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Nucleus Olivaris Inferior of the European Bison

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A description is given of the topography, formation and cell structure of *nucleus olivaris inferior* in the European bison. The studies were carried out on the *medullae oblongatae* of four bison from the Białowieża Primeval Forest. The *medulla oblongata* was cut into cross-sections 15 μm thick which were stained by the Nissl, and Klüver and Barrera methods. The inferior olivary complex was divided into three parts, the most strongly formed of which was the medial accessory olive, and most weakly formed the principal olive. The dorsal accessory olive occupies an intermediate position.

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1. INTRODUCTION

The present paper initiates a cycle of studies on the cytoarchitectonics of the brain in European bison, being carried out in the Department of Vertebrate Anatomy of the Teachers Training College, in Olsztyn, material being obtained from the Białowieża herd of European bison.

The purpose of the study was to obtain knowledge of the structure, position and cytoarchitectonics of *nucleus olivaris inferior* in the European bison, in view of the complete lack of data on this in world literature. This important co-ordinating centre of *medulla oblongata* has been described in several domesticated species of *Artiodactyla*, e.g. the cow (Kdda, 1928), pig (Lewandowski, 1952), and goat (Szteyn & Walento, 1963). Among the wild representatives of *Artiodactyla* the inferior olivary nucleus has been examined in the roe deer (Szteyn & Welento, 1967) and wild boar (Welento & Szteyn, 1967). The above studies revealed considerable differences in ungulates in comparison with representatives of other mammalian orders, such as *Carnivora* (Brodal, 1940; Yoda, 1940, 1941; Taber, 1961), *Rodentia* (Hoffmann, 1957; Szteyn, 1965) and *Lagomorpha* (Meessen & Olszewski, 1949).

The function of *nucleus olivaris inferior* is connected, *inter alia*, with locomotor capacity, the range of movement of the limbs and development of the sense of balance in different species of mammals. It would therefore seem interesting to compare the structure of *nucleus olivaris*

inferior in the European bison with the analogical nerve centre in other mammals.

2. MATERIAL AND METHODS

The studies were carried out on the *medullae oblongatae* of four European bisons from 6 months to 8 years old. The study material was fixed in formalin, dehydrated in ethyl alcohol and embedded in paraffin. The *medulla oblongata* was sectioned to 15 μm, taking every 4th section for examination. The sections were alternately stained by the Nissl and Klüver-Barrera methods.

3. RESULTS

In the European bison *nucleus olivaris inferior* consists of 3 distinctly separated parts: *nucleus olivaris accessorius medialis, nucleus olivaris accessorius dorsalis* and *nucleus olivaris principalis*. The inferior olivary complex is situated in the ventro-medial part of *medulla oblongata*. 57% of the inferior olivary nucleus lies in front of *calamus scriptorius*, and 43% to the rear of this place.

Nucleus olivaris accessorius medialis (Fig. 1—8) in the European bison is far more strongly formed than the remaining parts of *nucleus olivaris inferior*, and occupies a ventro-medial position in the inferior olivary complex. The medial accessory olive consists of 2 strongly folded laminae — horizontal and vertical. The vertical lamina ends at the top in a distinctly broader part forming what is known as the dorsal cap. *Nucleus olivaris accessorius medialis* stretches further to the rear than the medial accessory olive and principal olive and forms on its own almost 1/3 of the posterior part of the complex. The medial accessory olive extends over an area equal to 77% of the length of the whole inferior olivary nucleus. In the rear the horizontal lamina of the medial accessory olive first appears, being formed of a narrow band of cells arranged transversely from the dorso-medial side towards the ventro-lateral side. In a forwards direction the horizontal lamina enlarges and becomes folded. Near the anterior end of the medial accessory olive these folds become smoothed and the horizontal lamina again forms a narrow band of cells situated ventrally from the principal olive. The vertical lamina is accompanied by the medial part of the horizontal lamina and is about 3/5 of its length. It is formed by a band of cells arranged parallel to the raphae of the *medulla oblongata*. The lower margin of the vertical lamina is joined to the medial end of the horizontal lamina. Both laminae of the medial accessory olive are positioned in relation to each other at an obtuse angle. The vertical lamina, like the horizontal lamina, is strongly folded in its medial part and is distinctly thickened at the end to form the dorsal cap.

