NOTA HISTÓRICA

Cerebral localization of higher functions: anatomic structures before the identification of their memory function

Localização cerebral de funções superiores: estruturas anatômicas antes da identificação de suas funções de memória

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ABSTRACT

The nature of memory and the search for its localization have been a subject of interest since Antiquity. After millennia of hypothetical concepts the core memory-related structures finally began to be identified through modern scientifically-based methods at the diencephalic, hippocampal, and neocortical levels. However, there was a clear temporal delay between the finding of these anatomic structures ignoring their function, and their identification related to memory function. Thus, the core structures begun to be identified with a pure anatomical view in the late Middle Ages on, while the memory function related to them was discovered much later, in the late Modern Period.

Keywords: memory, anatomical structures, diencephalon, hippocampus, neocortex.

RESUMO

A natureza da memória e a busca de sua localização tem sido objeto de interesse desde a Antiguidade. Após milênios de conceitos hipotéticos as estruturas centrais relacionadas com a memória finalmente começaram a ser identificadas através de métodos modernos com base científica, nos níveis diencefálico, hipocampal e neocortical. Entretanto, houve um claro retardo temporal entre o achado dessas estruturas anatômicas ignorando sua função e sua identificação relacionada à função da memória. Assim, as estruturas centrais começaram a ser identificadas com uma visão puramente anatômica da Idade Média tardia em diante, enquanto a função da memória relacionada com as mesmas foi descoberta muito mais tarde, no Período Moderno tardio.

Palavras-chave: memória, estruturas anatômicas, diencéfalo, hipocampo, neocórtex.

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INTRODUCTION

The nature of memory and the search of its localization have been object of interest since antiquity[1]. After a long period of indecision about storage of memory between the heart and the brain, the latter prevailed. There, initially, the soul and the mind were localized in the ventricles of the human brain, as described by Herophilus from Chalcedon and Erasistratus from Chios (IV-III BC). Much later, Nemesius, possibly around the end of the IV century AD, and centuries later Albertus Magnus, also situated the functions of the human mind (senses, reasoning, and memory) in these cavities, placing memory in the posterior one [cerebellar ventricle], the latter providing additionally a schematic representation of the ventricles, seemingly for the first time (1506, chapter XIII – posthumous release)[2,3]. Such situation was maintained during the entire Middle Ages, until the Renaissance. At this point the faculties were understood to be in the solid parts of the cerebrum, as suggested by Johannes Jakob Wepfer (1658), and a short time later by ThomasWillis (1664), the latter localizing the memory in the external surface of the brain [cerebral cortex][2,3].

After such long preceding period of studies of presumptive localizations, begun a phase of more concrete and scientifically-based ones, trying to relate memory function and failure (forgetfulness [amnesia]) to anatomic brain structures in the late Modern Period (mainly XIX century, and extending to the XX), reaching close to the present day knowledge on the subject[4].

It is important to remember that most core anatomical structures, and later related to declarative memory function, were described at a much earlier time, as will be seen in the present approach.

THE MEMORY-RELATED ANATOMICAL BRAIN STRUCTURES

The present day knowledge on the anatomy of memory-related brain structures, which emerged from the studies performed in the late Modern Period (XIX-XX century), comprise the diencephalic, hippocampal, and neocortical ones. A short review of such structures related to declarative (explicit) memory, as seen presently, are summarized (Box 1).

Box 1. Memory-related anatomic structures, as seen in present days.

Diencephalic nuclei. The memory-related nuclei of the diencephalon comprise mainly the anterior (anterior ventral, anterior dorsal, anterior medial), medial dorsal, intralaminar and midline (reuniens, paraventricular, parataenialis, and rhomboid) thalamic nuclei, and the mammillary bodies of the hypothalamus, as revealed by clinical-pathological and experimental studies[42].
Hippocampus and related formations. These structures comprise the hippocampus (or hippocampal formation, comprising the hippocampus proper, dentate gyrus and subicular complex), and adjacent cortical areas that are anatomically related to the hippocampus (especially the entorhinal, perirhinal, and parahippocampal areas)[43,44].
Neocortex. Long-term memories are presumed to be stored mainly in neocortical areas (frontal and tempo-ro-occipito-parietal) (cortical networks), considering their bidirectional connections with the hippocampus and parahippocampal region[36,43,44,45].
Connections of the memory-related structures. Besides the intrinsic connections between the hippocampus and related cortical areas, the fornix and the mammillothalamic tract represent the main medial temporal lobe–diencephalic connections[42,46,47,48]. Additionally, the anterior thalamic peduncle connects the anterior nuclei and the medial dorsal nucleus to the prefrontal cortex[49], the anterior thalamic nuclei project to the cingulate gyrus[47,50], and the inferior thalamic peduncle connects the parahippocampal region the medial dorsal thalamic nucleus[42].

