TOPICAL REVIEW

History, anatomical nomenclature, comparative anatomy and functions of the hippocampal formation

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Abstract

The complex structures in the cerebral hemispheres is included under one term, the limbic system. Our conception of this system and its special functions rises from the comparative neuroanatomical and neurophysiological studies. The components of the limbic system are the hippocampus, gyrus parahippocampalis, gyrus dentatus, gyrus cinguli, corpus amygdaloideum, nuclei anteriores thalami, hypothalamus and gyrus paraterminalis

Because of its unique macroscopic and microscopic structure, the hippocampus is a conspicuous part of the limbic system. During phylogenetic development, the hippocampus developed from a simple cortical plate in amphibians into complex three-dimensional convoluted structure in mammals. In the last few decades, structures of the limbic system were extensively studied. Attention was directed to the physiological functions and pathological changes of the hippocampus. Experimental studies proved that the hippocampus has a very important role in the process of learning and memory. Another important functions of the hippocampus as a part of the limbic system is its role in regulation of sexual and emotional behaviour. The term "hippocampal formation" is defined as the complex of six structures: gyrus dentatus, hippocampus proprius, subiculum proprium, presubiculum, parasubiculum and area entorhinalis In this work we attempt to present a brief review of knowledge about the hippocampus from the point of view of history, anatomical nomenclature, comparative anatomy and functions *(Tab. 1, Fig. 2, Ref. 33)*.

Key words: hippocampal formation, history of medicine, nomenclature, comparative anatomy, function.

Hippocampus in the history of medicine

The history of medicine is rich in pioneers, who lighted the way of the modern science. In this part we present the role of some of them in studying the hippocampus.

Arantius (1587) described in his book "De Humano Foetu" the structure in the temporal horn of the lateral ventricles that looks like hippocampus (sea horse) or bombycinus vermis candidus (white silkworm), (Sano, 1997). In literature only the first term gained popularity and is in use till today. This term is extracted from the Greek hippokampos: hippos, horse; +kampos, sea monster (Pearce, 2001).

According Walther (2002) the careful reading of the entire original text of Arantius leads to the conclusion that it was not the hippocampus in our modern terms but the dentate gyrus, which he compared to a little sea horse or a silkworm.

Diemerbroeck in 1672 added a foot to each seahorse and called it pes hippocampi. In the 18th century, Vicq d'Azyr distinguished the hippocampus major and minor. He defined the hippocampus minor as an eminence in the floor of the occipital horn of the lateral ventricle, calcar avis in the modern nomenclature (Bentivoglio and Swanson, 2001).

The coronal section of the hippocampus reminded Winslow (1732) of the shape of the ram's horn, because of that he named it cornu arietis. De Garengeot (1742) chose more mystical term, cornu Ammonis (Sano 1997). Ammon, the hidden, is the chief god of Theba in ancient Egypt. It was presented as a ram headed man, or a ram headed sphinx.

Tarin (1750) differentiated structure, which he called fascia dentate, from the rest of the hippocampus. Huxley (1861) pro-

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Tab. 1. Hippocampus in the anatomical nomenclature.

Cajal (1911)	Rose (1926)	Lorente de Nó (1934)	Terminologia anatomica (1998)
Fasciadentata	Fascia dentata	Fascia dentata	Gyrus dentatus
Hilus fasciae	H3, H4, H5	CA4	Regio IV hippocampi proprii dentatae (CA4)
Regio inferior	H2	CA3	Regio III hippocampi proprii (CA3)
		CA2	Regio II hippocampi proprii (CA2)
Regio superior	H1	CA1	Regio I hippocampi proprii (CA1)
Subiculum		Subiculum	Subiculum
		Presubiculum	Presubiculum
		Parasubiculum	Parasubiculum

vided an alternative term, dentate gyrus (Bentivoglio and Swanson, 2001, Ledényi, 1937).

In 1873 Golgi introduced the reazione nera (the black reaction), the revolutionary silver impregnation method. This method was a great forward step in understanding the microscopic structure of the nervous system (Szentágothai, 1975, Swanson, 1999).

Ramón y Cajal (1911) and his student Lorente de Nó modified Golgi's method to increase its effectiveness and used it in studying the cellular architecture of the hippocampal formation (Bentivoglio, 2004, Woolsey, 2004). Their results are the keystone of knowledge of the archicortex till the present day.

