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A Particular Nucleus in the Mesencephalon of a Weakly Electric Fish, Gymnotus Carapo, Gymnotidae
I. Light Microscopic Structure*

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Summary. 1. A particular area of the midbrain called *magnocellular mesencephalic nucleus* (MMN), characteristic of several weakly electric fishes, was examined by different histological methods in *Gymnotus carapo*, Gymnotidae.

2. This area contains a dense network of thick fibers in which large neurons are scattered: it contains also a great number of small neurons.

3. The large neurons (25—35 μ) are unipolar with a profusely branching axon that gives rise to the main part of the network within the nucleus. At least one branch of the axonal arborisation leaves the nucleus towards the *torus semicircularis*, *i.e.* in the ventral direction. The small neurons (5—12 μ) are uni- or bipolar and display a profuse arborisation of their axon near the soma.

4. Large and small neurons are preferentially localized in the postero-ventral part of the nucleus.

5. Large neurons are contacted by multiple club endings originating partly from the rhombencephalon. The unipolar small neurons receive a single cup-like terminal.

6. The total number of club endings extablishing synaptic contacts on the surface of a large neuron was counted on serial semithin sections.

7. The present findings provide new information about the mesencephalic nucleus, which according to previous electrophysiological observations (Szabo, 1967; Szabo and Sakata, 1967) has been shown to represent a relay in the rapid electrosensory pathway.

Key words: Weakly electric fish — Midbrain nucleus — Unipolar (adendritic) neurons — Club endings — Cup-like terminals — Rapid electrosensory pathway

Introduction

A special area has been described recently in the anterior part of the mesencephalon of *Sternarchus albifrons* (Szabo, 1967). It is characterised by a dense network of thick fibers in which large neurons are scattered. In this and in several

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other gymnotid fishes *(Hypopomus, Gymnotus, Steatogenys, Electrophorus, Rhamphichthys, Eigenmannia app.)* field potentials as well as unitary responses could be detected by extra- and intracellular recordings from this area, both of which were phase related with a very short latency to each electric organ discharge (Szabo and Sakata, 1967). Consequently, this particular midbrain nucleus was considered to be a relay in the rapid pathway of the electrosensory reflex system (Szabo, 1967, 1972; Réthelyi and Szabo, 1971). The electrosensory fibers of the lateral line nerve which conduct the information to the mesencephalon do not reach this area directly. However, after lesion of the lateral lobe where the primary sensory neurons end, degenerated fibers could be traced up to the mesencephalon (Szabo, 1967).

A systematic histological investigation of the central nervous system of another weakly electric fish, *Gymnotus carapo*, also revealed the presence of this particular nucleus. The present report gives a detailed account of this structure, viz., its localization, its light microscopic structure. Its ultrastructural aspects will be considered in a subsequent paper (Réthelyi, Sotelo and Szabo, in preparation).

In the literature, there is no mention of a similar brain center in any other fish. A structure discernible in a frontal section of the mesencephalon of *Electrophorus electricus*, presented by Oliveira de Castro (1961) is a homologue, about which unfortunately no description is available. In view of its mesencephalic position and its large neurons, the designation of this structure as the *magnocellular mesencephalic nucleus* (MMN) appears to be justified.

A preliminary account has been given elsewhere (Réthelyi and Szabo, 1971).

Material and Methods

Fifteen *Gymnotus carapo* (15—20 cm length) were used. The brains were fixed, cut and treated according to various histological procedures as follows:

1. Paraffin sections stained by hematoxylin-eosin (or toluidine blue) mainly for mapping out the nucleus.

2. Two of the Golgi methods: Golgi-Cox and Golgi-Kopsch. The former was found to be better, impregnating many elements, whereas the latter stained only a few cell bodies.

3. Frozen sections impregnated according to Reumont-Lhermitte.

4. Semi-thin sections cut and stained with 1% toluidine blue from tissue blocks for electron microscopy containing only small pieces of the nucleus. — As the thick fibers in the MMN appeared to be of myelinated fibers (see Results) they can be easily seen in semi-thin sections. In order to obtain more information about these fibers the analysis of consecutive semi-thin sections was performed. Photomicrographs containing a neuron and the adjacent fibers were examined and the presynaptic fibers were traced back and drawn from the synapse "antidromically". The photomicrographs were then collected to give a three dimensional picture. In this way the exact number of the fibers presynaptic to a given neuron could be counted and their distribution on the surface of the perikaryon could be seen.

Preliminary data concerning the fiber connection were obtained in three specimens in which various portions of the rhombencephalon were destroyed. The animals were killed 7 days after the operation and perfused with 4% formalin. The brain was frozen and cut in serial sections subsequently treated according to Fink and Heimer (1967).

