VIA MEDICA

ORIGINAL ARTICLE

The amygdaloid complex of the rabbit — morphological and histochemical study

Hanna Jagalska-Majewska, Jerzy Dziewiątkowski, Sławomir Wójcik,
Anna Łuczyńska, Renata Kurlapska, Janusz Moryś

Department of Anatomy and Neurobiology, Medical University of Gdańsk, Poland

The aim of the present paper is to describe the morphology and topography of the nuclei of the amygdaloid complex in the rabbit. In the current study we also investigated the intensity of the enzymatic reaction for acetylcholinesterase (AChE) in the amygdaloid complex and the morphology of its neurones. Material consisted of 5 brains of adult New Zealand rabbit, stained either with cresyl violet or for AChE activity.

Although, as in other mammals, the rabbit amygdala consists of two main nuclear groups (corticomedial and basolateral), it reveals a peculiar morphology pattern, forming a transition structure between those observed in the cat and rat. Especially characteristic is the arrangement of the basolateral complex. Within that the ventromedial division of the lateral nucleus seems to be the largest, while its dorsolateral division — the smallest. The arrangement of the corticomedial complex in the rabbit is similar to both the cat and rat.

In the rabbit the highest acetylcholinesterase activity is found in the basolateral nucleus and the nucleus of the lateral olfactory tract. The lowest AChE staining is observed in the cortical and medial nuclei, amygdalohippocampal and anterior amygdaloid areas and intercalated masses.

key words: amygdala, rabbit, acetylcholinesterase and morphology

INTRODUCTION

The amygdaloid complex has attracted considerable attention over the last few decades and many of its organisational and structural features have been revealed. It belongs to the limbic system and is implicated in memory and emotional behaviour [42]. It occupies a central position of the telencephalon, lying medially to the endopiriform nucleus. In the rabbit it extends in frontal sections from the level of the anterior commissure to the lateral geniculate body [15].

The morphology and subdivisions of the amygdaloid complex have been studied in many species: the rat [14, 43, 51, 53, 64], mouse [65], squirrel [66], guinea pig [66], hamster [62, 66, 70], cat [20, 29, 63], dog [28], monkey [1, 2, 52, 64] and human [24, 41, 58]. In contrast to the rabbit amygdaloid complex, the morphology of this structure in the rat, cat, monkey and human is described by different staining techniques and methods. There are only limited data concerning the morphology of the amygdala in the rabbit [26, 67, 70]. The rabbit amygdala has been described only as a neighbouring structure in stereotaxic atlases [19, 57, 67] and these descriptions are decidedly insufficient for precise delineation of nuclear masses of the amygdaloid complex.

Acetylcholinesterase (AChE) plays a key physiological role in cholinergic synapses by rapid hydrolysis of the acetylocholine and termination of the syn-

Address for correspondence: Prof. Janusz Moryś, MD, PhD, Department of Anatomy and Neurobiology, Medical University of Gdańsk,
ul. Dębinki 1, 80–210 Gdańsk, Poland, tel: +48 58 349 1401, fax: +48 58 349 1421, e-mail: jmorys@amg.gda.pl

aptic transmission. It is present in cholinergic and noncholinergic neurones, which are in the focus of interests of neurobiology, because cholinergic innervation of the cerebral cortex and amygdala plays a critical role in the neuronal modulation of attention, arousal and memory [59]. Severe damage of cholinergic pathways is one of the earliest neuropathological features of Alzheimer's disease [9, 10, 38, 59], especially in the basolateral complex of the amygdala [5].

AChE activity of the amygdaloid complex was studied in man [16, 36, 58, 61], monkey [39], cat [48], guinea pig [21] and rat [3, 4, 47]. It is characteristic that the same nucleus in different species shows an approximately similar level of AChE activity. Thus AChE is a valuable and comparable substrate in morphological studies.

According to Humphrey [23] and Johnston [25], the amygdala consists of two main nuclear groups: the corticomedial and basolateral. The corticomedial complex, being phylogenetically older, is partitioned into: the central, medial nuclei, cortical amygdalohippocampal area, nucleus of the lateral olfactory tract, bed nucleus of the accessory olfactory tract and amygdalopiriform cortex. On the other hand the phylogenetically younger basolateral complex is divided into the basal and lateral nuclei. There are other amygdaloid areas such as the anterior amygdaloid area and intercalated masses.

It is well known that the corticomedial (superficial) division plays an important role in the convergence of sensory (especially olfactory), autonomic and endocrine inputs from the hypothalamus and brain stem, whereas the basolateral (deep) group receives direct sensory and limbic inputs, being an important structure in learning, memory, emotional and social behaviour [44]. The lateral and basolateral nuclei project to the central nucleus [13, 26, 30], which then projects to the hypothalamic and brain stem target areas [56] modulating some aspects of emotions. There are a lot of data concerning the amygdala as a crucial structure in classical Pavlovian conditioned fear [7, 8, 69] and emotional learning in long term potentiation mechanism [32]. The amygdala also plays an important role in unconditioned fear, anxiety, aggression and attention [13, 30]. Researchers started to indicate the lateralisation of the amygdala's involvement in emotionally influenced memory [6, 11]. It is responsible for recent but not remote memories [13] and is involved in memory consolidation [17].

There are many clinical aspects of studies on the amygdala. For example, there are some data sug-gesting that developmental malformations of the amygdala may underlie autism [22]. The amygdala is susceptible to development of the temporal lobe epilepsy [60, 68]. Pitkänen et al. [54] have proved that some parts of the amygdala (e.g. the medial division of the lateral nucleus, basomedial nucleus, accessory basal nucleus, posterior cortical nucleus, anterior cortical nucleus and medial nucleus) in the rat are regions sensitive to status epilepticus-induced neuronal damage.

The above-mentioned involvement of the amygdaloid nucleus in physiological and pathological processes taking part in a changeable external environment should be based on their morphological properties. Because of the lack of such a detailed description in one of the most common laboratory animals, the aim of the current study was to give a detailed description of the topography and morphology of the amygdaloid complex in the rabbit with the usage of classical techniques: cresyl violet and AChE staining.

MATERIAL AND METHODS

The material consisted of five brains of female New Zealand rabbits, aged 9–24 months and weighing 2650–4550 g. Care and treatment of animals were in accordance with the guidelines of the EC as well as of the Local Ethical Committee. Animals were deeply anaesthetised with a lethal dose of Thiopental (80 mg/kg of body weight i.p.), then transcardially perfused with 250 ml of 0.9% solution of saline containing 10000 units of Heparin, followed by 1000 ml of Baker fluid (4% paraformaldehyde solution in 0.1 M phosphate buffer with calcium chloride (22,350-6 Aldrich), pH 7.4). The brains after immediate removal from skulls were fixed in Baker fluid for 3 hours, kept in 15% and next in 30% sucrose solution in 0.1 M phosphate buffer (pH 7.4, 4°C) until sunk. Frontal 40-μm-thick, serial sections of brains were cut on JUNG 1800 cryostat (Leica, Germany). The first set of sections was collected on glass slides and dried at room temperature and finally stained with cresyl violet. The second group of sections was used for AChE histochemistry. The staining procedure was based on Koelle method in the modification of Gerebtzoff and was carried out at a pH of 7.4 [18, 36, 37, 45].

For selective inhibition of unspecific cholinesterases serial sections were incubated at a temperature of 37°C for two hours in a medium containing: acetyltiocholine iodide (01480 Biochemica), copper sulphate (C-1297 Sigma), glycine (G-7032 Sigma), acetate buffer (acetic acid, glacial A-6283 Sigma), distilled

water and ethopropazine (E-2880 Sigma) [18, 45]. Sections were rinsed 2–3 times in distilled water. Then sections were postincubated in ammonium sulphide (17,250-2 Aldrich) and rinsed again. Sections were plated on glass slides, allowed to dry and covered; then analysed under light microscope (Labophot 2, Nikon, Japan). The set of low magnification images was saved as bitmaps to display topographic relations between amygdaloid nuclei (light microscope (Leica DMLC, Germany) equipped with camera).

RESULTS

The corticomedial amygdaloid complex

In frontal sections the corticomedial amygdaloid complex appears at the level of the optic chiasm (Fig. 1) and extends throughout the whole amygdaloid com-

plex (Fig. 1–11). Its nuclei together with the anterior amygdaloid area build a rostral pole of the amygdala (Fig. 1). This complex in AChE staining is heterogeneous, although this differentiation is less visible then in the basolateral complex. Medial and cortical nuclei are poorly but homogeneously stained, while subdivisions of the central nucleus are characterised by poor to moderate intensity (Fig. 2b–9b).

