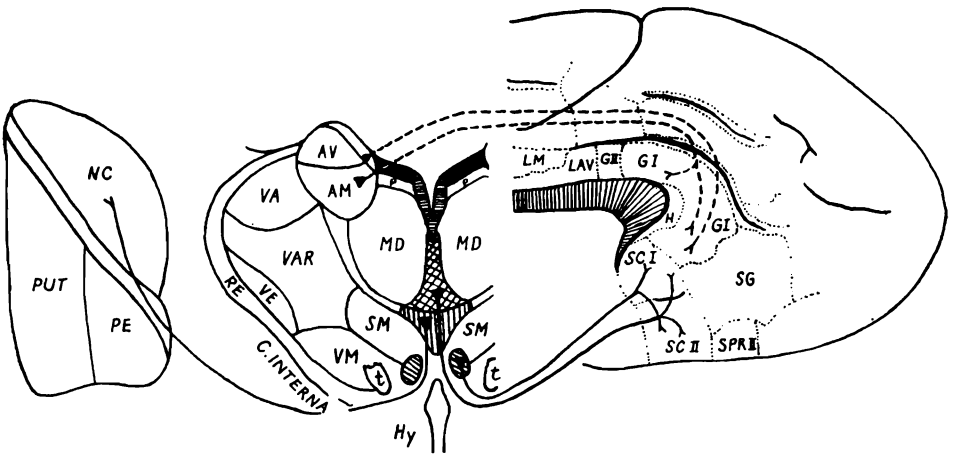

Fig. 2. Diagram to illustrate regions of the telencephalic terminations of the rhomboidal, centromedial and reuniens nuclei

In the oral section, the pars ventralis of the centro-medial nucleus occupies a slightly greater surface than the pars dorsalis, but in the remaining section of the nucleus these proportions are reversed. This is caused by the development of both n. submedius. The length of the centro-medial nucleus in the oro-caudal dimension is about 5500 μ. From the point of view of myeloarchitectonics, the surface of n. centralis medialis, similar in shape to a wedge with the sharp end turned ventrad, can be divided into a pars dorsalis and a pars ventralis. The pars dorsalis is a commissural "nucleus" for both laminae medullares internae, and partly for n. submedius. The pars ventralis, on the other hand, is the part through which the fibers linking the laminae medullares internae with the contralateral laminae medullares externae, and also both n. submedius, run.

The pars dorsalis of the centro-medial nucleus lies in the dorsal part of lamina medullaris interna, and remains in contact with numerous medium and thin-calibre, strongly myelinated fibers of the commissural type. These fibers are grouped around the dorsal side of the centro-medial nucleus (on the boundary with n. rhomboidalis and n. paraventricularis), and more numerously on its ventral side. They also penetrate the area of the pars dorsalis. The fibers arranged about the dorsal

side of the pars dorsalis of the centro-medial nucleus come from the dorso-lateral part of the lamina medullaris interna (they also pass through the n. paracentralis). At first running diagonally latero-mediad and slightly ventrad, they then make towards the medial line, arranging themselves almost horizontally. The layer which they form on the surface of the pars dorsalis of the centro-medial nucleus reaches from 15 to 20 μ in thickness, and is if anything thicker in its medio-caudal section. These are typical commissural fibers. The fibers penetrating the pars dorsalis of the centro-medial nucleus pass through closely packed nerve cells. Because of this, their course is a wave-like one, in different directions. Some of these fibers reach and cross the medial line. The remainder, of which there are a sizeable number, do not reach the medial line, turning ventrad instead, and joining the periventricular system.