Nucleus olivaris accessorius dorsalis (Fig. 4—12) is a long narrow band of cells situated on the dorso-lateral side of the remaining part of the olivary complex. The dorsal accessory olive extends further forwards than the medial accessory olive and principal olive, and forms on its own a short anterior part of the complex. In cross-sections the band of cells forming the dorsal accessory olive lies transversely from the dorso-medial side to the ventro-lateral side. The posterior part of *nucleus olivaris accessorius dorsalis* is situated above the horizontal lamina of the medial accessory olive, and its anterior part, after the appearance of the principal olive, is situated on the dorso-lateral side of this final part of *nucleus olivaris*. The length of the dorsal accessory olive is equal to 68% of the length of the whole inferior olivary complex.

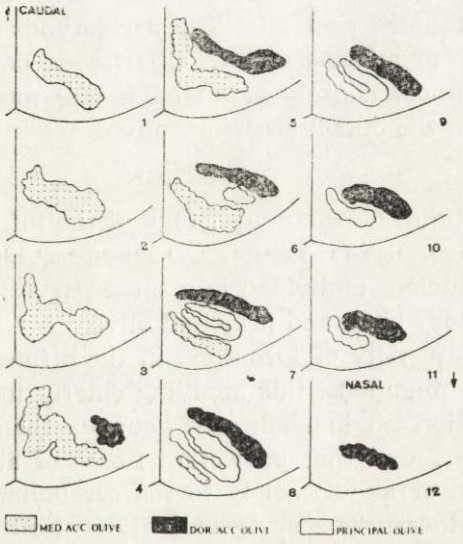

Fig. 1. Cross-sections of *nucleus olivaris inferior*. Nos. 1—12 show consecutive layers of the nucleus.

The principal olive (Fig. 6—11) is very weakly formed in the European bison and its extent is limited to the anterior half of the complex. *Nucleus olivaris principalis* lies between the medial and the dorsal accessory olives. In the rear this part of *nucleus olivaris* appears at a small distance forwards from half the length of the olivary complex. The anterior pole of the principal olive lies about 250 μm to the rear of the anterior end of the dorsal accessory olive, forming independently the anterior part of *nucleus olivaris inferior*. *Nucleus olivaris principalis* extends over a space equal to 47% of the length of the whole complex. The shape of the principal olive varies in the cross-

sections. The posterior part is elongated, similar in shape to an oval group of cells arranged transversely from the dorso-medial side to the ventro-lateral side. In its middle part the principal olive is more distinctly formed, having the shape of a letter U lying transversely, the open part of which is directed dorsal and medial. Between the arms of the letter U there is a narrow sinus without cells. *Nucleus olivaris principalis* exhibits this shape only for a short section, taking on in its anterior part the shape of an elongated band of cells situated on the ventro-medial side of the dorsal accessory olive.

Nucleus olivaris inferior in the European bison is formed from intensively staining multipolar and rounded cells from 25 to 40 μm in dimension and fusiform cells measuring from 30 to 45 μm along the long axis (Phot. 1, Plate I). The cells of the olive have large spherical nuclei with a nucleolus situated centrally. The perikaryons of the cells forming the different parts of *nucleus olivaris inferior* do not differ as to shape and size, but are most densely arranged in the medial accessory olive and most loosely in the dorsal accessory olive.

4. DISCUSSION

Comparative studies on the morphology of the inferior olivary nucleus have shown (Brunner, 1917; Kooy, 1917; Kappers, 1960 and others), that in mammals this nucleus is divided into three parts: the medial accessory olive, dorsal accessory olive and principal olive.

There is great diversity of formation in the different parts of *nucleus olivaris inferior* in mammals, this applying chiefly to the principal olive, which is a formation phylogenetically younger than the two accessory olives. It has been found that projection fibres of all parts of the olive are directed solely, or almost solely to the cerebellar cortex (Armstrong *et al.*, 1982 and others). The system of efferent fibres of the principal olive, however, is connected chiefly or solely with the cerebellar hemispheres, whereas the phylogenetically older accessory olives send fibres primarily to the vermis (*inter alia* Saigal *et al.*, 1983).