The central nucleus (CE)

In the frontal sections the central nucleus appears in the plane where the medial and anterior cortical nuclei are well developed (Fig. 2). It is of an easily distinguishable ovoid shape. Its ventrolateral boundary is formed rostrally by the external capsule and caudally by the basolateral complex (Fig. 2–8). Me-
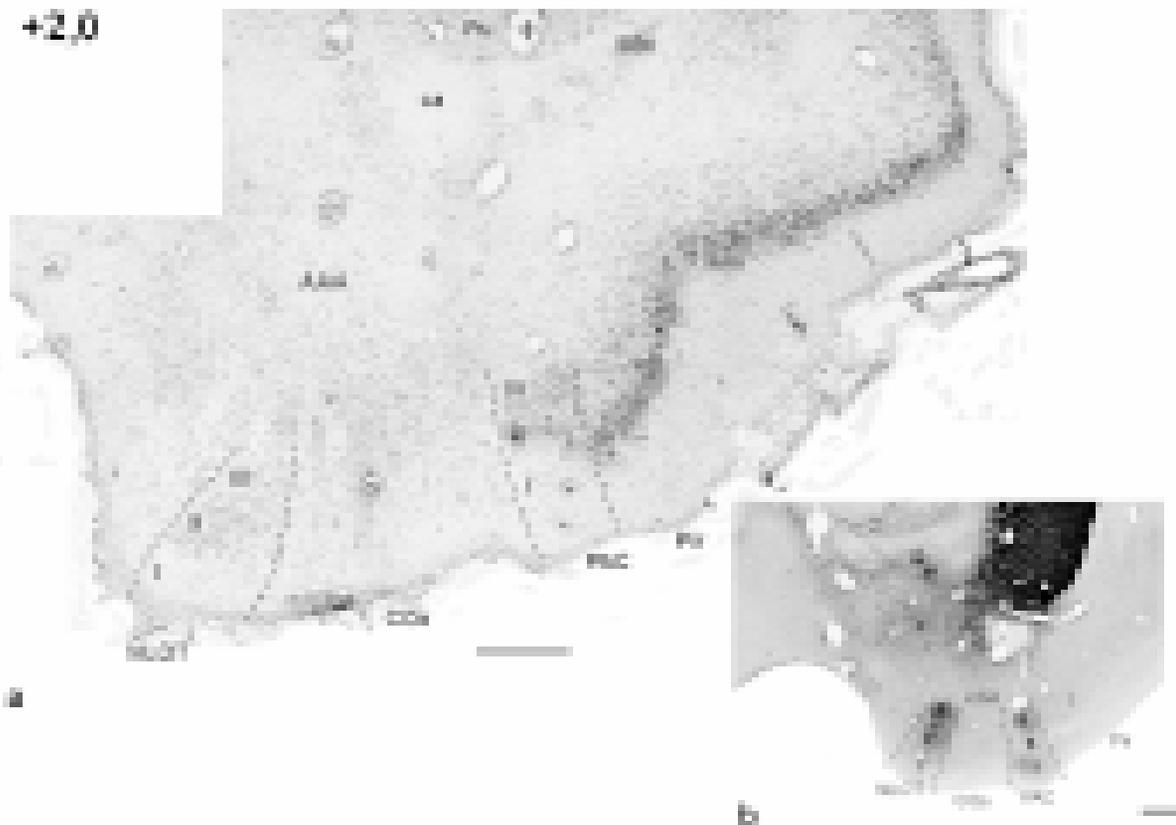

Figure 1–11. Photomicrographs of frontal sections through the amygdaloid complex in the rabbit: **a)** cresyl violet; **b)** AChE histochemistry. The number in the upper left corner means the distance with reference to Bregma [mm].
AAA — anterior amygdaloid area, AHA — amygdalohippocampal area, aot – accessory olfactory tract, BAOT — bed nucleus of the accessory olfactory tract, BL — basolateral nucleus, BM — basomedial nucleus (d, v — dorsal and ventral part, respectively), ca — anterior commissure, ce — external capsule, CE — central amygdaloid nucleus (CEm — medial, CEim — intermediate, CEc — capsular and CEl — lateral subdivisions), Coa — anterior cortical nucleus, COpm — posteromedial cortical nucleus, COpl — posterolateral cortical nucleus, EN — endopiriform nucleus, fi — fibres of hippocampus, Hi — hippocampus, IM — intercalated masses (IMa — anterior, IMl — longitudinal, IMm — medial), Ldl — dorsolateral division of the lateral nucleus, Lvm — ventromedial division of the lateral nucleus, M — medial amygdaloid nucleus (Md — dorsal, Mv — ventral subdivisions), NLOT — nucleus of lateral olfactory tract, PAC — periamygdaloid cortex, Pir — piriform cortex, Pu — putamen, rhs — rhinal sulcus, Suc — subicular complex, st — terminal stria, to — optic tract, V — lateral ventricle; scale bar = 50 μm.
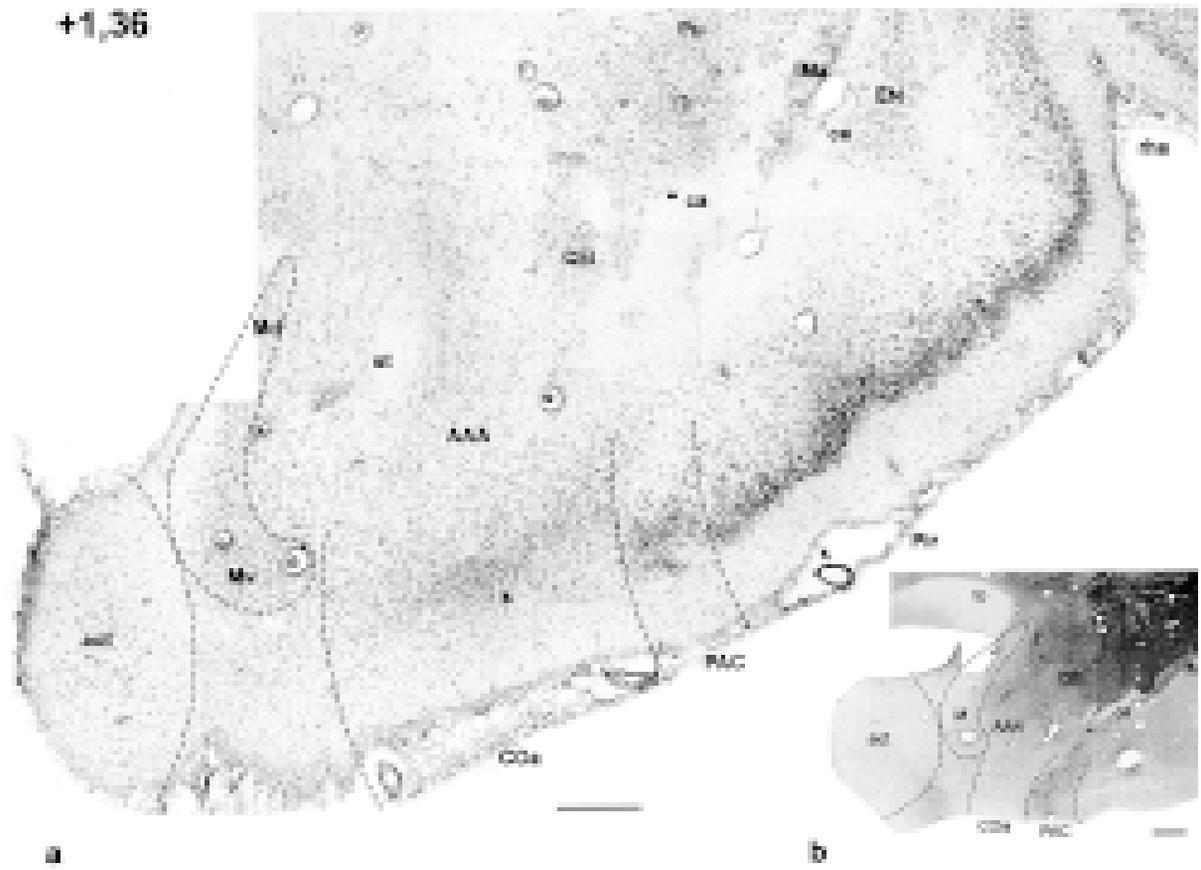
+1,36
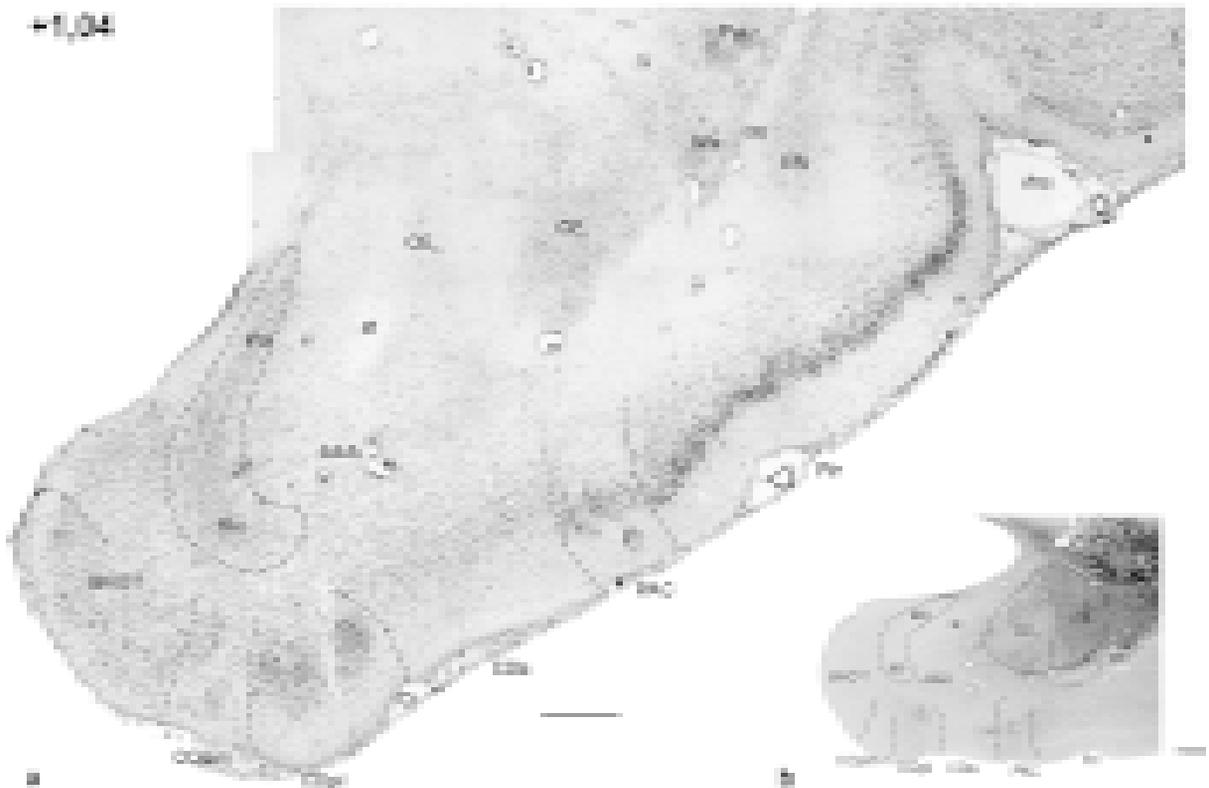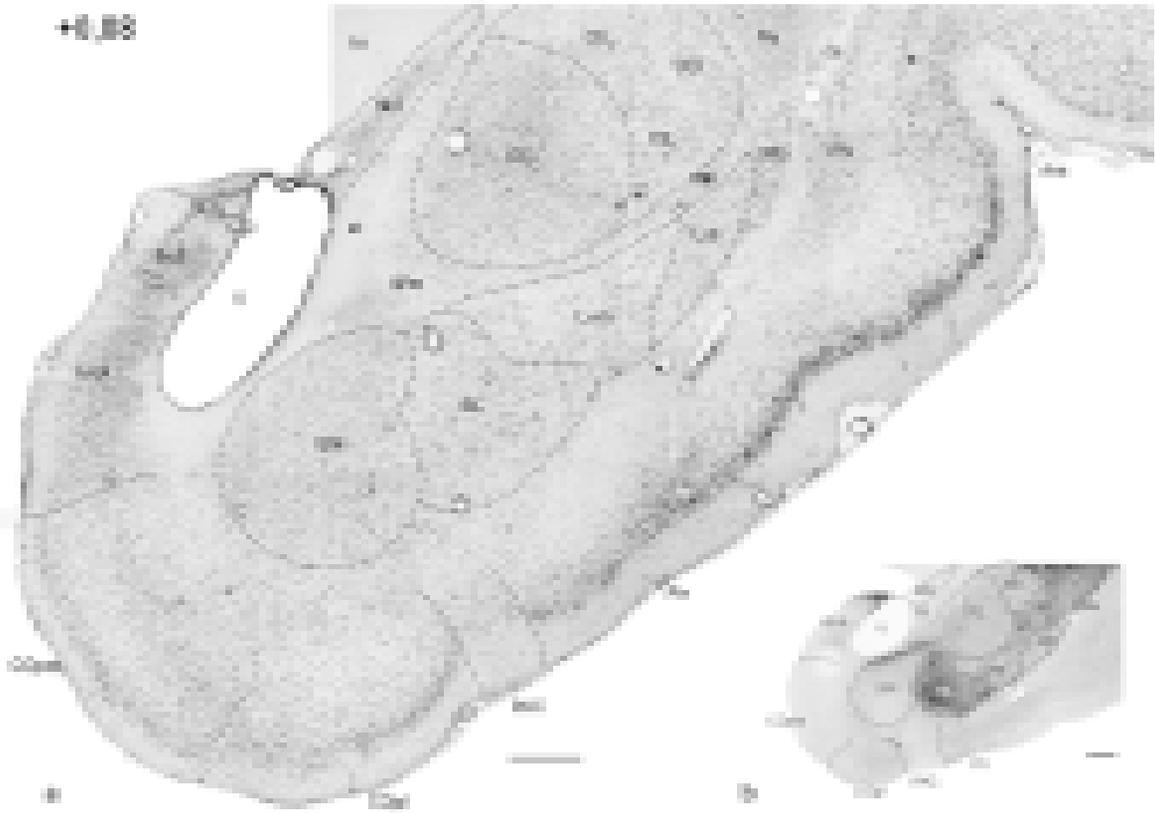