The system of commissural fibers of the lamina medullaris interna which are grouped around the ventral side of the pars dorsalis of the centro-medial nucleus contains more numerous and more strongly-diagonally running (medio-ventrad) fibers. These form (though not everywhere distinctly) the boundary between the two parts of the centro-medial nucleus. They are mainly thin, fine fibers, but also in some cases medium sized, and strongly myelinated. Running towards the medial line, which they fairly frequently cross, they form the ventral part of the "commissure" for both laminae medullares internae. Not all fibers behave in this way. Some of them which lie more latero-ventrally than the typical commissural fibers run more diagonally medio-ventrad and orad, and join the periventricular system, also returning again laterally to enter into contact with the lamina medullaris externa ipsilateralis, partly passing through the pars ventralis of the centro-medial nucleus. The pars ventralis of the nucleus under discussion is penetrated by numerous fibers coming from the "interior" of the lamina medullaris interna and also from its ventral part, which is of looser construction. These are strongly myelinated fibers, mainly thin or medium size which run diagonally medio-ventrad and somewhat orad. The most laterally-lying of these fibers (they run along the medial side of n. submedius) run latero-ventrally and form a capsule on the surface of n. submedius. Nearer the interior of the lamina medullaris interna are arranged fibers which are morphologically similar to those previously described, and which run diagonally medio-ventrad, and then, after passing through the pars ventralis of the centro-medial nucleus and crossing the medial line, reach the lamina medullaris externa contralateralis. The fibers originating from the "interior" of the lamina medullaris interna form together with the fibers of the dorsal

part of this lamina the boundary of the pars dorsalis of the centro-medial nucleus, and pass into the pars ventralis of this nucleus to come into contact with the periventricular system, while some of them also pass over to the opposite side. Fairly numerous fibers of the periventricular system run through the whole area occupied by n. centralis medialis. A loose system is also visible, composed of finer, somewhat less strongly myelinated fibers which pass mainly through the pars ventralis of the centro-medial nucleus (a looser arrangement of cells) to join both n. submedius together.

Besides the systems described above, n. centralis medialis is linked by numerous interconnectional fibers with its neighbours. These last mentioned connections are basically formed from fine fibers of various degrees of myelinization. The most numerous of these link n. centralis medialis with n. dorso-medialis and n. rhomboidalis. Visible orally are the junctions with n. interanteromedialis. For practically its whole depth it is joined by fine fibers to n. paracentralis. Fine fibers, averagely myelinated, run latero-ventrad, linking the region of the centro-medial nucleus with n. ventralis thalami. It is most weakly linked with its ventral neighbour, n. reuniens, by a few poorly myelinated fine fibers.

In the oral section, a few fine, thin fibers running on the medial side of the pedunculus thalami inferior reach n. centralis medialis, as do also a few fibers of the stria medullaris thalami.

The fibers of the periventricular system (vertically) originating from the hypothalamus but also from fasciculus longitudinalis dorsalis form a fairly distinct system running through the area of the centro-medial nucleus; these fibers run at right angles to the layer of commissural fibers of the lamina medullaris interna.

N. reuniens (Fig. 1ABCD, 2)

This is a double nucleus, and also the mid-line nucleus which is the most ventrally-situated. It is arched — the gentle curve of the bow is turned ventrally — from the frontal pole of the thalamus to n. interventralis. In its frontal section it is extended in the dorso-ventral direction, and in frontal section has the shape of an ellipse. Further caudad, this shape changes to almost a circle, while the measurements of the nucleus as a whole decrease so that at the level of the interventral nucleus it disappears. In this neighbourhood, both these nuclei intermingle. N. interventralis is forced between n. reuniens and n. centralis medialis, pushing the nucleus discussed here ventrad and somewhat laterad, so that the interventral commissural fibers are highly interwoven with the dorsal part of n. reuniens. For this reason, there is no distinct boundary between these two nuclei.

N. reuniens has its most visible boundary on the dorsal side — n. centralis medialis and the fibers of the lamina medullaris interna — and the medial side — the periventricular system. The lateral boundary is poorly visible because of the system of the pedunculus thalami inferior which passes through the lateral region of this nucleus, and also because of the contact of this nucleus with n. ventralis, and n. submedius.