THE DISCOVERY OF DIENCEPHALIC MEMORY-RELATED STRUCTURES

The scientifically-based studies of memory and the search of the underlying structures were triggered by Carl Wernicke (1881, 1900), and Sergei Sergeievich Korsakow (1887-1890)[3]. The latter described a condition of memory failure in alcoholic patients that was designated “Korsakow’s syndrome” or “Symptom Complex of Korsakow”, as proposed by Friedrich Jolly (1887)[5]. The Korsakow’s syndrome, for many years, constituted the main model for the study of memory disorders[6]. However, these outstanding researchers were not able to identify the underlying anatomical structures[3]. Two publications that followed were especially relevant for this subject, that of Hans Gudden and of Eduard Gamper, who provided important new anatomical data[3]. They presented neuropathological data of cases with Korsakow’s syndrome. Gudden (1896) found lesions affecting mainly the anterior tubercle of the thalamus, walls of the 3rd ventricle, and marked atrophy of the mammillary bodies, besides affecting also the dorsal vagus nucleus; additionally, the fornix and Vicq d’Azyr bundle were involved in some cases[3,7]. Three decades later Gamper (1928) described changes mainly of the mammillary bodies (constantly affected), thalamic nuclei comprising the submedial, parafascicularis, reuniens, medial, besides the dorsal vagus and oculomotor, and the Darkschewitsch and interstitialis nuclei[3,8]. Thus, these findings related explicitly the mammillary bodies to memory failure, as well as to damage of the anterior, midline, and medial thalamic nuclei[3] (Box 2).

THE DIENCEPHALIC STRUCTURES ANTEDATING THEIR MEMORY-FUNCTION DISCOVERY

The thalamus was partly depicted, not named, by Andreas Vesalius (1514-1564) in his *Fabrica* (1543) (Figure 7). However, Thomas Willis (1621-1675), in his *Cerebri Anatome* (Figs. 4 and 8), was the first to clearly localize and depict this structure, and to designate it as ‘optic nerve thalamus’ (*thalamus nervorum opticorum*) (1664)[9]. In the following decades some anatomical thalamic reliefs were recognized (anterior tubercle, pulvinar, geniculate bodies). The first clear internal division of the human thalamus was provided by Karl Friedrich Burdach (1776-1847), who described the internal medullary lamina, dividing the thalamus in superior, inner, and external nuclei (1822). He was followed by Jules Bernard Luys (1828-1897), who divided the thalamus in four centers connected to different parts of the hemisphere (1865). Later, in a more detailed manner, Constatin von Monakow (1853-1930) identified thalamic regions related to destructive lesions of different cortical areas (1895). Other studies followed in the subsequent years. Some of the individual thalamic nuclei that later would be revealed as memory-related were identified by different authors, comprising the anterior (Luys, 1865, 1873), mediodorsal (von Monakow, 1895), parafascicular (Vogt and Vogt, 1902), submedius (Vogt, 1909), reuniens (Malone, 1910)[10,11,12].The mammillary bodies were first identified also by Willis, who depicted and named the structure as ‘whitish glands’ (*glandulae candicantes*), localized below the infundibulum (Figure 1 - 1664)[9]. Later (1779), ‘mammillary bodies’ (*corpora mammillaria*) were described in the base of the human brain by Christian Friedrich Ludwig (1757-1823)[13]. More detailed information was provided by Felix Vicq d’Azyr (1748-1794), who described varied structures: [1] identified and depicted on a basal view of the human cerebrum the ‘mammillary eminences’ (*éminences mamillaire*) (Plate XVII – Fig 1 – 36 and Plate XXV – Fig 2 - 57), [2] described and depicted “…the anterior pillars [columns] of the fornix terminate there [mammillary eminences] merging with its substance…”; [3] described, without naming, a “…white cord (*cordon blanc*) that emerges from the mammillary eminence, forming a curve in the direction of the anterior and inner tubercle of the optic thalamus…” (Plate XXV – Fig 2 – a, b) [mammillo-thalamic tract] (1786) [named by Koelliker ‘fasciculus thalamo-mammillaris’ and ‘Vicq d’Azyr bundle’ (*Bündel von Vicq d’Azyr*)] (1896)][14,15]. The fornix (*fornice*) or tortoise (*testudine*) was first recognized in the human brain, although in an incomplete way, by Vesalius (1543), as a triangular body, constituting the roof of the 3rd ventricle, and part of the anterior and posterior limbs (Fig. 5)[16]. It was later studied by numerous authors, who identified its other parts, the more detailed being that of Vicq d’Azyr (1786), who described and depicted the ‘vault of the three pillars’ (*voute a trois pilliers*), distinguishing the body (*triangle médullaire*), the anterior and posterior pillars (*pillier anterieur* and *pillier postérieur*) [limbs], the posterior limb extending till the tip of Ammon’s horn, where it ended as a white strip, the ‘band of the hippocampus’ (*bandelette de l’hippocampe*) or ‘fimbriate body’ (*corpus fimbriatum*) [fimbria], and the anterior limb stretching to the mammillary bodies (*éminences mamillaires*) (Plate XX and XXV – Figs. 1-3)15 (Box 2).