Figure 2.

+1,04

Figure 3.

Figure 4.
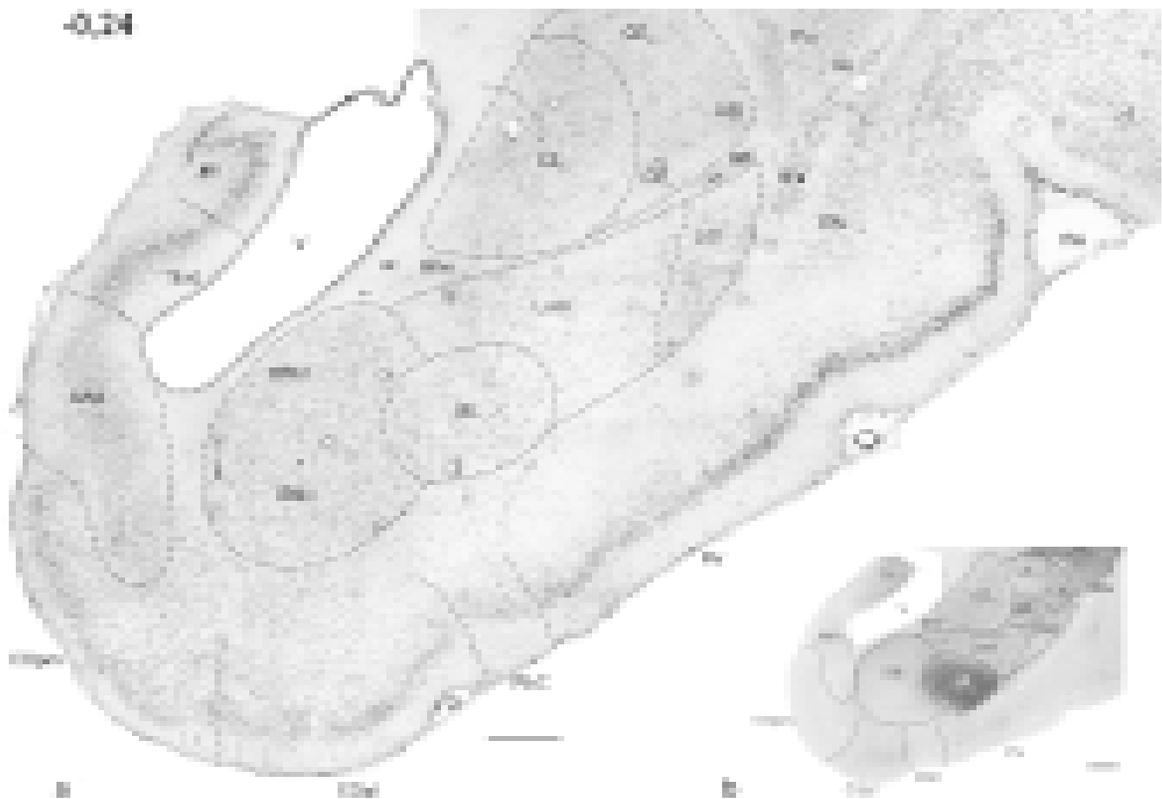
Figure 5.
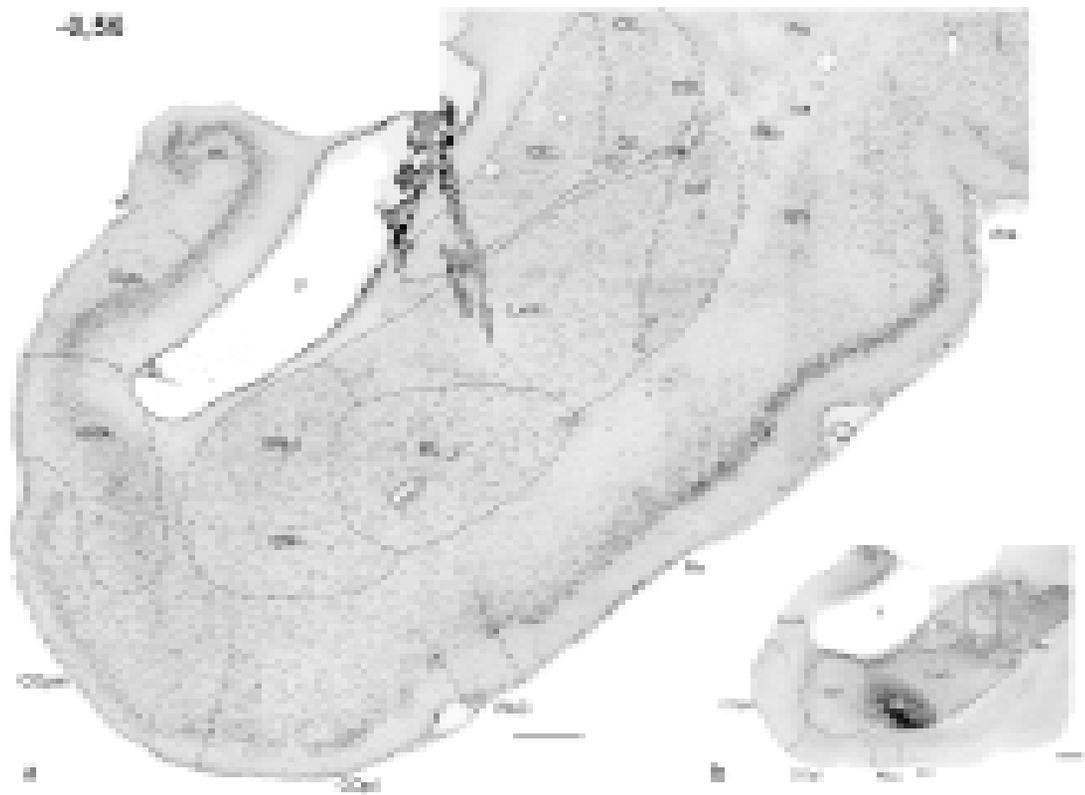
Figure 6.