The dimensions of n. reuniens in the oro-caudal axis are around 5000 μ in the average-sized dog brain. The best visible system of fibers running through the lateral part of n. reuniens is composed of the fibers lying medially in the region of the pedunculus thalami inferior. These fibers, fine, and of small calibre, staining well with the Weigert method, lie medially from the bundle of fibers (strongly myelinated, medium to thick in calibre) of the pedunculus thalami inferior (which runs to the ansa) and to the fibers of the stria medullaris thalami which are mixed with them. The fibers of the medial part of the pedunculus thalami inferior run practically vertically. A certain quantity of medial fibers of this system, which is a fairly loose system and is made up of fibers originating from n. ventralis thalami and from the region of the anterior thalamic nuclei group, spread out in the dorsal and lateral parts of n. reuniens. Numerous fibers of this system pass through these regions of n. reuniens, passing further ventro-orad to spread out partly in the area preoptica medialis and lateralis, and partly in the anterior hypothalamic area — mainly of n. hypothalamicus anterolateralis (together with the fibers of the stria medullaris thalami), but they also partly divert laterad and connect with the ansa peduncularis.

The same area of n. reuniens is reached by fairly numerous fine, somewhat thin fibers coming from n. ventralis medialis thalami. These fibers run diagonally (in a medio-orad direction) and penetrate the pedunculus thalami inferior to enter n. reuniens from the latero-dorsal and lateral sides. The fibers entering from the lateral side run parahorizontally in n. reuniens. They are partly spread over its dorsal part, and partly run further medially to reach the mid-line and enter into contact with the periventricular system. Identical fibers originating from the lamina medullaris run parallel the system described above, and divide n. reuniens from the pars ventralis of the centro-medial nucleus. A transitory system of fibers running from n. centralis medialis and n. rhomboidalis passes through the dorso-lateral "edge" of the oral part of n. reuniens, and joins with the pedunculus thalami inferior.

From latero-ventral and ventro-lateral sides, strongly myelinated, loosely arranged small-calibre fibers reach the frontal part of n. reuniens. They pass on the parahorizontal plane (in frontal section) and divert slightly oro-latero-ventrad. These fibers mingle with those coming from

n. ventralis medialis, having appeared from the medio-ventral part of the internal capsule (Fig. 2). The capsular fibers pass through the system pedunculus thalami inferior and continue at the level of the sulcus hypothalamicus (Kuhlenbeck's sulcus diencephalicus ventralis) above n. perifornicalis and further medially above n. paraventricularis hypothalami. The fibers between n. reticularis and n. reuniens run almost identically, but with stronger lateral deviation. Further dorsad from them are arranged the fibers of lamina medullaris externa, and these run identically. They enter n. reuniens from the lateral side. Some of these fibers join the periventricular system. From the dorsal part of the hypothalamic paraventricular nucleus appear fine, palely-stained fibers which run dorsad and slightly lateral to enter n. reuniens from the ventral side. The medial part of this nucleus is traversed by fine, strongly myelinated fibers of the periventricular system which run vertically (with dorso-orad deviation). These reach the medial line on the ventral margin of the massa intermedia (bounded by the area periventricularis defined by Bodian 1939 as periventricular gray or by Bleier 1961 as n. periventricularis), where they are partly crossed by a similar contralateral system. Running further in the medial line they pass between both n. reunientes towards the ventral surface of the pars ventralis of the centro-medial nucleus. The fibers of this system, and they are fairly numerous, which are not crossed, spread out in the medial part of n. reuniens. The crossed fibers mingle with fibers coming from n. ventralis medialis and the lamina medullaris interna on the dorsal side of n. reuniens.

The medial section of n. reuniens betrays in cross-section a circular form, occupying a smaller surface. In this section too, fibers of the pedunculus thalami inferior system, more loosely arranged, pass through the lateral parts of n. reuniens. Between the above mentioned system of pedunculus thalami inferior, lying medially, and the fasciculus princeps, lying laterally (but descending diagonally ventro-medio-caudad) and lamina medullaris interna, lying dorsally, is situated n. submedius. This nucleus is an almost direct neighbour of the latero-dorsal part of n. reuniens. These two nuclei are divided by the fibers of the pedunculus thalami inferior and the lamina medullaris interna which surrounds the medial surface of n. submedius. As in previous section, the fibers of the pedunculus thalami inferior and of the medial olfacto-habenular tract (which lies furthest medially) run through the lateral part of n. reuniens. Less numerous fibers than in the previous section, originating from the medial surface of the pedunculus thalami inferior, spread out in the dorso-lateral part of n. reuniens. Also visible are fine, loosely-arranged fibers running between n. reuniens and n. submedius.