In 1937 Papez described his circuit and he suggested that it might constitute the center of emotion. One of the structures integrated in this circuit was the hippocampus. In 1952 Maclean named this circuit the "limbic system" (Marshall and Magoun, 1998).

By the middle of the last century the limbic system and specially the hippocampus started to be one of the most studied structures in the nervous system. They were studied by application of multidisciplinary approach, in which combination of anatomic, physiologic and behavioural sources were used.

Hippocampus in the anatomical nomenclature

Pallium (the cerebral cortex) coats the surface of the cerebral hemispheres (Tab. 1). The cerebral cortex is divided according the development level, structure and function into neocortex and allocortex. The periallocortex or the mesocortex are the terms used to mark the transitional zone between neocortex and allocortex. The highly developed six-layered neocortex forms approximately 95.6 % of the cerebral cortex (Čihák, 1997).

The three-layered allocortex is divided into:

a) paleocortex, which is the oldest part of the cortex from the development view point;
b) archicortex, which comprises the hippocampus in a wider sense.

The terms "hippocampus" and "archicortex" are used in the literature as synonyms (Schwerdtfeger, 1984). Hippocampus proprius was separated in many regions according to the thickness of the layers and cell size and density. Today in literature we can find at least three differing nomenclatures of the hippocampus (Williams, 1995).

1) Nomenclature according Cajal

Cajal (1911) divided the hippocampus proprius in two regions:

a) regio superior, which is closer to the entorhinal cortex (gyrus parahippocampalis); and
b) regio inferior, which is nearer to the gyrus dentatus.

Cajal used the term fascia dentate for the gyrus dentatus. He used the term „hilus fasciae dentatae" to mark the region between the two arms of the gyrus dentatus.

2) Nomenclature according Rose

Rose (1927) divided the hippocampus in five regions (H1–H5). He designated these regions on the direction from the subiculum toward the gyrus dentatus.

3) Nomenclature according Lorente de Nó

Lorente de Nó (1934) used the term cornu ammonis (CA) for the hippocampus proprius. He identified four regions in cornu ammonis:

a) CA1 is the nearer to the entorhinal cortex;
b) CA2 is a narrow region between CA1 and CA3;
c) CA3 continues until the hilus fasciae dentatae; and
d) CA4 is the region between the arms of the fascia dentate.

4) Terminologia anatomica

Terminologia anatomica (1998) is the newest anatomical nomenclature. It divides the hippocampus proprius in four regions marked CA1–CA4 or regio I–IV. Instead of the term fascia dentata used by the previous nomenclatures it uses the term gyrus dentatus.

The subiculum is the transitional region between the hippocampus proprius and the entorhinal cortex (Cajal, 1911). The subiculum itself was divided from the entorhinal cortex toward the CA1 into the parasubiculum, presubiculum and subiculum proprium (Lorente de Nó, 1934).

The term "hippocampal formation" is a complex of six structures: gyrus dentatus, hippocampus proprius, subiculum proprium, presubiculum, parasubiculum and area entorhinalis (Bayer, 1985).

Hippocampus in comparative anatomy

Amphibians, reptiles and birds have a tissue homologous to the hippocampus, but its cytological composition is different from that of mammals.

The pallium of amphibians consists of three longitudinal areas, namely the area lateralis pallii, area medialis pallii and area dorsalis pallii. From the morphological point of view, the area medialis pallii can be interpreted to represent the primordial hippocampi (Kuhlenbeck, 1977).

The cortex medialis of reptiles corresponds to the primordium hippocampi of amphibians. In comparison with mammals,

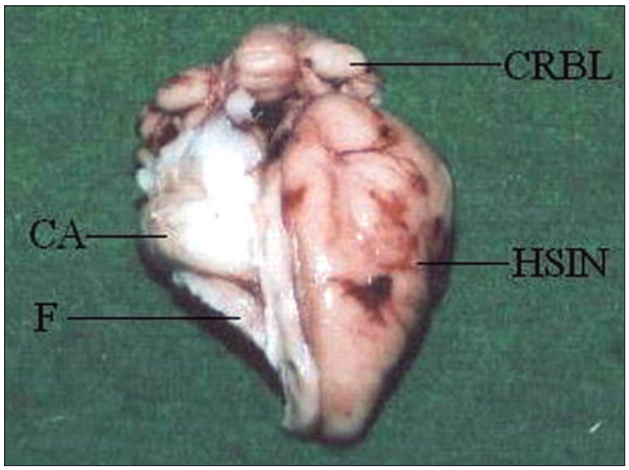

Fig. 1. The rabbit's brain after removal of the neocortex of the right hemisphere to illustrate the position of the hippocampus. HSIN – hemispherium sinistrum, CRBL – cerebellum, CA – cornu Ammonis, F – fornix et fimbria hippocampi.