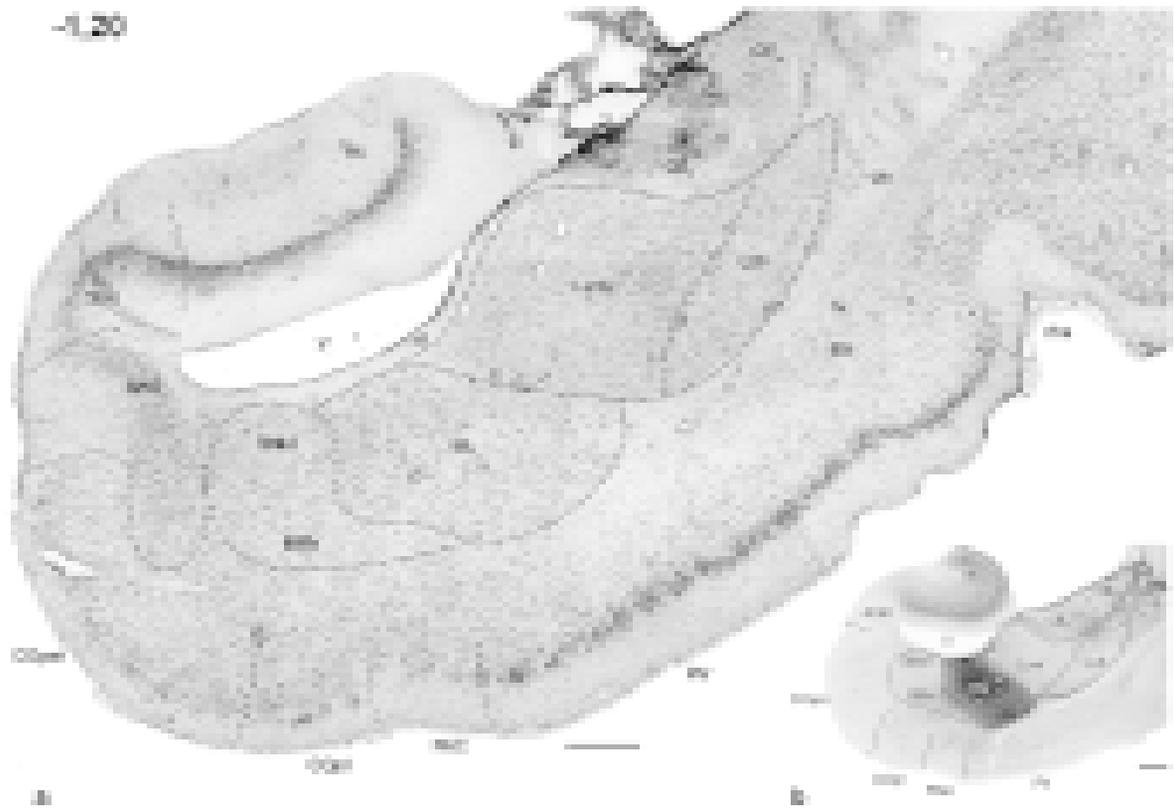**Figure 7.**
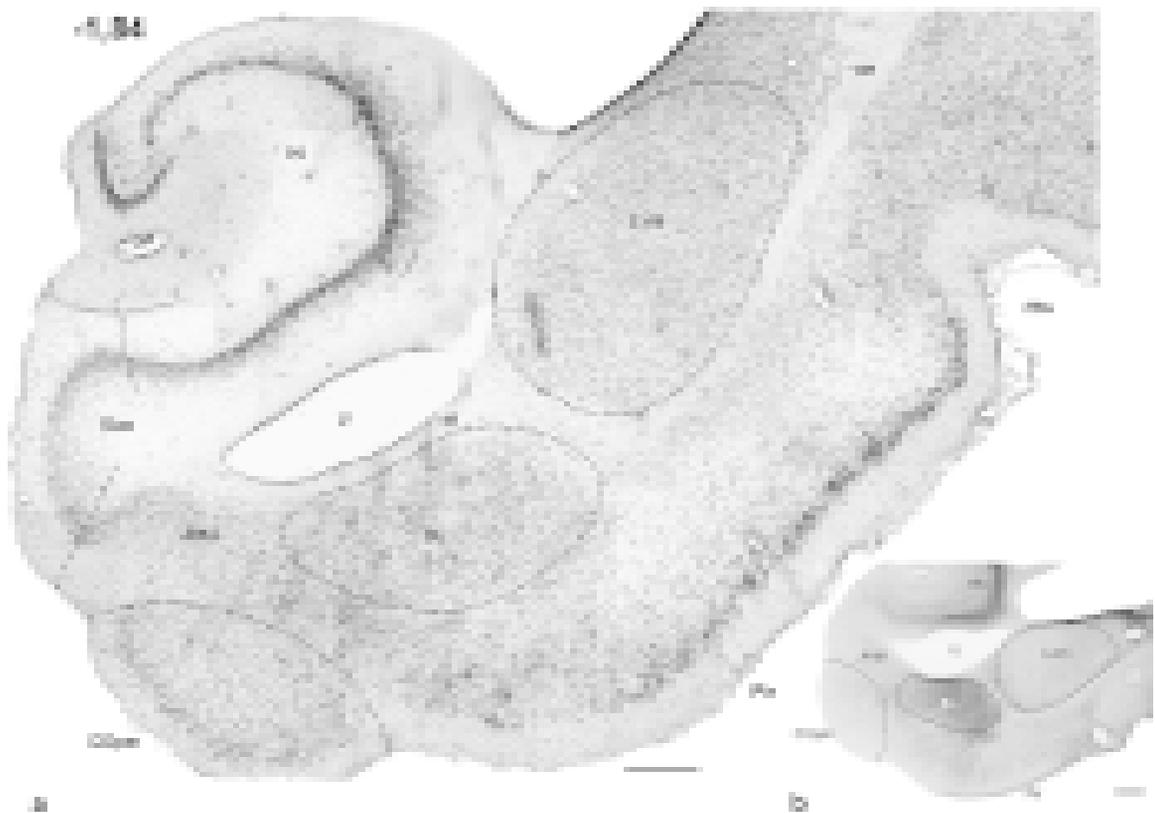
Figure 8.
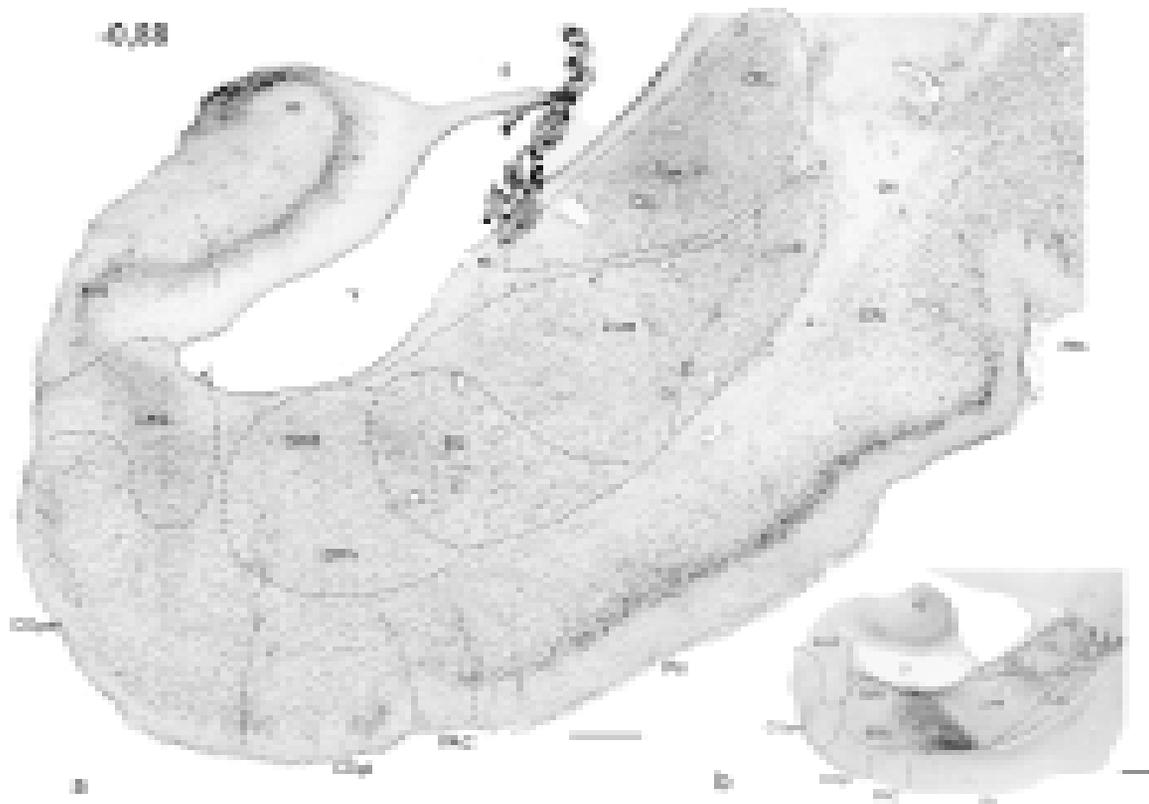
Figure 9.
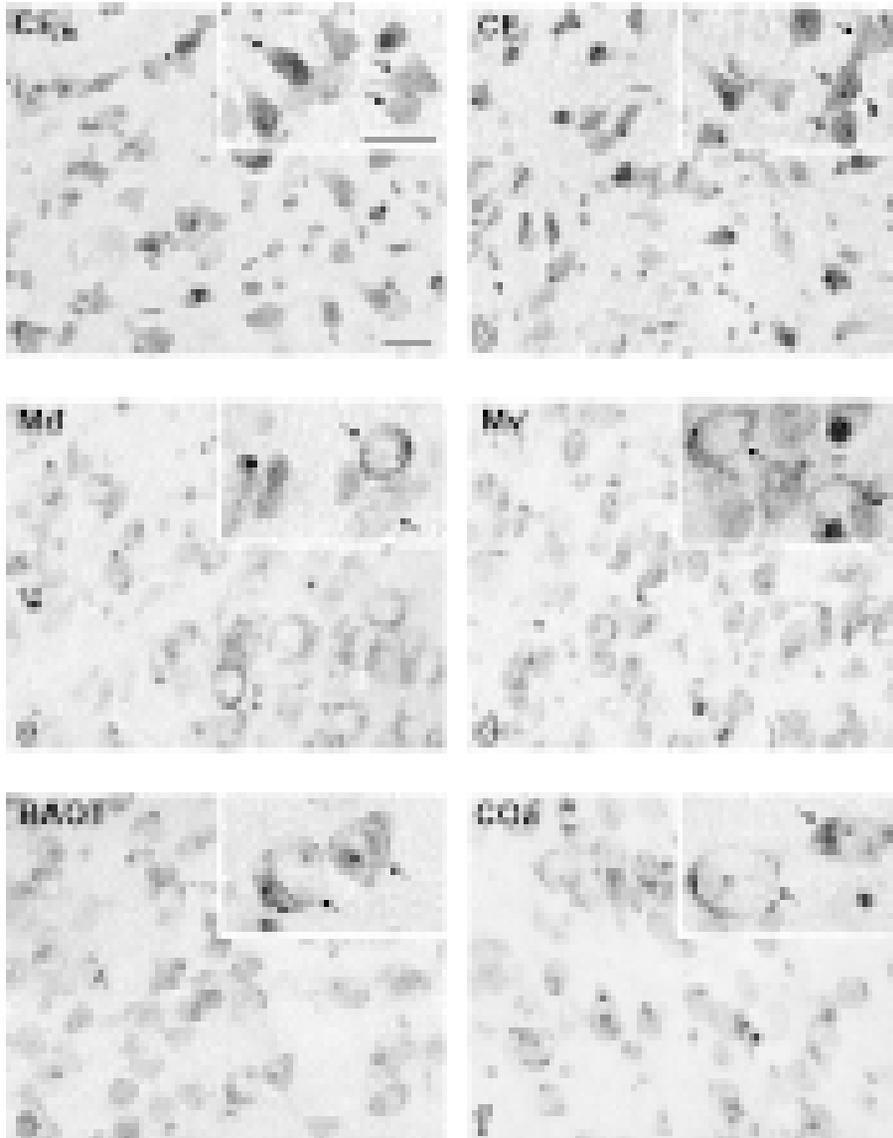
Figure 10.