In ungulates the principal olive is very weakly formed. This also applies to the European bison, which even among ungulates is distinguished by an exceptionally small principal olive. This is shown, *inter alia*, by the ratio of length of *nucleus olivaris principalis* to the length of the whole complex, this being illustrated by the following table:

Capreolus capreolus	57%	*Bos taurus*	50%
Capra domestica	55%	*Sus domestica*	50%
Ovis domestica	54%	*Bison bonasus*	47%
Equus caballus	51%	*Sus scrofa*	46%

The length of the principal olive in the European bison is similar

to the length of this part of the olive in the wild boar, but the picture in cross-sections shows that it is far less developed. In the wild boar the principal olive is formed on the long part from two arms connected with each other in the form of a letter U and is folded. In the European bison the principal olive is shaped like the letter U only for a very short part.

The majority of researchers connect the development of the principal olive with the locomotor capacity of the limbs. Kappers (1960) connects the strong development of the principal olive in *Primates* with the formation in these mammals of limbs of the prehensile type with a wide range of movement and manipulative capacity of the digits, but Tilney (cited after Kappers, 1960) with the so-called "eye-head-digital" group of movements, in which the movement of the limbs and digits are connected with movements of the head and eyes. Lewandowski (1952) assumes that the weak formation of *nucleus olivaris principalis* in ungulates is to a great extent due to the polarization of joints, reduction of muscles and digits of the limbs. Welento & Szteyn (1967) in analyzing the results of studies by Brouver & Coenen (1919), Brodal (1940) and Larsell & Berthelsdorf (1941), and also on the strength of their own observations, consider that one of the tasks of the principal olive is to co-ordinate the work of the muscles of limbs and spine. No confirmation has been found for Brunner's assumption (1917) that the function of the principal olive is connected only with the movements of the fore limbs. The observations made by Swanson & Castro (1983) showed in the rat the presence of projection fibres running from *nucleus ruber* to the principal olive, which suggests that the principal olive participates in the functions of the extrapyramidal system. The exceptionally weak development of the principal olive in the European bison is probably connected with the low mobility of the spine and the small range of movements and uncomplicated action of the limbs in this animal.

The most strongly-formed part of the inferior olivary nucleus is the medial accessory olive. It is not only the longest part of the complex, but also exhibits the most complicated structure, since it is formed of 2 strongly folded laminae. In comparison with other ungulates *nucleus olivaris accessorius medialis* in the European bison is, however, relatively short, as is shown by the comparison given below, presenting the ratio of length of the medial accessory olive to the length of the whole complex of the inferior olivary nucleus in ungulate mammals:

Sus scrofa	95%	*Capra domestica*	81%
Capreolus capreolus	94%	*Bos taurus*	81%
Ovis domestica	86%	*Equus caballus*	80%
Sus domestica	85%	*Bison bonasus*	77%

It is difficult to interpret these relations on account of the great difference of opinion as to the function of the medial accessory olive. Kappers (1960) and Lewandowski (1952) connect the development of the medial accessory olive with the mobility of the spine, while Schober (1959/1960) connects it with the motor capacity of the forelegs. These two views difficult to reconcile. Among mammals with a very strongly developed medial accessory olive there are animals characterized by great mobility of the spine with relatively low capacity of the forelegs (seals, cetaceans — Kooy, 1917) and those in which the basic locomotor organ consists of the fore limbs, while the mobility of the spine is negligible (bats — Schober, 1959/1960). These two groups of mammals, on the other hand, are linked by a highly developed sense of balance. Taber's studies (1961) showed that, like aquatic mammals and bats, the cat, in which the sense of balance is also very well developed, also has a strongly formed medial accessory olive. Connection of the medial accessory olive with this sense is supported by the results of studies by Swenson & Castro (1983), who described the projection fibres running from the vestibular nuclei to the medial accessory olive. Observations made by Nakamura, Kitao & Okoyama (1983) showed that the medial accessory olive also receives nerve fibres from the motor cortex through the nucleus of Darkschewitsch, which suggests the participation of the medial accessory olive in functions of the cortico-medullary tract, although this is at present difficult to determine.