Results

The Magnocellular Mesencephalic Nucleus

The MMN appears in frontal sections as a median nucleus bifurcating into two separate symmetrical areas in the rostral and caudal parts. The rostral extensions

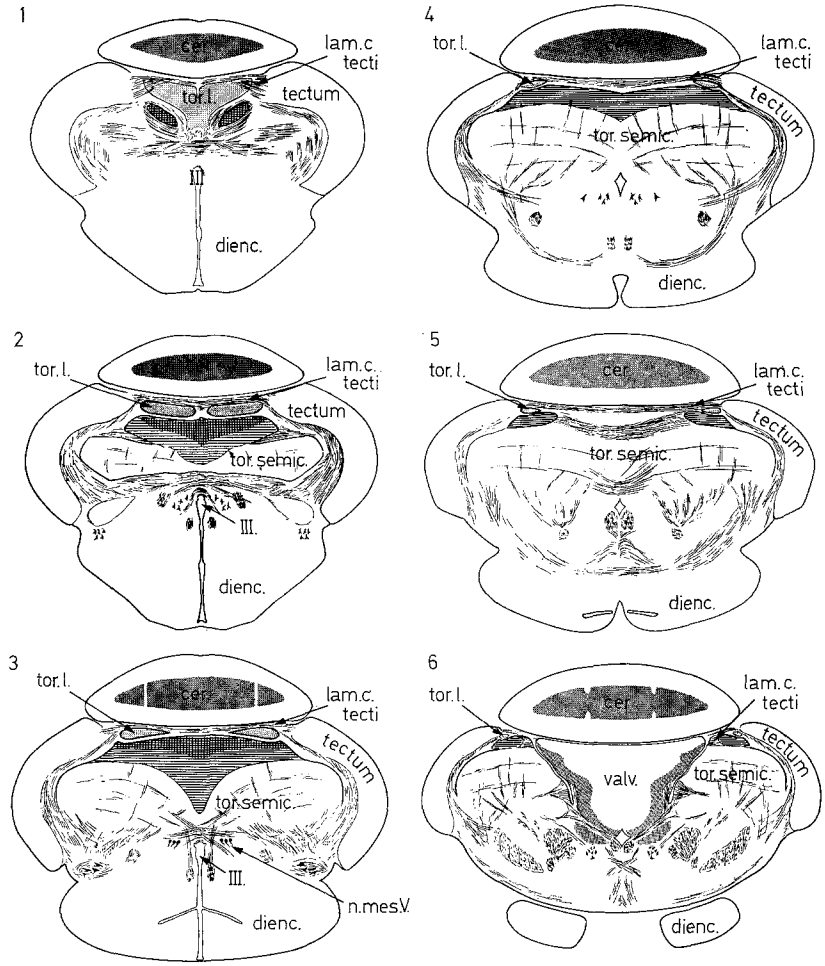


Fig. 1—6. *Schematic drawings of successive (antero-posterior) coronal sections showing the localization of the magnocellular mesencephalic nucleus (MMN) and that of some related structures.* Antero-dorsal area of the MMN — cross hatched; postero-ventral area of the MMN — horizontally hatched. Fig. 1 indicates the reference level, from which the other sections were taken at the following distances: Fig. 2, 100 μ; Fig. 3, 300 μ; Fig. 4, 600 μ; Fig. 5, 700 μ; Fig. 6, 1100 μ. cer = cerebellum; valv = valvula cerebelli; tor. l. = torus longitudinalis; tor. semic. = torus semicircularis; tect. = optic tectum; lam. c. tecti = lamina commissuralis tecti; dienc. = diencephalon; n. mes. V. = mesencephalic root of the Vth nerve; III. = third ventricle. For further explanation, see the text

reach the most anterior level of the mesencephalon. Surrounded by a commissural fiber system they lie ventrally to the *torus longitudinalis* and to the *lamina commissuralis tecti* (Fig. 1). Caudally the rostral extensions grow rapidly in volume and finally fuse in the midline forming a single triangular area (Fig. 2), the base of which is turned upwards. At this level as well as at more caudal levels the MMN is separated from the overlying *torus longitudinalis*, from the *lamina commissuralis tecti* and from the optic tectum by a narrow tissue space. The two sides of the