Fairly numerous fine and medium calibre fibers originating from the region of n. ventralis thalami enter the area of this nucleus from the ventro-lateral side. These partly spread out in n. reuniens; the rest of them pass further mediad towards the middle line and mingle (on the dorsal surface of this nucleus) with the periventricular system.

Reaching n. reuniens on the dorsal side, running practically along the medial line, is a system composed of thin, fine, well myelinated fibers. These compose the vertical part of the horizontal fibers of the periventricular system. They pass through the area of the paraventricular nucleus, turn ventrad, then pass through n. rhomboidals and n. centralis medialis to reach n. reuniens. They comprise part of the fibers belonging to the fasciculus longitudinalis dorsalis (Zyo et al. 1962).

From the area of the reuniens nucleus and also from n. centralis medialis appear loosely-arranged, fine, fairly strongly myelinated fibers which make ventro-latero-orad through the medial section of the ventromedial nucleus (below the fasciculus princeps and the lamina medullaris externa) to reach n. reticularis and the zona incerta. A few, fine, weakly-staining interconnectial fibers run between n. reuniens and n. centralis medialis, which lies dorsally.

Ventrally n. reuniens is linked by a system of fine fibers with the dorsal hypothalamic nucleus. Medially from it run the fibers of the periventricular system, behaving as described above.

Through the caudal section of n. reuniens there run single small bundles of fibers emerging from n. rhomboidalis and n. dorsalis medialis, and passing towards the internal capsule, and less numerous bundles belonging to the medial olfacto-habenular tract. These pass through the dorso-lateral part of the reuniens nucleus.

Numerous strongly myelinated fibers of the oral section of the interventral nucleus are arranged above n. reuniens along the ventral surface of the submedius nucleus (above the fasciculus princeps). These fibers divide the nucleus under discussion from n. centralis medialis, forcing it somewhat laterad. On the medial side, as before, lie numerous thin, delicate fibers of the periventricular system.

Also visible are fairly numerous thin, fine fibers coming from the ventro-lateral and ventral sides and entering the area of the reuniens nucleus from the region of the dorsal hypothalamic nucleus, and further caudally from the dorso-caudal hypothalamic nucleus. Laterally from them run fibers linking the lamina medullaris externa and the zona incerta with the area of the hypothalamus. A certain number of these fibers run beneath the fasciculus princeps, diverting dorso-medio-caudad (above the dorso-lateral surface of the dorso-caudal hypothalamic nucleus) to enter n. reuniens. These fibers remain partly in this nucleus,

and partly run further medio-dorsad to mingle with the periventricular system and the fibers descending from the lamina medullaris interna.

In the final section n. reuniens is mixed with the highly-developed n. commissuralis interventralis and n. ventralis medialis, so that its further investigation is impossible.

No junctions of the commissural type were noticed between the right and left n. reuniens in this material.

Area periventricularis (Fig. 1ABCD, 3)

The medial surface of the thalamus, which also constitutes part of the lateral wall of the third ventricle, is covered with a single-layer ependymal epithelium. Directly below the ependymal layer, which measures about 15 μ in thickness, lies a none too thick layer of nerve cells which stretches dorso-ventrally. The dorsal part of this layer is better formed. This layer as a whole constitutes part of the very large region surrounding the third ventricle, which stretches almost the whole depth of the thalamus, and descending ventrally takes in the region of the area preoptica and hypothalamica.

In the region of the thalamus this layer is interrupted by the mid-line thalamic nuclei concentrated in the massa intermedia. As a result, in this section it is the dorsal part of this area which is best visible, showing more numerous concentrations of neurons which make up the n. paraventricularis described by many authors.