Fig. 2. Wax embedded preparation of the human brain illustrating the position of the hippocampus. LF – lobus frontalis, Cd – nucleus caudatus, COVL – cornu occipitale ventriculi lateralis, LO – lobus occipitalis, CC – corpus callosum, F – fornix et fimbria hippocampi, CTVL – cornu temporale ventriculi lateralis, CA – cornu Ammonis, LT – lobus temporalis, CFVL – cornu frontale ventriculi lateralis.

the larger dorsolateral portion of the cortex medialis is comparable to cornu Ammonis, and the smaller dorsomedial part is homologous to gyrus dentatus (Kuhlenbeck, 1977).

The hippocampal formation in birds consists of the curved cortical strip on the dorsomedial surface of the hemispheres. It is composed of the hippocampus and the area hippocampalis, which presents a transitional zone between hippocampus and other regions of telencephalon (Tömböl et al., 2000).

During the phylogenetic development of mammals, topographic changes in position of the hippocampus occurred (Figs 1, 2). The cause of these changes was the intensive development of the neocortex and corpus callosum. The result was displacement of the hippocampal formation rostrally and to the depth of temporal lobe (West, 1990).

According the Nomina Anatomica Veterinaria (1974), the hippocampus in mammals presents three regions.

a) Pars retrocommissuralis (hippocampus proprius or cornu Ammonis) is the largest and most developed portion of the hippocampus.

b) Pars retrocommissuralis (indusium griseum or gyrus supracallosus) is located on the corpus callosum as a thin layer of grey matter. Striae longitudinales corporis callosi are paired elevated tracts of the indusium griseum. These striae together with indusium griseum and gyrus fasciolaris (part of the periarchicortex) continue behind the corpus callosum into the hippocampus proprius. Because of the extensive development of the corpus callosum in Primates, the indusium griseum from the functional viewpoint is a vestigial structure (Carpenter,1973).

c) Pars precommissuralis (taenia tecta or anterior hippocampus) is the rostral continuation of the indusium griseum. It is placed below the genu corporis callosi and reaches the pedunculus olfactorius. The taenia tecta is rarely a macroscopically visible structure and it can include the dorsal portion of the gyrus paraterminalis (Switzer et al., 1985).

Functions of the hippocampus

In 1953, Dr. W. Scovill bilaterally removed H.M.'s medial temporal lobe structures for the relief of epileptic attacks. After the operation the frequency of seizures decreased, but later the patient suffered severe and persistent amnesia. This experimental operation opened the way for other studies, which proved the role of the hippocampus as the cerebral structure most involved in the process of memory and learning. Other cortical structures in the medial portion of the temporal lobe with high participation in the process of memory and learning are the entorhinal cortex, the perirhinal cortex and the parahippocampal cortex. (Barr and Goldberg, 2003, DeJong, 1973).

Some new theories argue that the hippocampus plays a selective role in creation of the episodic memory and the spatial memory while the entorhinal, perirhinal and parahippocampal cortices play major roles in semantic memory (Suzuki and Clayton, 2000, Jarrard, 1995, Teyler and DiScenna, 1985).

Studies observed an alteration of the pattern and duration of eating in animals with damaged hippocampus. Increased food consumption was also reported following electrical and chemical stimulation of the hippocampus. These studies concluded clear role of the hippocampus in the control of behaviour related to food and appetite (Tracy et al., 2001).

The hippocampal formation as a part of the limbic system participates in the control of emotion. (Mysliveček and Myslivečková-Hassmanová, 1989, Hara and Myers, 1973). The emotional impulses created in the limbic system must be transmitted to the neocortical regions to add emotional colouring to the psychic process (Carpenter, 1972).

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Received March 4, 2006.
Accepted March 24, 2006.