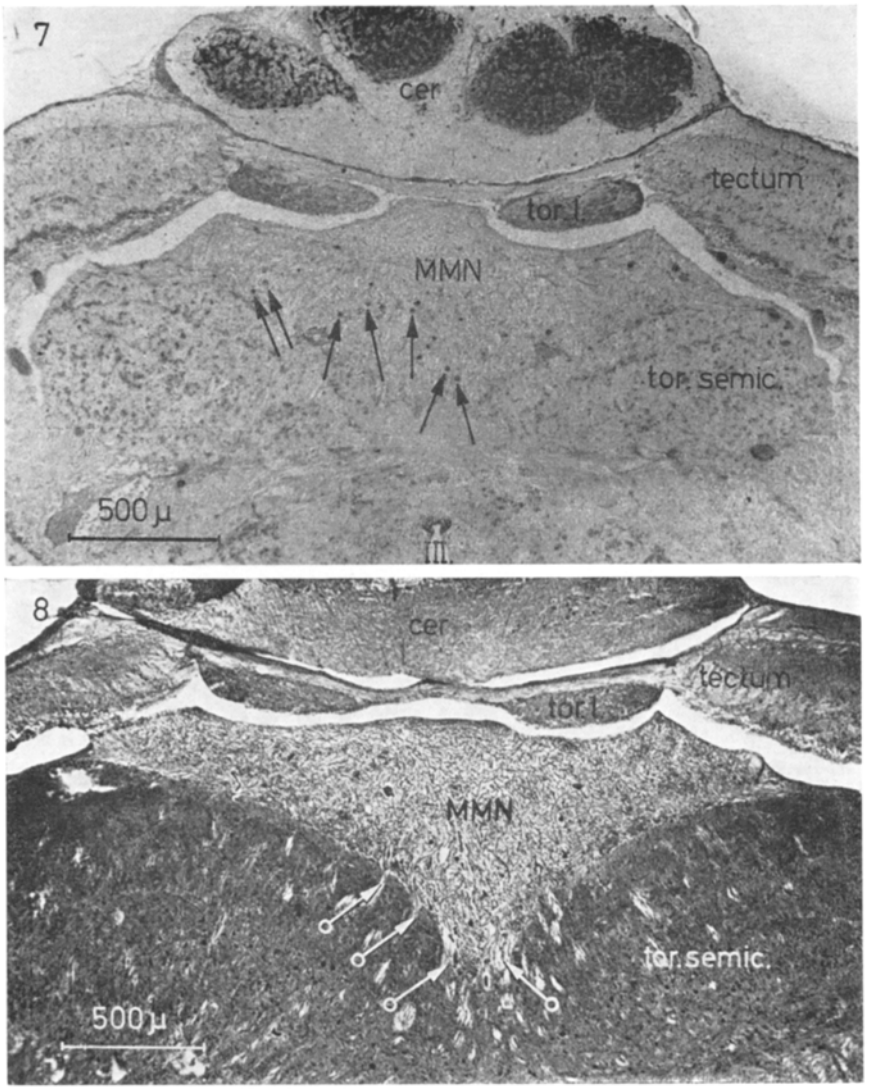


Fig. 7 a. 8. *Coronal sections through the magnocellular mesencephalic nucleus.* Fig. 7. Paraffin section, Nissl stain. Fig. 8. Frozen section, Reumont-Lhermitte stain. Large neurons are clearly seen, especially in Fig. 7 (arrows). Fibers connecting the torus semicircularis and the MMN are indicated by ringed arrows in Fig. 8. For abbreviations, see Figs. 1—6

triangular area adjoin the *torus semicircularis*. The border between the MMN and the latter area is always very sharp irrespective of staining method used (Figs. 7 and 8). At about 300 μ from the rostral end the MMN reaches its greatest volume. The apex of the above mentioned triangle penetrates deeply into the *torus semicircularis* and lies rather close to the roof of the 3rd ventricle (Fig. 3). More caudally the MMN diminishes in size and appears as a transverse band covering the *torus semicircularis* (Fig. 4). At about 700 μ from the rostral end the MMN bifurcates

again into two symmetrical areas. They lie beneath the *torus longitudinalis*, the latter also being considerably reduced at this level (Fig. 5). Although the most posterior parts of the MMN are shifted laterally, they still remain in contact with the *tori semicirculares* and maintain the same topographical relations with the neighbouring structures as in more anterior levels (Fig. 6). The whole rostro-caudal dimension of the MMN is about 1000—1200 μ depending, however, upon the length of the animal.

The Structure of the Magnocellular Mesencephalic Nucleus

There are two striking histological features that distinguish this nucleus from other areas not only in the brain of *Gymnotus carapo*, but also in the CNS of higher vertebrates sofar studied:

1. A particular network of thick nerve fibers resembling the white matter rather than the gray matter (compare in Fig. 8 the *torus semicircularis*, as a characteristic example of the gray matter, with the MMN). This network is fed and drained by small bundles of fibers which approach the nucleus through its ventral surface.