THE DISCOVERY OF HIPPOCAMPAL MEMORY-RELATED STRUCTURES

The hippocampus was identified as a memory-related structure initially by Vladimir Michailovich Bechterew, who reported a case with memory impairment (1900), where the autopsy revealed a state of softening comprising the anterior (gyrus uncinatus), and the internal part (gyrus cornu Ammonis) [constituted by cornu Ammonis (hippocampus proper) - fascia dentata – subiculum (according to Bechterew [1887]1899)] of both temporal lobes, as well as the underlying parts[3,17]. Bechterew's report was the first that related memory impairment with lesion of the hippocampal region[18]. Half a century later this feature was confirmed surgically by William Beecher Scoville and Brenda Milner. They reported a patient, later known as the HM (Henry Molaison) case, with refractory epileptic crises, who after bilateral medial temporal resection, destroying probably the anterior ⅔ of the hippocampus and the [para]hippocampal gyrus bilaterally, as well as the uncus and the amygdala, presented an unexpected and persistent severe loss of memory (1954). He presented, on a neuropsychological assessment, severe loss of anterograde memory [recent], and partial retrograde memory, maintaining early memories [long term memory], and general intelligence. Such findings pointed to the importance of the hippocampal region [hippocampus and related structures] for the normal functioning of the anterograde memory [new memories formed, and new long-term memories stored] (1957)[19]. It is meaningful to stress that the removed hippocampal region included the hippocampus proper, dentate gyrus, and subiculum, as well as nearby temporal lobe structures, as revealed later by neuroimaging, and also by autopsy study[3]. Further studies proceeded in the next decades to distinguish the role of the various components of the hippocampal region in memory processing – the hippocampus proper[18], the dentate gyrus[20], the subiculum complex, and the immediately surrounding regions, the perirhinal, entorhinal and para-hippocampal cortical areas[21] (Box 2).