The cells of n. paraventricularis, which is a double nucleus, lie scattered between the fibers of the periventricular system, and are in direct contact with them. N. paraventricularis can be seen as an arched body embracing the massa intermedia thalami on the ventro-oro-dorsal

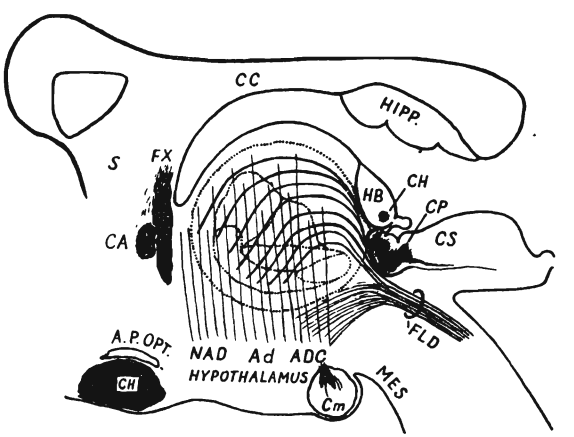

Fig. 3. Diagram, in the sagittal plane, to illustrate the vertical and horizontal components of the periventricular system

side. Caudally from this commissure the n. paraventricularis bends gently ventrally, so that at the level of the caudal pole of the centromedial nucleus it reaches towards and comes into contact with n. commissuralis interventralis. Orally, the paraventricular nucleus reaches the region which lies beyond the anterior commissure and as a paired structure stretches along the whole medial surface of the third ventricle lying beneath the ependymal layer. Caudally, this nucleus becomes smaller in the dorso-ventral dimension and melts into the substantia grisea centralis of the pretectal region (this junction is very fluid, without any distinct boundary).

The periventricular area is characterized by the occurrence of fine, and thin fibers of varying degrees of myelination, which run in two basic directions. Some of them run vertically, while the remainder are arranged horizontally at varying depths of the thalamus in the oro-caudal dimension, and divert vertically to mix with the vertical fibers (Fig. 3). The horizontal fibers betray in their vertical stretch a somewhat different direction of course than the vertical fibers. The latter bend away from the vertical axis in an oro-dorsal direction, while the vertical section of the horizontal fibers shows an oro-ventral bending away from the vertical.

The fibers of this system are fairly loosely arranged, although they do, mainly in the dorsal section of the area periventricularis, group themselves in discrete bundles. They are grouped more numerously laterally from the commissural nuclei of the mid-line, and partly pass through the region of these nuclei. The vertical fibers diverting oro-dorsad which can be traced in the hypothalamus enter into contact with all the nuclei of the mid-line, also with the medial thalamus nuclei, and mainly with the dorso-medial nucleus. They are more numerously arranged parasagittally, but a certain quantity of them run in the mid-sagittal layer itself. These fibers stretch along the whole length of the thalamus from the medial structures of the dorsal thalamus. They next pass through the lamina medullaris interna, and — for a small distance — the medial parts of the thalamus ventralis, and make towards the mid-line, passing through the dorsomedial part of the reuniens nucleus, latero-ventrad in relation to the centro-medial nucleus, and join the fibers running in the mid-sagittal line. In the area bounded laterally by n. reuniens, from above by the pars ventralis of the centro-medial nucleus, and ventrally by the third ventricle, the majority of these fibers cross together and pass over on to the opposite side to reach the area periventricularis hypothalami, n. paraventricularis hypothalami, n. dorsalis and n. dorso-caudalis hypothalami (Śmiałowski 1966, 1968). The fibers which do not cross, of which there are fewer, run to the

ipsilateral structures of the hypothalamus which have been mentioned above. In the forward part they can be traced with some difficulty as far as the caudal parts of the medial and lateral preoptic area. These fibers mingle with the more strongly myelinated fibers of the medial olfacto-habenular tract which lie slightly lateral of the region of the periventricular area. In the area of the dorsal thalamus the fibers of the periventricular system enter into contact with n. paraventricularis (which lies dorsally from the massa intermedia), n. interparataenialis, n. interanteromedialis, n. rhomboidalis, n. centralis medialis and n. reuniens. In the frontal sections of the thalamus they lie medially from the stria medullaris thalami and pedunculus thalami inferior, partly mingling with them.

Caudad from the massa intermedia the fibers of the periventricular system run medially from the parafascicular nucleus, partly joining it, and can be traced as far as the region of the decussatio supramammillaris. Here part of them pass on, and part run caudad of this decussation to pass further caudally and become lost in the central gray substance of the pretectal region. Between them are visible fibers which reach the Forel's region H. The whole of this system forms a dispersed system stretching through the whole depth of the thalamus, and linking the hypothalamus with the thalamus independently of the hypothalamo-thalamic connections gathered in the fasciculus intrathalamicus, mainly from the ventral thalamus (the ventral and lateral nuclei and n. dorsomedialis). Because of the connection between this system and the mid-line thalamic nuclei, especially with the centro-medial nucleus which is connected with the lamina medullaris interna, to which run fibers carrying the protopathic sensation of pain, they may play an important part in the vegetative reactions which are so strongly connected with the experience of pain.

