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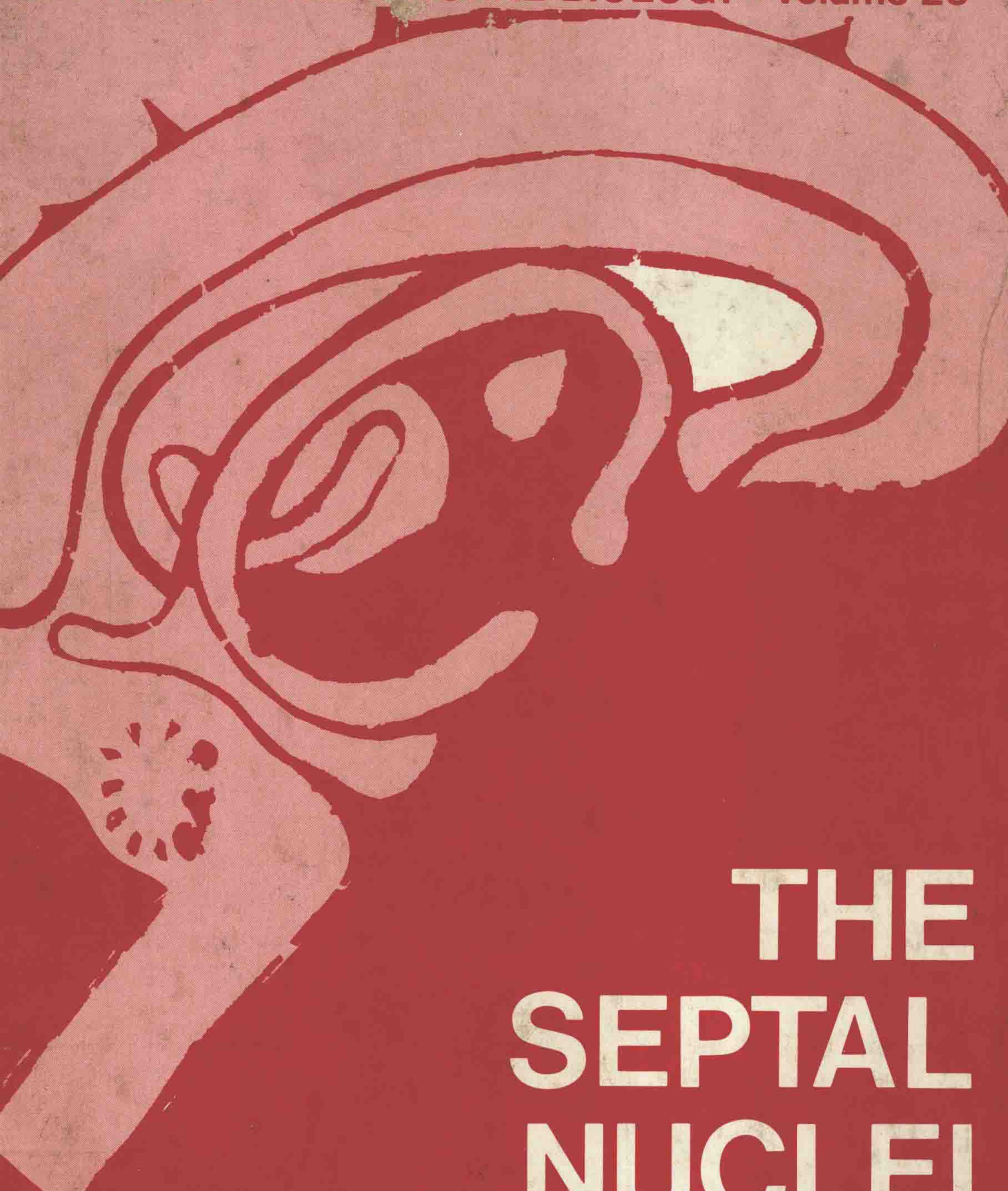

THE SEPTAL NUCLEI

Edited by

Jon F. DeFrance

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Detroit, Michigan

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Finally, I want to thank all the participants. Their interest and enthusiasm made it all worth while.

JDF

Preface

The "septum pellucidum" has been described since antiquity. Even though people such as Vicq d' Azyr (12) and Burdach (3) pictured the septal region in their drawings, the nuclei associated with the pellucidum--the septal nuclei--were not described until Meynert (10).