THE HIPPOCAMPAL STRUCTURES ANTEDATING THEIR MEMORY-FUNCTION DISCOVERY

About four centuries before the description of its function as a memory-related structure, Giulio Cesare Aranzio (Arantius) (ca. 1530-1589) described a protrusion inside the inferior cavity ('ventricle of the hippocampus') [temporal horn] he designated as 'hippocampus' (1587)[22,23]. About one century and a half later Johann [Johannes] Georg Duvernoy (1691-1759) reiterated the description and presented the first illustration of this structure (1729)[23,24]. The term Ammon's horn (corne d'Ammon) [cornu Ammonis] was introduced by René Jacques Croissant de Garengeot (1688-1759), initially to designate the distal part of the posterior limbs (crura) of the fornix (1742)[25], later extended to the entire hippocampus. The 'hippocampus' described by Arantius and depicted by Duvernoy, probably embraced, at least, the hippocampus proper (cornu Ammonis) and the dentate gyrus (gyrus dentatus), seen as part of the 'hippocampal formation', which includes also, according to some authors, the subiculum and the entorhinal cortex[26]. The dentate gyrus was identified in human dissection as a structure related to the hippocampus, described and depicted first by Pierre (Petro) Tarin (ca 1725-1761), and named as 'subrotund eminences' (*eminentiae subrotundae*), in a horizontal section of the hippocampus (Plate II - Figs. 5 and 6) (1750)[27]. Later, Vicq d'Azyr described and depicted (Plate XX) the hippocampus (major) (*grande hippocampe*) (Ammons's horn – according to Garengeot), and its 'dentate' or 'gadrooned' internal border (*bord interne dentelé* or *godronné*), formed by grey matter (1784)[15]. Some time later, Ignaz Döllinger (1770-1841) described and depicted this structure he designated 'dentate stripe' (*'fascia dentata'*) (*gezähnte Leiste*) (1814)[28] (Box 2).

THE DISCOVERY OF NEOCORTICAL MEMORY-RELATED STRUCTURES

The first to attribute the memory function to the cerebral cortex was Willis (1664), although in a conjectural manner[9,29]. Further speculative studies followed. Much later, new approaches established that the neocortex represented the seat of storage of long term memory, as considered experimentally by Karl Lashley, who inferred that it must be widely distributed, and further, that dispersed neuronal assemblies represented such memories or "engrams" (1950), a concept he revived from Richard Semon (1904). A similar view of large-scale cortical networks (or "maps") representing all experience acquired through the senses was proposed theoretically by Friedrich Hayek (1952)[30,31].

Later, the Scoville and Milner's HM case, who maintained long term memory ('early memories') after the surgery he underwent[19], suggested that its storage was outside the removed regions, i.e., extra-hippocampal, presumably localized in the neocortex[32] .

The first to demonstrate experimentally that the human cerebral cortex was related to memory was Wilder Graves Penfield (1891-1976), who obtained, through electrical stimulation of the exposed brain (superior temporal gyrus, and the temporo-occipital region), mainly on the left side, of vigil patients undergoing surgery for epilepsy treatment, auditory and visual past experiences (memory--like) [memory] (1959, 1963)[33,34,35].

It is presently presumed that the frontal and the temporo-parieto-occipital neocortical areas are the main structures related to the neural networks underlying the storage of long term memory[32,36] (Box 2).

THE CORTICAL AREAS ANTEDATING THEIR MEMORY-FUNCTION DISCOVERY

A 'superficial yellowish-gray matter' [cerebral cortex - gyri and convolutions], and a 'deep white matter' were first recognized in the human brain by Vesalius (1543) who depicted them clearly separated in his *Fabrica* (Figure 5) (1543)[16]. He was followed by Archiangelo Picollimini (1526-1586), who is usually credited for the first clear distinction between the 'cerebrum' or 'gray-colored body' (*corpus cineritium*) [cerebral cortex] and the closely envolved underlying 'white matter' (*candidum corpus*) (1586)[37], and other authors that followed, making such gross anatomical distinction. The microscopic studies appeared, and Marcello Malpighi (1628-1694) was the first to provide an account on the 'cortex of the cerebrum' (*cerebri cortice*), describing there "…a mass of numerous tiny glands stacked and joined together…" [pyramidal cells?] [artefacts?], and also "…these glands, where white roots of the nerves are inserted…or from which they originate…" [axons?] (1666)[39]. This view was accepted by other authors for a very long time. The next step was the discovery of the lamination of the cortex, and Jules Gabriel François Baillarger (1806-1890), examining thin sections of the cerebral cortex with transmitted light, identified six alternately transparent and opaque layers, two of the white layers being later named after him (external and internal lines of Baillarger) (1840)[38]. A further step was made by Rudolf Albert von Koelliker (1817-1905), who examining the cerebral cortex after fixation and with staining methods, identified and described the nerve cells and fibers arranged in layers (1852)[38]. A differential view was taken by Theodor Meynert (1833-1892), seen as the first to notice regional variations in the neuronal arrangements (cytoarchitectonics) of the cerebral cortex, where he identified 2 types, a 'common type' (5 layers) (convexity of the brain) [neocortex], and 'special types' (occipital, Sylvian depression, Ammon's horn, olfactory bulb) (1872)[38,40]. Next, Korbinian Brodmann (1868-1918) extended the cytoarchitectonic knowledge, and identified 52 distinct areas in the human brain, divided in 11 regions. Additionally, he divided the cerebral cortex in 'heterogenetic' (lack of six-layered pattern) [including the allocortex- according to Vogt and Vogt, 1919] [archicortex], and 'homogenetic' (six-layered pattern), the latter further divided in 'homotypical' [including frontal, parietal, temporal and occipital region] [isocortex – according to Vogt and Vogt, 1919] [neocortex] [including associative areas], and 'heterotypical' [primary sensory and motor cortex] . He also commented on the 'functional localization' for some faculties (1909)[38,41] (Box 2).