The horizontal system is composed of thin fibers, somewhat more strongly myelinated, passing medio-ventrally from stria medullaris thalami. They are more numerously grouped in the dorsal and caudal part of the paraventricular nucleus. They stretch through the whole oro-caudal dimension of the massa intermedia to turn ventro-orally and pass on vertically (at an oro-ventrad angle from the vertical) to mingle with the fibers of the previously described system.

More of the horizontal fibers change course to the vertical half-way through the caudal part of the massa intermedia. Frontally they stretch almost to its forward pole, although their number progressively decreases due to the ventro-oral furrow in the massa intermedia. Half-way through the caudal massa intermedia they are grouped in fine, small bundles which run parasagittally between the fibers of vertical system. The

majority of the horizontal fibers run to the rhomboidal, central-medial and reuniens nuclei. Caudally, those fibers grouped in the dorsal part of the paraventricular nucleus, lying medio-ventrally in relation to the medial habenular nucleus, run below the habenular commissure and the posterior commissure to the dorsal part of the pretectal region. They make up thalamic division of Schütz's fasciculus longitudinals dorsalis (vel fasciculus longitudinalis posterior, vel fasciculus periependymalis) which runs towards the area of the brain stem. Running slightly ventrally from the posterior commissure, this system gives up some of its fibers to this commissure through which they traverse the contralateral side of the thalamus.

DISCUSSION

On the basis of a myeloarchitectonic analysis of the mid-line thalamic nuclei of the dog, the following nuclei of this group have been distinguished: n. interanterodorsalis, n. interanteromedialis, n. interparataenialis n. centralis medialis, n. rhomboidalis, n. reuniens and n. paraventricularis.

It was observed that from the area of the reuniens nucleus, and also from the rhomboidal nucleus and the centralis medialis of the dog, there appear systems of fibers which run oro-ventrad and slightly laterad. These mingle with the fibers of the pedunculus thalami inferior (vel radiatio thalamica inferior) and run through the medial part of n. ventralis thalami and n. reticularis to the ventro-medial part of the internal capsule. These observations confirm the results obtained by other authors on normal material (Gurdjian 1927, Rioch 1931, Kappers et al. 1965) and on experimental-degenerational material (Rose and Woolsey 1943, 1948, Jasper 1949, Droogleever–Fortuyn 1950, Stefens and Droogleever–Fortuyn 1953, Nauta and Whitlock 1954, Powell and Cowan 1954, 1955, 1956, Akimoto et al. 1956, Mc Kegney 1958). In the last group of investigations it was noted that n. reuniens, n. rhomboidalis and n. centralis medialis (and also the intralaminar nuclei) send their projections out orally across the pedunculus thalami inferior to the ventro-medial third of the internal capsule. In the area of the latter, these fibers from the above-mentioned nuclei run anteriorly, dividing up into the caudate nucleus (n. centralis medialis), and into the area infralimbica (n. reuniens and n. rhomboidalis).

My observations on the junctions of the reuniens nucleus with the reticular nucleus are to a certain extent confirmed by the experimental results of Akimoto et al. 1956. In addition, I ascertained that these nuclei send their fibers to the pedunculus thalami inferior (independently of the oral group of nuclei and the parataenial nucleus) and enter into

contact with the oral parts of the amygdaloid complex and the substantia innominata, which confirms the results of Rioch 1931, Kuhlenbeck 1954, McKegney 1958, Miodoński 1966.