Figure 11.

Figure 12. Photomicrographs of cells in the central, medial, anterior cortical nuclei and bed nucleus of the lateral olfactory tract in the rabbit: **a)** medial division of the central nucleus (CE_m) with oval, pyramidal-like and round neurones (arrows); **b)** lateral division of the central nucleus (CE_l) with denser pyramidal-like and oval neurones (arrows); **c)** the dorsal division of the medial nucleus (Md) with loosely packed large oval and round neurones (arrows); **d)** the ventral division of the medial nucleus (Mv) with round densely packed cells (arrows); **e)** the bed nucleus of the lateral olfactory tract, arrows indicate large oval and round neurones; **f)** the anterior cortical nucleus, oval and round neurones (arrows); cresyl violet; scale bar = 25 μm.

dially, the central nucleus is surrounded by fibres of the terminal stria and medial nucleus (Fig. 3–10). In rostral sections clear delineation of the central nucleus from the dorsolaterally located striatum is difficult due to the similarity of their cellular structure (Fig. 2–4). The only difference is that neurones of the central nucleus are less dense. Nevertheless, in middle sections the dorsal aspect of the central nucleus is surrounded by fibres marking the boundary with the putamen (Fig. 6–8).

The central nucleus is well developed at the level of appearance of the lateral nucleus (Fig. 4). Caudally it grows smaller as the basal nucleus enlarges (Fig. 7–9).