Since Meynert's description, this portion of the limbic system has been troublesome in terms of nomenclature. Scientists about the turn of the twentieth century proposed quite diverse terminologies. For example, Elliot Smith first wrote of the precommissural area (4) and then later of the paraterminal body (5). These terms, however, were meant to extend beyond the septal nuclei of our understanding. Unger (11) and Herrick (8) proposed the familiar terms--nucleus lateralis septi and nucleus medialis septi; but again they were somewhat broader in definition than is accepted for current usage. These terms, however, were rejected by Johnston (9). In Johnston's great paper, he pointed out that the hippocampus seems to evolve out of large portions of the septal nuclei. It was appropriate then to borrow a term previously used by Elliot Smith (6), but in another context--primordium hippocampi. Johnston's primordium hippocampi corresponds to the lateral septal nucleus of current usage. He introduced the terms medial and lateral parolfactory area to refer to the remaining portions of the septal nuclei of Herrick (8). Hence, the lateral parolfactory area refers to the nucleus accumbens septi of Ariens Kappers (2). But, Johnston's terminology received little acceptance. The majority of investigators still favor the terms: medial septal nucleus and lateral septal nucleus. Fox (7) extended this notion to a medial and lateral septal region. The lateral septal region which included the nucleus accumbens septi.

The recent study of Andy and Stephan (1) has again changed the face of the terminology. They distinguish four basic septal groups--the medial, dorsal, lateral, and caudal. For the most part, the dorsal, lateral, and caudal septal groups of Andy and Stephan correspond to the lateral septal nucleus of Herrick (with the nucleus accumbens septi removed).

In spite of the problems of terminology, the septal nuclei have been the subject of intense investigation, spurred by their apparent role in emotional, motivational, and memory processes. A major aim of the current symposium is to bring recent research into focus so that a consensus can accrue with regard to the most appropriate terminology, and with that, a better understanding of the role of the septal nuclei in brain.

Detroit JDF

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Part I

Anatomy

SEPTUM DEVELOPMENT IN PRIMATES

O. J. Andy[1] and H. Stephan[2]

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INTRODUCTION

It has been commonly believed that the septum underwent a reduction in size during evolution. Previous investigators (18,19, 20) thought that the septum became a functionless atrophic cortical structure in association with a general atrophic process of the olfactory system. More recent studies, based on utilizing insectivores as a reference since they represent the forerunners of the primate, reveal that the septum actually undergoes a progressive increase rather than a decrease in size in primate development (3,4,22). Among primates it attains its greatest degree of development in the human brain (Fig. 1).

METHODOLOGY

Brains of living animal forms are utilized. The evolutionary levels of the animals under consideration are established in accord with the degree of development and differentiation of the neocortex. The basal forms of insectivores consist of terrestrial and nonspecialized species. They possess the simplest cortical pattern and smallest cortical volume. The higher insectivores tend to be more specialized. They may be semi-aquatic, may burrow or may possess a specialized visual system. All animal brains are profused with Bouin's solution immediately after sacrifice.

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[1]Supported in part by NIH grant 04510.

[2]Supported in part by Deutsche Forschungsgemeinschaft.