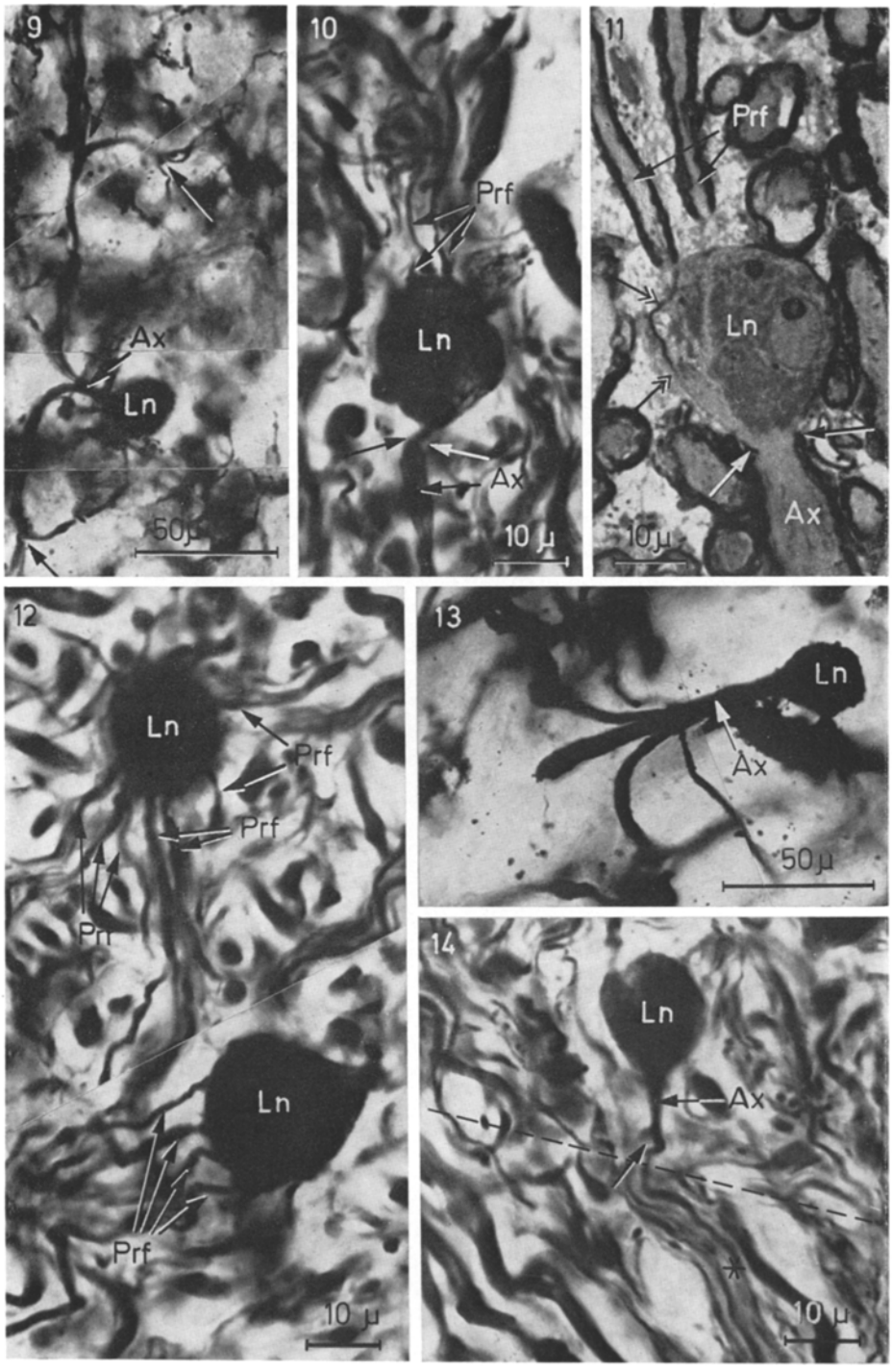
2. Small numbers of large and round, sometimes piriform perikarya and a multitude of small, round neurons. In Nissl or hematoxylin sections no dendritic processes appear to originate from the perikarya of the large neurons.

The distribution of the fibers and that of the large neurons is non-homogeneous and as a consequence the MMN can be divided into an antero-dorsal and a postero-ventral regions (Figs. 1—3). The latter is composed of large neurons surrounded by fibers of various thicknesses, whereas the former contains only thicker fibers. The antero-dorsal division disappears at the frontal level where the MMN begins to decrease (working backwards).

A) Large Neurons

Although they are generally scattered all over the postero-ventral division they tend to accumulate near the ventral surface of the nucleus. Their perikaryon is round or slightly elliptical, 25—35 μ in diameter (Figs. 9—14). The large neurons are provided with a single process, *i.e.* with a relatively thick axon (Figs. 10, 11, 13 and 14) covered with myelin right from its origin (Fig. 11). The axon branches immediately or close to the perikaryon and the branches repeatedly divide producing a great number of fibers within the nucleus (Figs. 9 and 13). Some of the secondary or tertiary branches leave the nucleus and penetrate the *torus semicircularis*. A good example of this can be seen in neurons situated near the ventral border of the MMN (Fig. 14).

The large neurons make contact with many thick fibers which approach the neuron in bundles (Fig. 12). The fiber either have a small terminal expansion or, more often, they terminate without any bulbous thickening (Figs. 10, 13). Although the 25 μ thick Reumont-Lhermitte sections reveal the above mentioned features, the much thinner (1 μ) semi-thin sections show the terminal part of the presynaptic fibers with greater accuracy. (It must be emphasized that the collection of the presynaptic fibers into bundles is unequivocal even in such a thin section [Fig. 15]).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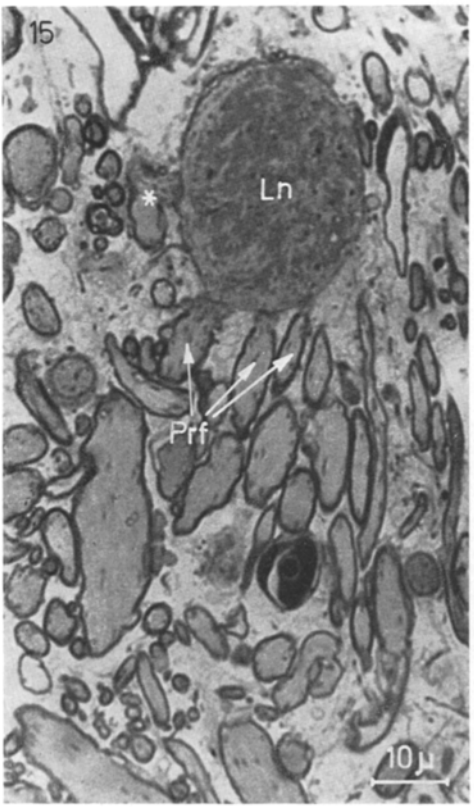