The dorsal accessory olive in the European bison, in comparison with the analogical part of *nucleus olivaris* in other ungulates is relatively weakly formed (Kolda, 1928), but is clearly shorter than *nucleus olivaris accessorius dorsalis* in the roe deer (Welento & Szteyn, 1967). This ratio of length of the dorsal accessory olive in ungulates to the length of the whole *nucleus olivaris* complex is shown in the following table:

Sus scrofa	91%	*Ovis domestica*	72%
Capreolus capreolus	83%	*Capra domestica*	71%
Equus caballus	81%	*Bos taurus*	69%
Sus domestica	75%	*Bison bonasus*	68%

On the other hand the dorsal accessory olive in the European bison is relatively far more strongly developed than the corresponding olive in some rodents, e.g. nutria (Szteyn, 1964) and beaver (Szteyn, 1974). It is difficult at present to define the role of the dorsal accessory olive. Brunner (1917) connects its development with the locomotor activity of the pelvic limbs. This statement cannot, however, be accepted without some reservation. Among mammals the bat, for instance, is distinguished by a very strongly formed part of nucleus olivaris (Schober, 1959, 1960) and in the bat the role of the pelvic limbs in locomotion is slight. New

light is thrown on the role of the dorsal accessory olive by the studies made by Kitao, Nakamura & Okoyama (1983), who found in the cat numerous nerve fibres running from the motor cortex through *nucleus pretectalis anterior* to *nucleus olivaris inferior*. These fibres and mainly in the dorsal accessory olive, and it is therefore possible that the dorsal accessory olive forms, in the cortico-olivary-cerebellar circuit an indirect link in the creation of somatomotor reactions to the incoming visual stimuli.

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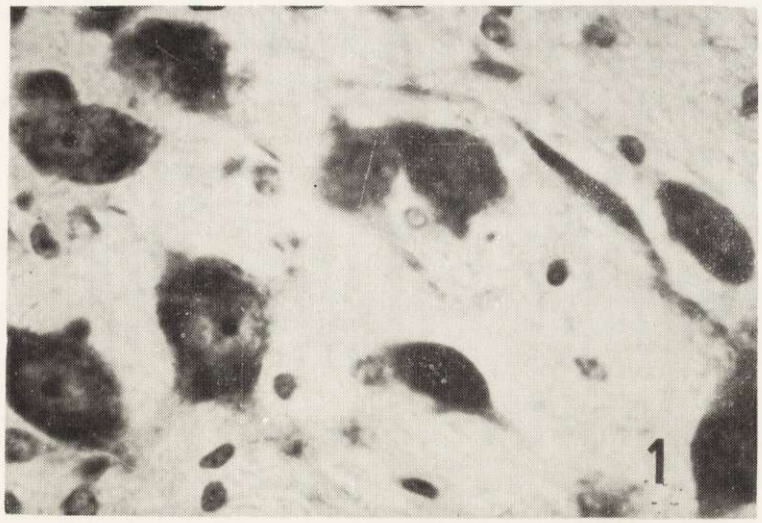
NUCLEUS OLIVARIS INFERIOR ŻUBRA

Streszczenie

Badania wykonano na rdzeniach przedłużonych 4 żubrów w wieku od 6 miesięcy do 8 lat. Materiał do badań utrwalano w formalinie, odwadniano w alkoholu etylowym, zatapiano w parafinie i cięto na skrawki poprzeczne grubości 15 μm. Skrawki barwiono metodami Nissla i Klüvera-Berrery.

Nucleus olivaris inferior żubra leży w brzuszno-przyśrodkowej części rdzenia przedłużonego. Oliwa dolna żubra podzielona jest na 3 części: przyoliwę przyśrodkową, przyoliwę grzbietową i oliwę główną. U żubra najlepiej wykształcona jest przyoliwa przyśrodkowa, która utworzona jest z 2 silnie pofałdowanych blaszek — poziomej i pionowej. Przyoliwa przyśrodkowa tworzy samodzielnie tylny odcinek kompleksu. Jej długość równa się 77% długości całej oliwy dolnej. Przyoliwa przyśrodkowa zajmuje w kompleksie oliwy położenie grzbietowo-boczne i ma postać pojedynczego, płaskiego pasma komórek. Przyoliwa grzbietowa sięga do przodu dalej niż pozostałe części oliwy i rozciąga się na przestrzeni równej 68% długości całego kompleksu. Oliwa główna jest u żubra wykształcona bardzo słabo. Tylko w środkowym odcinku utworzona jest z 2 ramion, które łączą się ze sobą w kształcie litery U. Oliwa główna leży między przyoliwą przyśrodkową i przyoliwą grzbietową w przedniej połowie kompleksu. Długość oliwy głównej równa się 47% długości całej oliwy dolnej.



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EXPLANATION OF PLATE I.

Phot. 1. Cells of *nucleus olivaris inferior.*