The large paraventricular nucleus, connected with the periventricular system, is divided by certain authors (Rioch 1931, Ingram et al. 1932, Crouch 1934, Solnitzky 1938, Walker 1938, Ban et al. 1967) into the anterior paraventricular nucleus and the posterior paraventricular by others (Clark Le Gross 1930, Castellanos 1949, Olszewski 1952, Dekaban 1953, Jasper 1954, Kuhlenbeck 1954, Sychowa 1961) it is treated as a whole, which corresponds to my observations. The cytoarchitectonic differences on which this division is chiefly based are not very convincing. Toncray (1946) expresses a similar opinion: "Nowhere can be seen a dividing line between the anterior and posterior paraventricular nuclei and the cell types of the two regions are not different".

The vertical fibers of the periventricular system which I describe, and also the fibers from the paraventricular nucleus which belong to this system, enter into contact with all the mid-line thalamic nuclei (Fig. 3). On the other side, stretching ventrad, they link the nuclei of this group with the preoptic area (mainly laterally), the hypothalamus (area periventricularis hypothalami, n. periventricularis hypothalami, n. dorsalis and dorso-caudalis hypothalami), and with the parafascicular nucleus and the region of the decussatio supramammillaris. These observations agree with my earlier works (Miodoński 1963) and also with the observations of other authors (Rioch 1931, Kuhlenbeck 1954, Śmiałowski 1966, 1968). The degeneration works (Zyo et al. 1962, Ban et al. 1967) complete my observations by confirming that besides the above-mentioned connections this nucleus projects into the septum (n. lateralis and medialis septi), n. accumbens and the tuberculum olfactorium. In addition to this, they confirm my observations on the subject of the junctions the septum with the preoptic area and the hypothalamus (Miodoński 1963, 1967): which partly constitute a continuation of the projection of the paraventricular nucleus into these regions.

The horizontal fibers of the periventricular system which I have described form the thalamic division of the fasciculus longitudinalis dorsalis, and separate into n. centralis medialis, n. reuniens, n. rhomboidalis (and n. dorso-medialis) (Fig. 3). On the other side, they stretch caudad to reach the substantia grisea mesencephali. These observations are consistent with the results of Gurdjian (1927), Rioch (1931), Kuhlenbeck (1954), Zyo et al. (1962), Ban et al. (1967).

All the mid-line thalamic nuclei are linked by a system of interconnecting fibers with other nuclei of the thalamus dorsalis (mainly)

and thalamus ventralis, and also with each other. Commissural-type nuclei which link identical nuclei of the oral group and both nuclei parataeniales are not always distinguished by other authors as separate anatomical units, and are frequently included in the area of the paraventricular nucleus. In addition, connections between these nuclei and n. paraventricularis most probably run through the area of the commissural nuclei of the group of anterior nuclei of the thalamus.

It seems highly probable (though this has not been confirmed in our material) that the fasciculus mammillaris princeps may send its collaterals or some fibers to the reuniens nucleus, which in one section is in direct contact with the medial surface of this bundle. This is suggested by the observation of Fry et al. (1963), that this bundle gives up a certain number of its fibers to the n. ventralis thalami region through which they pass, and also to the cortical region to which the projection of the reuniens nucleus runs, since it lies in the region of the cingular gyrus to which projections from all the nuclei of the anterior group, which is the terminal point for the Vicq d'Azyr bundle, and finally come.

SUMMARY

The present paper is dealing with the myeloarchitectonics analysis of the massa intermedia in the dogs' brain. For this study six dogs' brains have been used. Observations were conducted on materials stained with the Weigert, as well as the Klüver and silver methods.

In the dogs' massa intermedia, which links the two halves of the dorsal thalamus, in every investigated case, several nuclei have been observed. Myeloarchitectonically there have been distinguished: the interanterodorsal nucleus, the interanteroventral, the interparataenial, the rhomboidal, the centro-medial, the reuniens and the paraventricular. Several of them are single nuclei of the commissural type. The rest of them are double. The mid-line nuclei are surrounded by the anterior thalamic nuclei, the medial thalamic nuclei group, the ventro-medial thalamic group, the hypothalamus and the third ventricle. The connections of the investigated nuclei are described and shown in the diagrams. Direct connections were found among the reuniens nucleus, the rhomboidal, the centro-medial and medio-ventral part of the internal capsule. Besides, the periventricular system and its connections with the mid-line thalamic group nuclei have been described. Also during a detailed, full analysis, the fiber pattern within particular nuclei, as well as their connections with adjacent structures have been considered.