Neurones of the central nucleus are mainly oval and pyramidal-like, some are multipolar and round (Fig.12a, b). On the basis of AChE activity four divisions: medial, intermediate, lateral and capsular, can be distinguished. Among all of them only the medial one is distinguishable in cresyl violet. It extends throughout the whole central nucleus except very
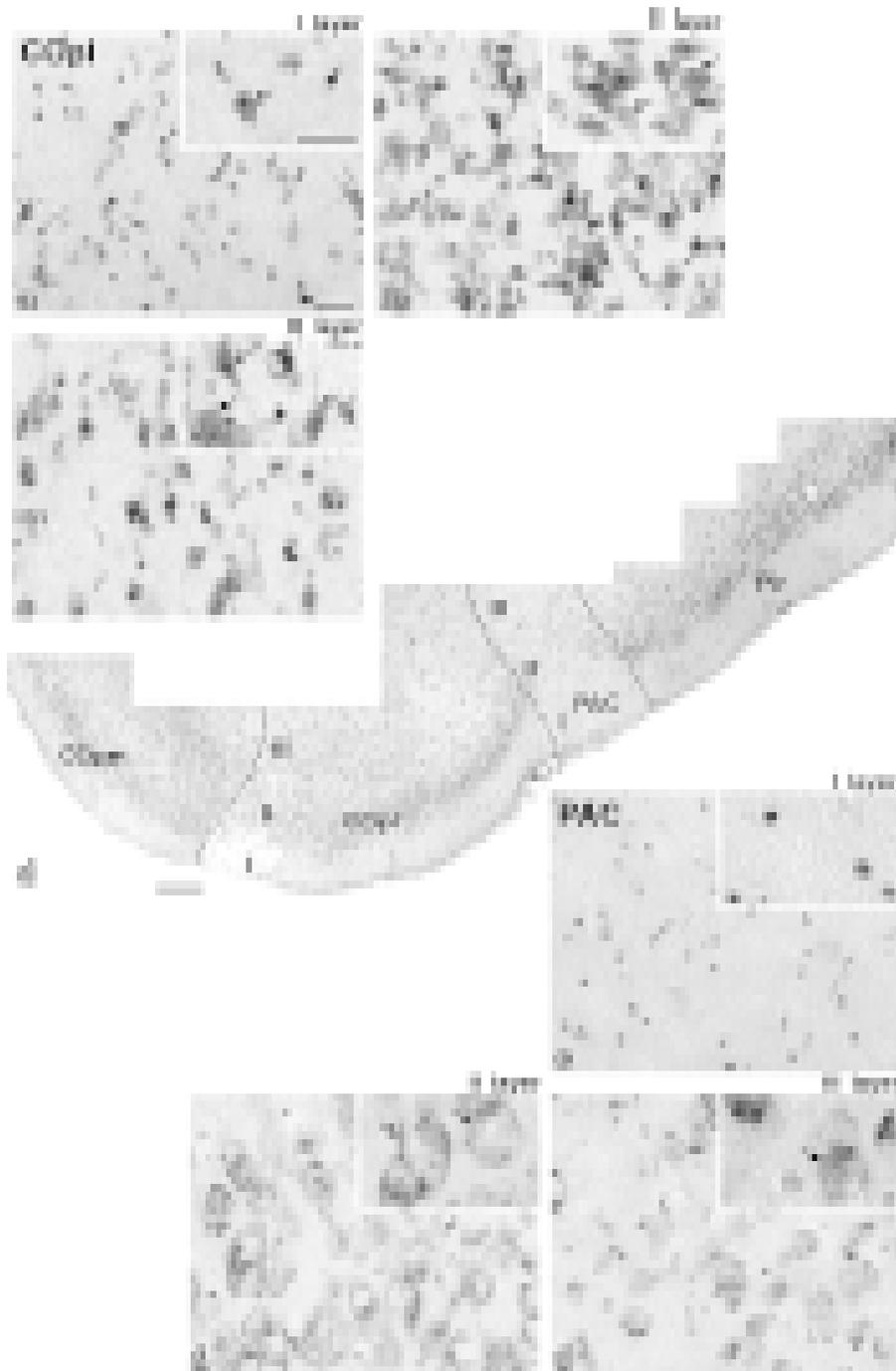
Figure 13. Photomicrographs of cortical area in the rabbit: a, b, c — the posteromedial cortical nucleus; **a)** layer I with loosely packed pyramidal-like neurones (arrows); **b)** layer II with densely packed oval, fusiform and pyramidal-like cells (arrows); **c)** layer III with oval, fusiform and pyramidal-like neurones (arrows); **d)** the chosen superficial cortical structures of the amygdaloid complex; e, f, g — the periamygdaloid complex; **e)** layer I, only glial cells; **f)** layer II with densely packed oval and round neurones (arrows); **g)** layer III with loosely packed oval and round neurones (arrows); scale bar = a, b, c, e, f, g = 25 μm; d = 50 μm.

rostral sections and is characterised by low neuronal density (Fig. 12a) and low AChE activity (Fig. 3b–4b).

The remaining divisions of the central nucleus are characterised by the homogeneity of the cellular structure, however some cytoarchitectonic differences are visible. The lateral division has smaller and more densely packed cells (Fig. 12b) and shows moderate heterogeneous AChE activity (Fig. 3b–7b).

It appears in the very rostral pole of the central nucleus and extends through the anterior and middle portions of the amygdala (Fig. 2–8).

The capsular and intermediate divisions appear from the middle portion of the amygdaloid complex (Fig. 6). The capsular division constitutes the ventrolateral aspect of the central nucleus (Fig. 6–8). It is well visible in AChE preparations as it performs moderate enzymatic activity (Fig. 6b–8b), although higher than in the lateral division.

The intermediate division appears in the dorsal aspect of the central nucleus and is inserted between the medial and lateral ones (Fig. 6–8). It shows the lowest AChE activity of all divisions of the central nucleus (Fig. 6b–10b), which makes it easily distinguishable from the putamen. In caudal sections only medial and intermediate divisions are present (Fig. 9–10).

The medial nucleus (M)

The medial nucleus is a group of cells that appears in the anterior aspect of the amygdaloid complex (Fig. 2). At rostral levels it neighbours the terminal stria, the anterior amygdaloid area — laterally, the bed nucleus of the accessory olfactory tract — medially and the anterior cortical nucleus — ventrolaterally (Fig. 2–3). At this level it has the outline of a bow, surrounding the anterior amygdaloid area from the ventral side (Fig. 2–3). Its vertical part inserts between the optic tract and terminal stria, while its horizontal one is directed to the anterior cortical nucleus (Fig. 2–3). More caudally the medial nucleus is inserted between the amygdalohippocampal area medially, the central nucleus, intercalated masses and basomedial nucleus — laterally (Fig. 5). Its most posterior portion is situated above the inferior horn of the lateral ventricle (Fig. 6).

Cytoarchitectonical features enable the division of the medial nucleus into two fields: dorsal and ventral, but the boundary between them is not clear. The dorsal division is characterised by loosely-packed, bigger, oval and round, palely-stained neurones (Fig. 12c). The ventral division consists of neurones of similar shape, but they are more densely packed, smaller and darkly stained (Fig. 12d).

The reaction for AChE is homogeneously low throughout the medial nucleus (Fig. 2b–6b).

The cortical nuclei

The cortical nuclei appear at the level of the optic chiasm and extend caudally throughout the whole amygdaloid complex lying superficially and ventrally to the anterior amygdaloid area and basolateral complex (Fig. 1–11).

On the basis of cytoarchitectonics as well as topographic relations, the following cortical nuclei can be distinguished: the anterior cortical nucleus (COa), posterior cortical nuclei (COp) (which splits into the posterolateral (COpl) and posteromedial cortical nucleus (COpm)).

In the cresyl violet staining cortical nuclei, except the anterior cortical nucleus, are composed of three cellular layers: layer I — containing small scattered cells, layer II — of densely-packed neurones and layer III — consisting of less densely packed cells (Fig. 13a–d). These nuclei are characterised by heterogeneous (from negative to moderate) AChE activity (Fig. 1b–11b).

The anterior cortical nucleus (COa)

The anterior cortical nucleus constitutes the most rostral aspect of the cortical nuclei, appearing at the level of the optic chiasm. At this level it borders the nucleus of the lateral olfactory tract medially and the periamygdaloid cortex — laterally (Fig. 1). More caudally the accessory olfactory tract and medial nucleus build the medial border of the anterior cortical nucleus (Fig. 2). Further, the anterior cortical nucleus is replaced by growing posterior cortical nuclei (Fig. 4)

The anterior cortical nucleus is characterised by its almost total lack of laminar structure. Darkly stained oval and round numerous cells are situated more deeply than some scattered neurones of the superficial part (Fig. 12f).

In AChE preparations the anterior cortical nucleus shows a negative staining, distinct from the dark staining of the nucleus of the lateral olfactory tract (Fig. 1).

The posterior cortical nuclei (COp)

The posterior cortical nuclei appear just before the basolateral complex, and from the very beginning they constitute the posterolateral (COpl) and posteromedial cortical nuclei (COpm) (Fig. 3). They lie superficially and extend anteroposteriorly to the very caudal pole of the amygdaloid complex (Fig. 3–11).