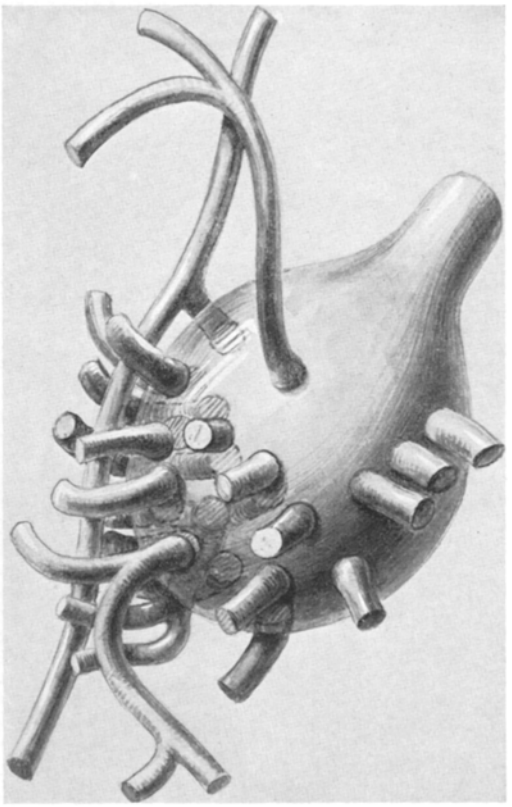

Fig. 15 Fig. 16

Fig. 15. *Semi-thin section showing a large neuron (Ln) with several presynaptic fibers (Prf) terminating with club endings.* The fiber with asterisk indicates a "contact de passage"

Fig. 16. *Stereodiagram showing the same neuron as in Fig. 15 with all the fibers terminating upon it.* The fibers are cut shorter than their real length given in the serial reconstruction of thirty-three 1 μ semi-thin sections. Only fibers with divisions or side branches near the neuron are indicated in the whole extension

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Fig. 9—14. *Photomicrographs showing different aspects of large neurons.* Ln = perikarya of large neurons. Ax = axons of the large neurons, Prf = presynaptic fibers establishing synapses with the large neurons. Fig. 9. The axon of a large neuron bifurcates, the branches run in rostro-caudal direction and split repeatedly (arrows). Golgi-Cox stain, sagittal section. Fig. 10. The perikaryon of a large neuron is contacted by three presynaptic fibers. The axon of the large neuron emerges at the lower pole and soon becomes myelinated (arrows). Reumont-Lhermitte stain, coronal section. Fig. 11. Large neuron with myelinated axon, the myelin sheath begins near the perikaryon (arrows). The neuron is contacted by two myelinated presynaptic fibers (top). Note the cytoplasm is partially covered with myelin (between double arrows). Semi-thin section, toluidine blue stain. Fig. 12. Bundles of presynaptic fibers approaching two large neurons in radial manner. Reumont-Lhermitte stain, coronal section. Fig. 13. Large neuron with trifurcating axon. Golgi-Cox stain, coronal section. Fig. 14. Large neuron at the border between the MMN and the torus semicircularis (dashed line). Its axon bifurcates (arrow); the recurrent branch is not in the plane while the other leaves the MMN by entering a fiber bundle (asterisk) connecting the MMN and the torus semicircularis. Reumont-Lhermitte stain, coronal section