A comparison of the names used by different authors for the mid-line thalamic nuclei group

N. reuniens

nucleus of mid-line (Sachs 1909)
(pars) noyau rhomboidal (Ramon y Cajal 1911)
mid-line grup (3 and 4) (d'Hollander 1913)
noyau paracommissural (Glorieux 1929)
nucleus reuniens 4 (Miura 1933)
n. reuniens anterior and n. reuniens posterior (Aronson and Papez 1934)
nucleus ventro-medialis (Rose and Woolsey 1943)
nucleus paramedianus and nucleus submedius (Droogleever-Fortuyn 1950)
nucleus endymalis (Schaltenbrand and Bailey 1959)

N. centralis-medialis

(pars) noyau rhomboidal (Ramon y Cajal 1911)
nucleus centralis a (Winkler and Potter 1914)
(pars) noyau réunissant (Glorieux 1929)
nucleus medialis posterior 1 (Grünthal 1934)
nucleus commissuralis (Schaltenbrand and Bailey 1959)

N. rhomboidalis

noyau rhomboidal (Ramon y Cajal 1911)
mid-line group 3 (d'Hollander 1913)
(pars) nucleus reuniens (Winkler and Potter 1914)
(pars) noyau réunissant (Glorieux 1929)
nucleus reuniens 2 (Miura 1933)

N. paraventricularis

nucleus paramedianus thalami (Malone 1910)
noyau supérieur du raphe (Ramon y Cajal 1911)
mid-line group 1 (d'Hollander 1913)
nucleus paraependymalis (Winkler and Potter 1914)
nucleus medianus anterior b (Grünthal 1934)
nucleus stellatocellularis, nucleus rotundocellularis (Krieg 1944)
nucleus paramedianus oralis, nucleus paramedianus principalis, nucleus paramedianus caudalis (Schaltenbrand and Bailey 1959)

N. interanteromedialis

(pars) noyau interdorsal (Ramon y Cajal 1911)
(pars) noyau réunissant (Glorieux 1929)
nucleus medianus anterior b (Grünthal 1934)

N. interanterodorsalis

(pars) noyau interdorsal (Ramon y Cajal 1911)
(pars) noyau réunissant (Glorieux 1929)

N. interparataenialis

nucleus medialis anterior 1 (Grünthal 1934)
(pars) noyau réunissant (Glorieux 1929)

Abbreviations

AD, Anterodorsal nucleus
Ad, Dorsal area
ADC, Dorsocaudal area
AM, Anteromedial nucleus
A.P.OPT., Preoptic area
AV, Anteroventral nucleus
CA, Anterior commissure
CC, Corpus callosum
CH, Optic chiasm
Ch, Habenular commissure
C. Interna, Internal capsule
CL, Centrolateral nucleus
CM, Centromedial nucleus
Cm, Corpus mammillare
CP, Posterior commissure
CS, Superior colliculus
FLD, Fasciculus longitudinalis dorsalis
FX, Fornix postcommissuralis
G I, Area genualis I
G II, Area genualis II
H, Hippocampus precommissuralis
HB, Habenular complex
HIPP, Hippocampus
Hy, Hypothalamus
IA, Interanterodorsal nucleus
IM, Interanteromedial nucleus
IP, Interparataenial nucleus
IV, Interventral nucleus
LAT, Lateral nucleus
LAV, Area limbica anterior ventralis
LM, Area limbica media
MD, Mediodorsal nucleus
MES, Mesencephalon
NAD, Anterior dorsal nucleus
NC, Nucleus caudatus
NG, Supragenicular nucleus
P, Parataenial nucleus
PC, Paracentral nucleus
PE, Entopeduncular nucleus
PUL, Pulvinar
PUT, Putamen
RE, Reticular nucleus
Re, Reuniens nucleus
S, Septum
SC I, Area subcallosa I
SC II, Area subcallosa II
SG, Area subgenualis
SM, Submedial nucleus
SPR II, Area subprorea II
t, Mammillo-thalamic tract
VA, Ventralis anterior nucleus
VAR, Ventralis arcuatus nucleus
VE, Ventralis externus nucleus
VM, Ventromedialis nucleus

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