The layered structure of the posterior cortical nuclei (Fig. 13d) is similar, but the posterolateral cortical nucleus is characterised by a clearer laminar appearance and darker staining. The superficial layer I is the narrowest and contains small scattered neurones and glial cells (Fig. 13a). Layer II is formed by densely packed neurones (Fig. 13b), while the widest deep layer III consists of less densely packed cells (Fig. 13c). Neurones of these layers are pyramidal-like, oval and fusiform (Fig. 13a–d).
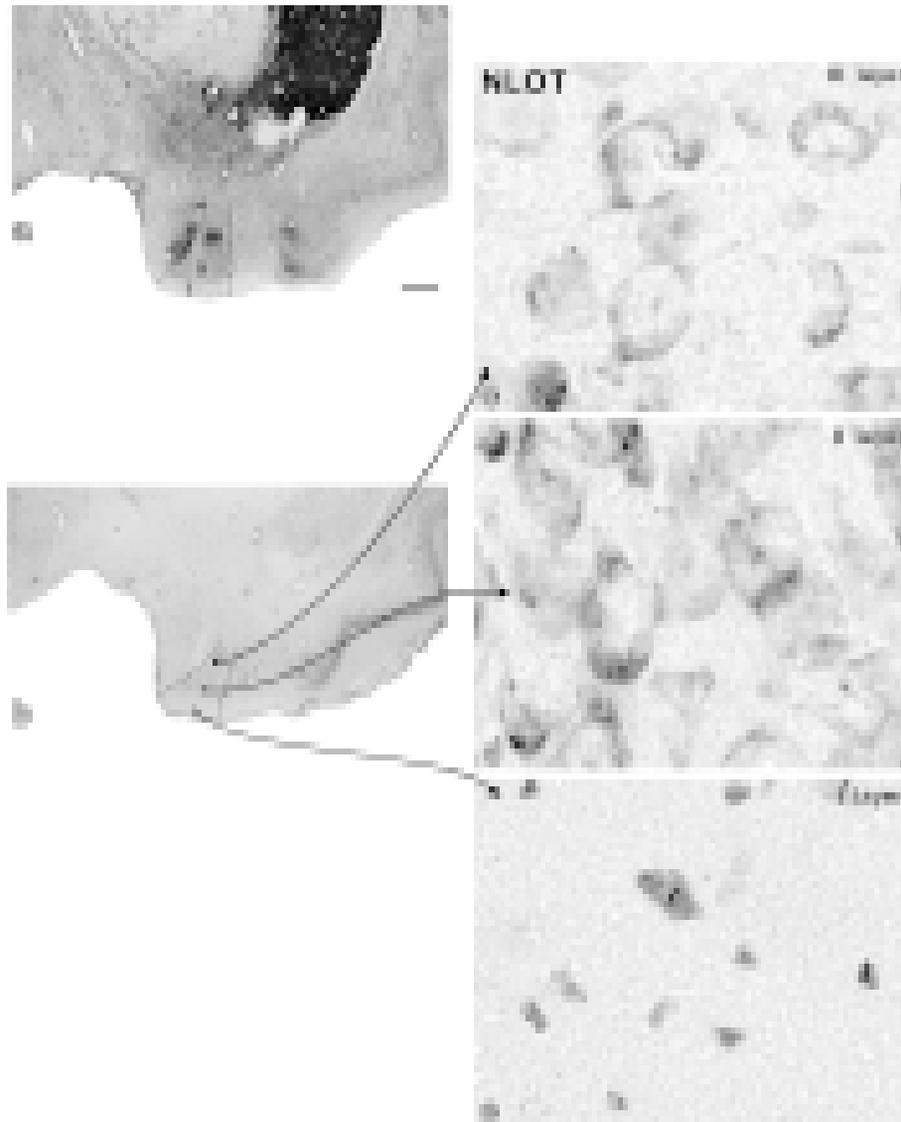
269

Figure 14. Photomicrographs of the nucleus of the lateral olfactory tract in the rabbit: **a**) cresyl violet and AChE staining; **b**) cresyl violet staining; **c**) layer III with loosely arranged, oval and round cells; **d**) layer II with large densely packed oval and round cells; **e**) layer I with few scattered neurones; c, d, e — cresyl violet; scale bar = a, b = 50 μm; c, d, e = 25 μm.

The posteromedial cortical nucleus appears as a well-delineated mass of cells situated in the ventromedial edge of the hemisphere. It borders laterally the posterolateral cortical nucleus (Fig. 3–10). Dorsomedially it abuts the bed nucleus of the accessory olfactory tract nucleus and amygdalohippocampal area (Fig. 3–5) and dorsolaterally — the basomedial nucleus (Fig. 5–11). The posteromedial cortical nucleus together with the ventrolateral division of the lateral nucleus builds the most caudal aspect of the amygdala (Fig. 11).

The posterolateral cortical nucleus merges rostrally with the anterior cortical nucleus (Fig. 3). It is inserted between the periamygdaloid cortex laterally and the posteromedial cortical nucleus — medially (Fig. 4–10). Dorsally it borders the medial nucleus at rostral levels and the basal nucleus — at middle and caudal levels.

The low AChE activity of the posterolateral cortical nucleus is different from that in both the anterior and posteromedial cortical nuclei, where it is negative (Fig. 3b–5b).

The periamygdaloid cortex (PAC)

The periamygdaloid cortex is a transition area between the piriform cortex and cortical nuclei (Fig. 1–11).

Rostrally the periamygdaloid cortex borders the anterior cortical nucleus medially (Fig. 1–3), whereas caudally — the periamygdaloid cortex abuts the posterolateral cortical nucleus (Fig. 4–10).

The periamygdaloid cortex possesses a characteristic laminar structure: layer I is wider and layers II and III are not clearly separated. The latter consist of big darkly stained cells and differ significantly from the pale and small cells of the anterior cortical nucleus as well as from the distinct laminar structure of the posterolateral cortical nucleus (Fig. 13d–g).

The periamygdaloid cortex is characterised by differentiated AChE activity — its anterior portion shows laminar distribution of moderate activity, while its posterior one — negative (Fig. 1b–10b).

The nucleus of the lateral olfactory tract (NLOT)

The nucleus of the lateral olfactory tract begins at the very rostral pole of the amygdaloid complex, at the level of the optic chiasm. At this level it is locat-ed superficially in the medioventral edge of the hemisphere (Fig. 1), further it is replaced by the bed nucleus of the accessory olfactory tract (Fig. 2). It is surrounded by the anterior amygdaloid area, and laterally neighbours the anterior cortical nucleus (Fig. 1).

The nucleus of the lateral olfactory tract consists of three layers: layer I — contains few scattered neurones (Fig. 14e), layer II — is characterised by large densely packed oval and round cells (Fig. 14d), layer III — consists of more loosely arranged, oval and round cells (Fig. 14c). These layers are also easily distinguishable in AChE preparations: the increase of the AChE activity is observed from superficial to deep layer (Fig. 1, 14a). Medially to the nucleus of the lateral olfactory tract the area of high AChE activity rich in fibres is found.

The bed nucleus of the accessory olfactory tract (BAOT)

The bed nucleus of the accessory olfactory tract is a homogeneous group of loosely packed darkly stained cells, which appears ventromedially at the level where the optic tract begins. It is closely con-
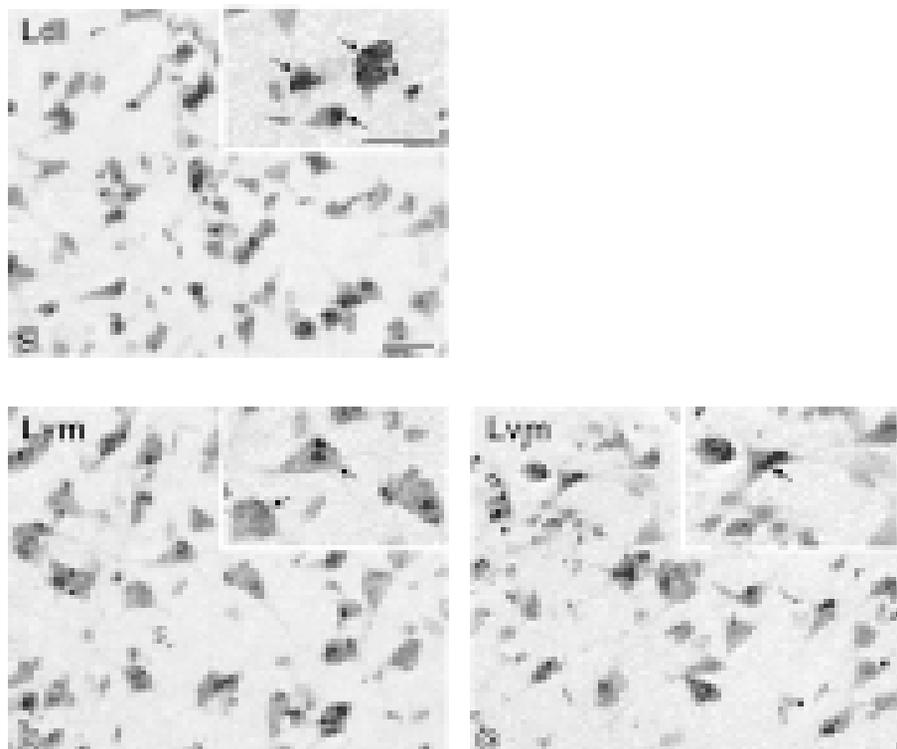
Figure 15. Photomicrographs of cells in the lateral nucleus in the rabbit: **a)** dorsolateral division (Ldl), arrows indicate small darkly stained pyramidal-like and oval neurones; **b)** anterior part of the ventrome-dial division (Lvm) with large loosely packed pyramidal-like neurones (arrows); **c)** posterior part of the ventromedial division (Lvm) with smaller and more dense pyramidal-like neurones (arrows); cresyl violet; scale bar = 25 μm.

nected with the accessory olfactory tract (aot) (Fig. 2). Cells of this nucleus are round and oval, they do not form layers (Fig. 3–5, 12e).

The bed nucleus of the accessory olfactory tract shows no AChE activity similarly to neighbouring structures: the posteromedial cortical nucleus — laterally, the medial nucleus and further amygdalo-hippocampal area — dorsomedially (Fig. 3–5).