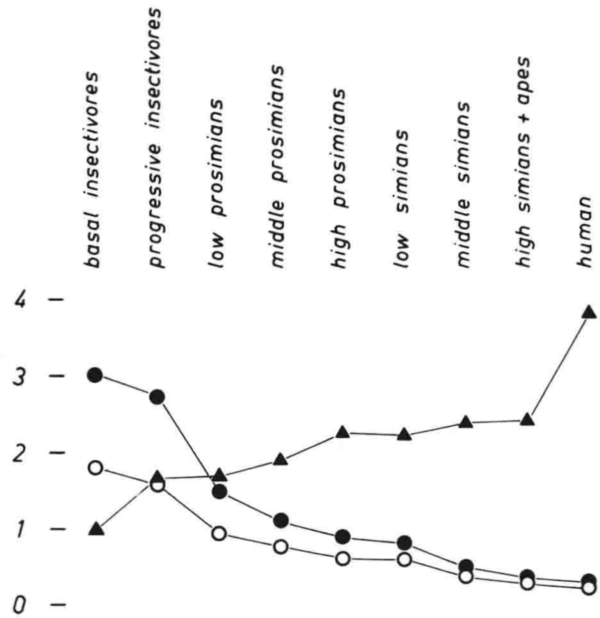

Figure 1. Comparison of the size of the septum at ascending levels of the primate scale by two different methods. The numbers on the left side indicate the percentage proportion of the septum related to the total brain (open circles) and telencephalon (solid circles). The same numbers represent progression indices for the septum in relation to body weight (triangles). These indices determine the enlargement multiple of the septum in the progressive group in comparison to that in basal insectivores (the latter have the index = 1). For more details refer to material, techniques and to discussion in Andy and Stephen (4).

The various insectivores and primate groups utilized are as follows:

Basal Insectivores

(Sorex, Crocidura, Suncus, Echinops, Hemicentetes, Setifer, Tenrec, Erinaceus)

Progressive Insectivores

(Solenodon, Nesogale, Limnogale, Potamogale, Neomys, Talpa, Galemys, Desmana, Chlorotalpa, Elephantulus, Rhynchocyon)

Tupaiidae

(Tupaia, Urogale)

Prosimians

(Microcebus, Cheirogaleus, Lepilemur, Hapalemur, Lemur, Avahi, Propithecus, Indri Daubentonia, Loris, Perodicticus, Galago, Tarsius)

Simians

Hapalidae

(Hapale, Leontocebus)

Aotes

Cebidae and Cercopithecidae

(Saimiri, Cebus, Ateles, Colobus, Macaca, Cercopithecus)

Pan

Homo

The brain of each animal is cut in either the frontal, horizontal or sagittal plane. The cytoarchitectonics are studied in serial paraffin sections in the frontal plane, 10 to 28 mm. thick. Every other section is stained with cresyl violet and Heidenhain Woelche stains in order to study nuclear and fiber components. All sections are stained in the smaller brains and every tenth section in the larger brains. Photographs magnified up to 35 X are made of 50 to 60 serial sections taken at equal intervals in each brain. For further details on technique refer to Stephan (23, 24).

Nuclear Cytoarchitectonics

In the insectivores the nuclear cytoarchitectonics of the septum is based upon detailed studies in 12 brains (2). Seven brains represent the sub-family Soricinae (red tooth shrew); five from the Genus Sorex Aranius (common shrew); one from the Genus Sorex Minutus (a dwarfed form of common shrew); and one from Neomys Fodiens (old world water shrew). Five brains are from the sub-family Crocidurinae (white tooth shrew); two from the Genus Crocidura

Russula (house shrew); three from the Genus Crocidura Occidentalis (an African musk shrew). The average body and brain weights in grams are as follows: Sorex Aranius, 10.3 and 0.2; Sorex Minutus, 5.3 and 0.11; Neomys Fodiens, 15.0 and 0.32; Crocidura Russula, 11.0 and 0.18; Crocidura Occidentalis, in males 32.0 and 0.45; in the females 24.0 and 0.43.

Detailed nuclear cytoarchitectonic studies representing the prosimian brain was performed on the Galago Demidovii (1). It belongs to a lower family of primates and possesses a body weight of 81.0 grams and a brain weight of 3.38 grams (Fig. 2). It lives in tropical Africa where it thrives on various forms of living matter and vegetation. Among higher primates the nuclear cytoarchitectonics was studied in the cercopithecus ascanius and colobus badius (25). Colobus badius body weight is 7,260 grams and brain weight 74.3 grams. Cerecopithecus ascanius body weight is 3,670 grams and brain weight 65.2 grams (Fig. 3).

Developmental size changes of the septum and its component nuclei are based on volumetric determinations, made by outlining various brain structures on the histologic serial photographs (Fig. 4). The various structures are then cut out and weighed. The volume of each structure is determined in accord with the weights of each structure translated to volume by taking into consideration the distances between the histologic photographs. Distances between

Figure 2. Galago demidovii from Durrell, G. M., 1955. Granckhsche Vertagshandlung, Stuttgart, 1955. Galago demidovii is a prosimian which represents a transition between the insectivores and the higher primates (overall body weight 10 grams, brain weight 3 grams). It has a relatively well differentiated brain and its septum demonstrates characteristics of both insectivores and higher primates. Taken from Andy and Stephan (1).