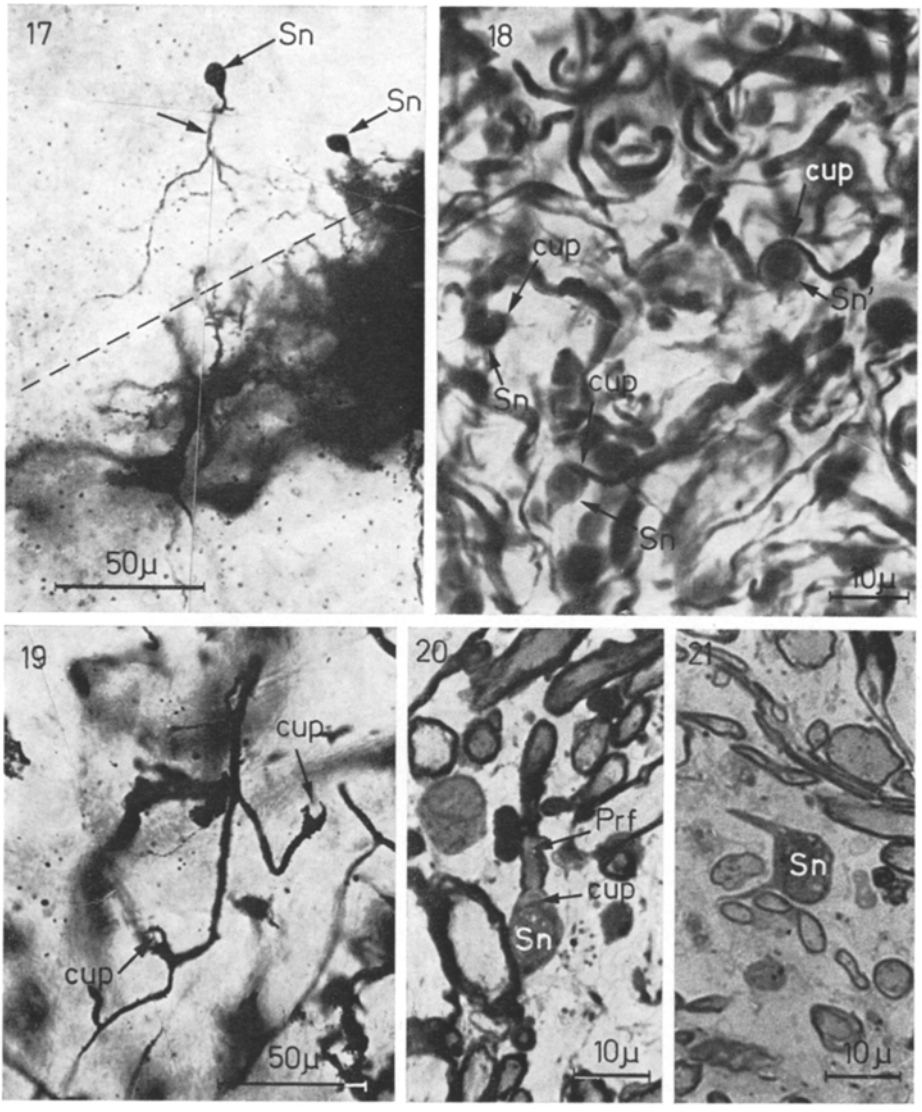

Fig. 17—21. *Small neurons and their presynaptic structures.* Sn = perikarya of small neurons, Ax = axons of small neurons, Prf = presynaptic fibers establishing cup-like terminals (cup) with the small neurons. Fig. 17. Two small unipolar neurons on the ventral border (dashed line) of the MMN. Golgi-Kopsch stain, coronal section. Fig. 18. Three small neurons of unipolar type with their cup-like terminals. In one of them (Sn') the terminal surrounds more than half of the neuron. The thin axon of these neurons or at least their initial parts are seen. Reumont-Lhermitte stain, coronal section. Fig. 19. Detail from a thick fiber displaying side branches with cup-like terminals (cup). Golgi-Cox stain, coronal section. Fig. 20. Semi-thin section showing a small neuron with cup-like terminal of a fairly thick myelinated fiber. Toluidine blue. Fig. 21. Semi-thin section showing a multipolar small neuron. Toluidine blue

The presynaptic fibers are myelinated and curiously enough, the myelin surrounds the axons for nearly the whole of their length (Figs. 11, 15). There is no "preterminal fiber" because the synaptic portion which in most cases hardly exceeds the diameter of the fiber, emerges from the myelinated fiber itself. The myelin sheath seems to terminate abruptly as if were a semi-node of Ranvier. All these features led us to the conclusion that the presynaptic fibers terminate with club-endings.

The fact that the presynaptic fibers could be followed on semi-thin sections allowed us to make three-dimensional reconstructions and to get quantitative data on the number of presynaptic elements terminating upon a single large neuron. The three large neurons reconstructed from serial sections have 14, 23 and 27 presynaptic terminals. Sometimes the terminals emerge from the parent fiber passing by the neuron (synapse *de passage*) but the majority of them are real terminals where the parent axon can be followed back for several microns. The synaptic terminals are densely grouped on the surface of the neuron but large empty surface areas can be found (Fig. 16) which are covered by a thin myelin-like layer (Figs. 11 and 15) the exact nature of which should be cleared up by ultrastructural analysis.

B) Small Neurons

The large neurons do not represent the only cellular element of the MMN. They are outnumbered several times by small neurons of 5—12 μ in diameter. The distribution of the small neurons follow that of the large ones: *i.e.* they accumulate in the postero-ventral division of the nucleus whereas their number diminishes towards the antero-dorsal area. They almost fill the entire caudal part of the nucleus but a few small neurons are also present in the rostral regions.

The small neurons do not represent a homogeneous population because both uni- and bipolar small neurons can be found (Figs. 17 and 21). As our material seems to be sufficient only for the examination of the unipolar small neurons (the majority of the small neurons) further description concerns them only.