CONCLUSION

The core memory-related structures (declarative type), comprise those localized in the diencephalon, the hippocampal region, and the neocortex, as well as their connections. There was a clear temporal delay in the identification of the structures and their relation to memory function, and the finding of these anatomic structures ignoring their function. The core structures begun to be identified anatomically in the late Middle Ages on, while the memory function related to them was discovered much later, in the late Modern Period.

Box 2. Anatomical structures, first related to memory, and those described with unknown function at the time, in the human brain (references as in the text).

structure	**1st described (related to memory)**	**1st described (function unknown)**
thalamus (nuclei)	anterior tubercle [anterior nuclei] [Gudden,1896] nucleus parafascicularis [parafascicular nucleus] submedial nucleus [submedius nucleus (part of midline nuclei)] nucleus reuniens [reuniens nucleus] medial thalamic nucleus (part) [medial mediodorsal nucleus] [Gamper, 1928]	anterior nuclei [Luys, 1865] parafascicular nucleus [Vogt and Vogt, 1902] submedius nucleus [Vogt, 1909] reuniens nucleus [Malone, 1910] mediodorsal nucleus [von Monakow, 1895]
mammillary bodies	mammillary bodies [Gudden, 1896]	'whitish glands' (*glandulae candicantes*) [Willis, 1664]
mammillo-thalamic tract	bundle of Vicq d'Azyr [mammillothalamic tract] [Gudden, 1896]	'white cord (*cordon blanc*) (emerges from the mammillary eminence) [Vicq d'Azyr, 1786]
hippocampu	hippocampal region [stroke] [Bechterew, 1900] hippocampal region [surgery] [Scoville and Milner, 1957] hippocampus proper [Zola-Morgan et al., 1986]	'hippocampus' [described] [Arantius, 1587] hippocampus [depicted] [Duvernoy, 1729]
dentate gyrus	dentate gyrus [included in the hippocampal region] [Scoville and Milner, 1957] dentate gyrus [Baker et al., 2016]	'subrotund eminences' (*eminentiae subrotundae*) [Tarin, 1750]
fornix	fornix [Gudden, 1896]	'fornix' or 'tortoise' [part] [Vesalius, 1543] vault of the three pillars (*voute a trois pilliers*) [Vicq d'Azyr, 1786]
cerebral cortex	substantia corticalis [cerebral cortex] (presumptive) [Willis, 1664] cerebral cortex (superior temporal gyrus, and temporo-occipital area) (electrical stimulation) [Penfield, 1959] cerebral cortex (neocortex) [Eichenbaum, 2000]	'superficial yellowish-gray substance' [cerebral cortex] [Vesalius, 1543] 'substantia corticalis' [cerebral córtex) [Willis, 1664] cortex of the cerebrum' (cerebri cortice) (microscopic structure) [Malpighi, 1666] cerebral cortex - citoarchitecture [Meynert, 1872] cerebral cortex - citoarchitecture (homotypical) [neocortex] [Brodmann, 1909]

CONFLICT OF INTEREST

The author declare that there is no conflict of interest.

FUNDING STATEMENT

There is no financial support.

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