The axon of the unipolar small neurons is myelinated and divides repeatedly (Fig. 17). A particular kind of presynaptic axon terminal forming a cup or a calyx surrounds the soma. This often covers up to more than half of the soma (Fig. 18) and is the ending of a fiber that bears a myelin sheath up to the neck of the cup (Fig. 20). In Golgi preparations the cups and their fibers can be recognized as short side branches of thick fibers (Fig. 19).

C) Fiber Structure

There is hardly any doubt that the fibers are essential constituents of the MMN. Their large number and tortuous course must be of special significance in the function of the nucleus.

Some of the fibers derive from the neurons localised within the nucleus, since the axon of both the large and small neurons branches repeatedly inside the nucleus thus producing a great number of fibers (Figs. 9, 13 and 17). As only some of these branches leave the nucleus (Fig. 14) it must be assumed that others terminate in the MMN. This might mean that the neurons are interconnected by the collaterals of their axons.

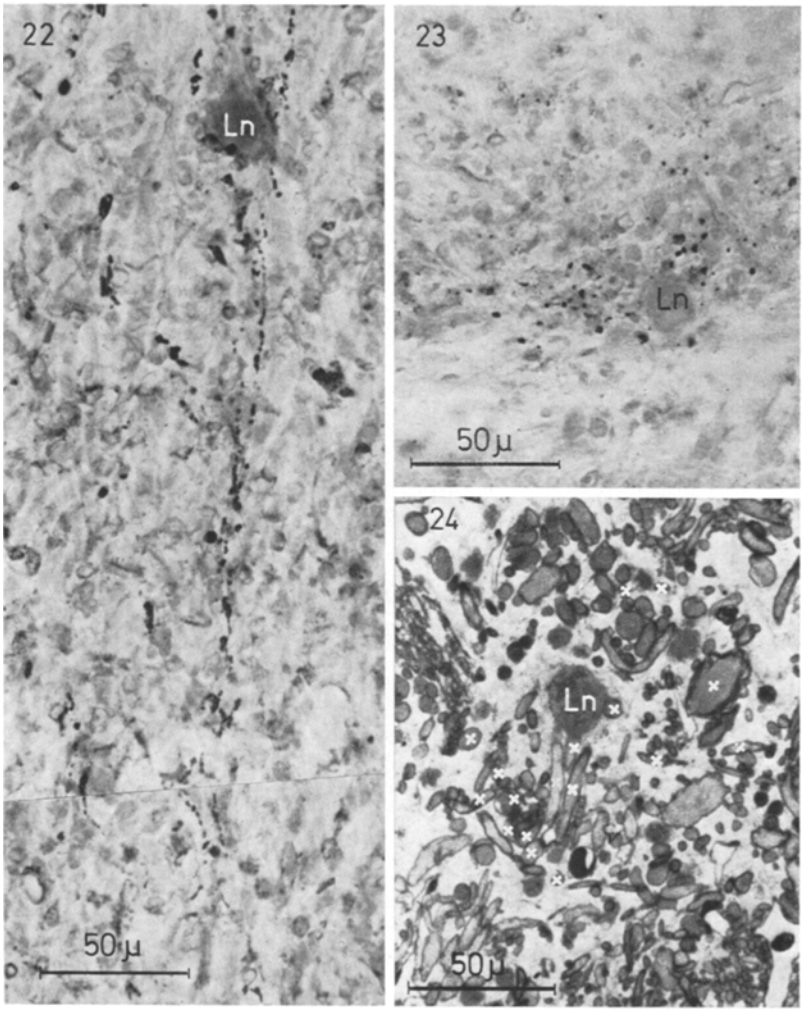

Fig. 22—24. *Fiber structure of the magnocellular mesencephalic nucleus.* Ln = perikarya of large neurons. Fig. 22. Degenerated fibers 7 days after massive destruction of the rhombencephalon. They have a straight course within the nucleus. Fink-Heimer procedure, coronal section. Fig. 23. Degenerated fragments surrounding a large neuron (same experiment as Fig. 22). Fink-Heimer procedure, coronal plane. Fig. 24. Semi-thin section demonstrating a large neuron and the adjacent myelinated fibers. Fibers establishing synaptic contacts with the large neuron in this or in any other planes are indicated by small asterisks. Note the similarity in the distribution of degenerated axon fragments in Fig. 23 and asterisks

Another group of the fibers originates from more or less distant brain structures. As it has been shown, fibers can be followed from the lateral lobe of the rhombencephalon to the MMN (Szabo, 1967). By repeating this experiment a small number of degenerated fibers could be found in the MMN after the destruction of large parts of the lateral lobe. Lesions of small areas in the caudal and lateral part of the lateral lobe did not result in any fiber degeneration in the MMN. The

distribution of degenerated fibers in the MMN displays three characteristic patterns. (i) Degenerated fragments could be found in the ventral part of the MMN corresponding to the area where the large neurons are localized (postero-dorsal division); (ii) Degenerated fibers are often arranged in straight lines (Fig. 22), reflecting the straight course of the rhomencephalic fibers in the MMN; (iii) Degenerated fragments tend to concentrate around large neurons (Fig. 23). It is interesting to compare the distribution of degenerated fibers around a large neuron (Fig. 23) with that of the presynaptic fibers surrounding a large neurons (*i.e.* fibers establishing synapses with the neuron) in a semi-thin section (Fig. 24). As the distribution of the degenerated fragments and that of the presynaptic fibers of a given large neuron is similar, it can be assumed that one part of the club endings belongs to presynaptic mesencephalic fibers.

Discussion

Before going into the discussion of the neuro-architecture of the MMN, the findings presented in the previous section have to be analyzed at a more basic neurohistological level. This should be attempted because both unipolar neurons and specialized terminals (club endings and cup-like terminals) occur rarely in the CNS of vertebrates.

1. Unipolar (Adendritic) Neurons

On the basis of their receptor surface the unipolar large and small neurons in the MMN represent a special group of neurons. Unipolar neurons occur frequently in the invertebrate nervous system (Horridge and Bullock, 1965) but here the presynaptic fibers terminate on the axon and not on the soma as they do in the MMN. Unipolar are the majority of the primary sensory neurons, but here again the soma is devoid of any synaptic terminals (Pineda *et al.*, 1967).

The neurons can be arranged in a continuum on the basis of the dendritic arborization and this sequence has been thought to indicate the level of differentiation. At one end of this continuum the less differentiated neurons have many dendritic processes distributed in random. The dendrites of more differentiated neurons diminish in number and show characteristic arborization patterns. At the other end the total reduction of the dendritic tree leads to the most differentiated unipolar (adendritic) neurons (Szentágothai, 1966; this concept was worked out and published earlier in Hungarian [Szentágothai, 1952]). Szentágothai (1952) demonstrated this sequence of differentiation giving as an example the peripheral autonomic neurons from the less differentiated Dogiel II type neurons (superior cervical ganglion in the cat) up to the unipolar neurons (ciliary ganglion in the pigeon). Although the tendency towards the reduced and characteristic dendritic arborization was clear enough in the central nervous system he failed to find real unipolar neurons.

Thus the unipolar neurons in the MMN might be of highly differentiated nervous elements. This fits well with the findings of Szabo (1967, 1971) who considered this nucleus to be a relay in the electrosensory reflex path. Perhaps the MMN is not a relay nucleus but the highest center in the reflex path where the sensory information is converted into special motor commands.

2. Special Synaptic Terminals

Both club endings and cup-like terminals are rare in the vertebrate CNS.

Club endings were first described on the lateral dendrite of Mauthner's cell (Bartelmez, 1915; Bartelmez and Hoerr, 1933) and these findings were extended later to other species by Bodian (1937). Fibers terminating with club ending have no terminal thickening and the myelin covers the whole lengt of the fiber. Robertson *et al.* (1963) have shown that so-called tight junctions occur at the synaptic level of club endings, thereby suggesting electrotonic transmissions between these and the postsynaptic membrane.

Cub-like terminals occur in rather different structures: in the tangential nucleus of the goldfish (Bodian, 1937), in the trapezoid body (Ramón y Cajal, 1909) and in the ciliary ganglion of birds (Lenhossék, 1911).

In one of his reviews Bodian (1952) gave a fascinating description of the club endings and cup-like terminals. According to him "...the synaptic junctions of large area and simple design..." like the above mentioned two types of synaptic terminals "...are commonly associated with neurons which are of simple form and which receive small number of synaptic contacts...". The unipolar neurons in the MMN are perhaps the best example of Bodian's (1952) observation, and this raises the question whether club endings and cup-like terminals are associated preferentially with unipolar neurons. If so, it would be interesting to know whether the presynaptic fibers determine the form of the postsynaptic neuron or whether the small receptor surface of the postsynaptic neuron involves specialized presynaptic endings. Besides these theoretical considerations one point seems to be clear: club endings and cup-like terminals must work with high synaptic efficiency because the presynaptic fiber to postsynaptic neuron ratio is very low, from 15—30 : 1 to 1 : 1.

3. Neuroarchitecture of the MMN

The present light microscopic findings give but a preliminary and very fragmentary picture of the interconnection of the neurons and the afferent and efferent fibers of the nucleus. Electron microscope and degeneration studies should complete the gaps of the following conclusions: (i) fibers from the rhomencephalon enter the MMN as straight fibers and the side branches of these fibers terminate preferentially on large neurons; (ii) at least one branch of the rich axonal arborization of the large neurons leaves the MMN in the ventral direction; (iii) many of the axonal branches of the large neurons are restricted to and terminate in the nucleus. Thus it seems that it is mainly the large neurons which are reached by incoming impulses and that the axons of the large neurons are the efferent elements of the nucleus. The dense fiber network which is characteristic for the nucleus appears to represent a multiple interconnection between large neurons.

Reconstruction of the large neurons with all the presynaptic fibers might prove eventually to be of considerable help for providing morphological correlates for physiological data on single neurons.

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