The amygdalohippocampal area (AHA)

The amygdalohippocampal area is a transitory area between the subicular complex and the amygdala. It appears in the medial aspect of the amygdala just before the ventral hippocampus (Fig. 5). Laterally it borders the medial, basomedial nuclei and inferior horn of the lateral ventricle and ventrally — the posteromedial cortical nucleus (Fig. 5–10). Caudally the amygdalohippocampal area fuses the periamygdaloid and piriform cortices.

The amygdalohippocampal area is a heterogeneous group of neurones consisting of deeply situated small oval and bigger round cells (Fig. 17d).

In cresyl violet staining its limits are clearly distinguishable, whereas low and homogeneous AChE activity does not allow their clear delineation (Fig. 5–11).

The basolateral complex

The basolateral complex — a large component of the amygdala — extends from the level just behind the optic chiasm almost to the joining of the ventral and dorsal hippocampi (Fig. 4–11). It is well developed at the level where the inferior horn of the lateral ventricle appears (Fig. 6). The nuclei of the basolateral complex are differentiated cellular masses and are characterised by variable AChE activity. AChE staining is especially useful for delineation of its nuclei, as we found big regional differences in the distribution of AChE enzyme in the basolateral complex.

The lateral amygdaloid nucleus

The lateral amygdaloid nucleus in the rabbit is well developed at the level of the beginning of the inferior horn of the lateral ventricle (Fig. 6). It extends throughout the amygdaloid complex lying medially to the external capsule separating it from the endopiriform nucleus, and ventrolaterally to the central nucleus (Fig. 4–11).

On the basis of the morphology and topographic relations in the lateral amygdaloid nucleus we distinguished two main divisions: dorsolateral and ventromedial. The border between these divisions is clear in the anterior portion (Fig. 4–7), but posteriorly it is not so obvious (Fig. 8–10). This division is also supported by different intensity of AChE. In the dorsolateral division AChE activity is slightly higher than in the ventromedial one (Fig. 5b–8b); moreover the boundary between these divisions in the most rostral sections is clearly marked by a bundle of darkly stained fibres (Fig. 5b–6b).

The dorsolateral division of the lateral nucleus (Ldl)

The dorsolateral division of the lateral nucleus begins the most rostrally among all nuclei of the basolateral complex. It borders laterally the external capsule and intercalated cells, but the border between the intercalated masses and the dorsolateral division of the lateral nucleus is not sharp (Fig. 4–7). Medially it abuts the central nucleus (Fig. 4, 5) and more caudally the ventromedial division of the lateral nucleus (Fig. 6–10). The dorsolateral division of the lateral nucleus prolongs ventrally to form something like a shell of the nucleus (Fig. 6–10). Finally, in the most caudal sections, it is replaced by the growing ventromedial division of the lateral nucleus (Fig. 11).

The dorsolateral division is composed of darkly stained small pyramidal-like, oval and occasionally round neurones. These cells are densely packed. Axes of neuronal cell somata have no specific orientation (Fig. 15a). There are many glial cells among the neurones.

The enzymatic reaction for AChE in the dorsolateral division is moderately intensive, higher than in the ventromedial division, especially in rostral sections (compare Fig. 4b, 7b).

The ventromedial division of the lateral nucleus (Lvm)

The ventromedial division of the lateral nucleus is the most caudally extended portion of the amygdala. It almost reaches the level of the fusion of the dorsal and ventral hippocampus. The ventromedial division of the lateral nucleus occupies the mediodorsal aspect of the basolateral complex. It borders the piriform cortex and dorsolateral division of the lateral nucleus — laterally, the central nucleus — dorsomedially, the basal nucleus — medially and ventrally (Fig. 4–11).

The border with the basolateral nucleus is clearly distinguishable, especially at the level of the beginning of the inferior horn of the lateral ventricle (Fig. 6–7). More caudally it is rather difficult to delineate the ventromedial division, which in cresyl violet fuses the central nucleus. Larger cells, their lower density and the homogeneity of AChE intensity enable its delineation (Fig. 8–10).
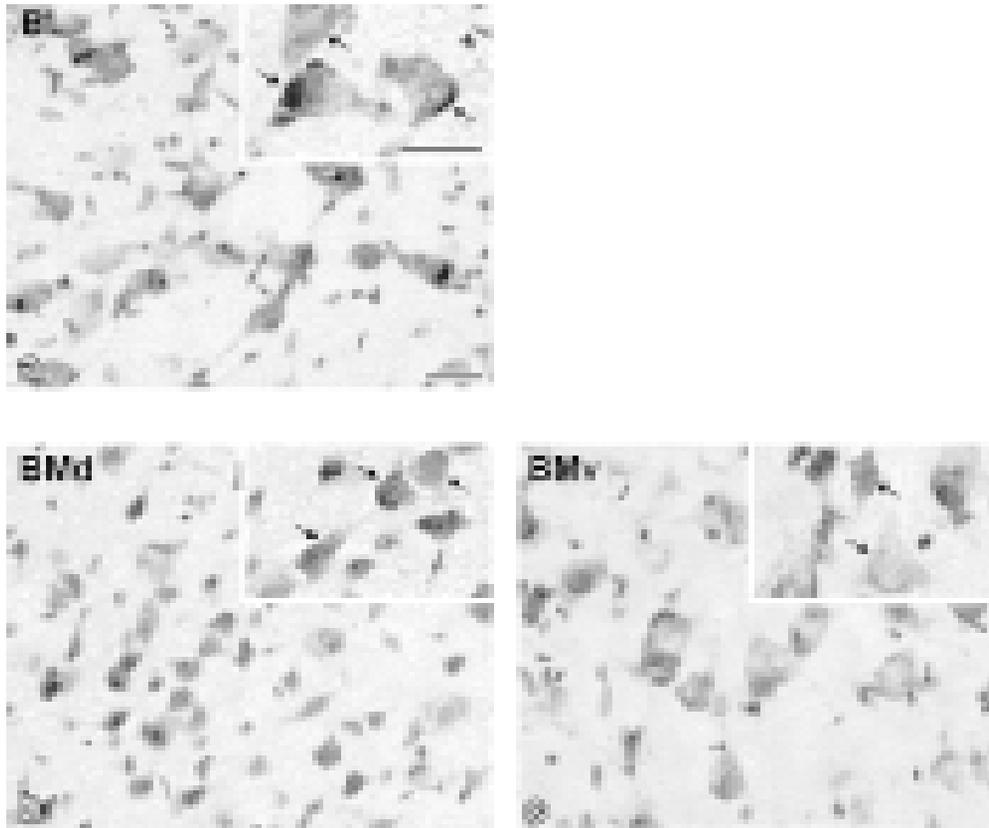
Figure 16. Photomicrographs of cells in the basal nucleus in the rabbit: **a)** the basolateral nucleus (BL), arrows indicate large oval, multipolar and pyramidal-like neurones; **b)** dorsal subdivision of the basomedial nucleus (BMd) with pyramidal-like and oval neurones (arrows); **c)** ventral subdivision of the basomedial nucleus (BMv) with larger then in BMd pyramidal-like neurones (arrows); cresyl violet; scale bar = 25 μm.

In rostral sections neurones of the ventromedial part are large, palely stained and loosely packed (Fig. 15b), while caudally they become smaller and denser (Fig. 15c). These neurones are mainly pyramidal-like and occasionally fusiform; there are many glial cells among them (Fig. 15b, c).

The basal amygdaloid nucleus

The basal nucleus is located in the ventromedial aspect of the basolateral complex (Fig. 4–11). Anteriorly it reaches the anterior amygdaloid area (Fig. 6). It borders the central nucleus and intercalated masses dorsally, the terminal stria, inferior horn of the lateral ventricle and amygdalohippocampal area — medially, the bed nucleus of the lateral olfactory tract, posterior cortical nuclei and periamygdaloid cortex — ventrally (Fig. 5–11).

Two main cellular groups: basolateral and basomedial are clearly visible in the basal nucleus. The AChE intensity in two parts of the basal nucleus is different and allows their clear delineation (Fig. 4b–11b).

The basolateral nucleus (BL)

The basolateral nucleus appears at the lateral aspect of the basal nucleus (Fig. 5–10). Fibres of the external capsule reach the lateral side of this nucleus.

Dorsally it borders the central nucleus (Fig. 4–6) and more caudally — the ventromedial division of the lateral nucleus (Fig. 7–11); its medioventral edge is surrounded by the basomedial nucleus. Further caudally the basolateral nucleus is located under the inferior horn of the lateral ventricle (Fig. 7–11). The ventromedial division of the lateral nucleus borders the basolateral nucleus dorsolaterally, whereas the piriform cortex and periamygdaloid cortex — ventrally (Fig. 5–11).

Due to the presence of the largest neurones the basolateral nucleus is easily distinguishable. It possesses scattered darkly stained pyramidal-like, multipolar and oval neurones (Fig 16a), of smaller density in comparison with the lateral amygdaloid nucleus. It also has the highest AChE activity (Fig. 4b–11b).
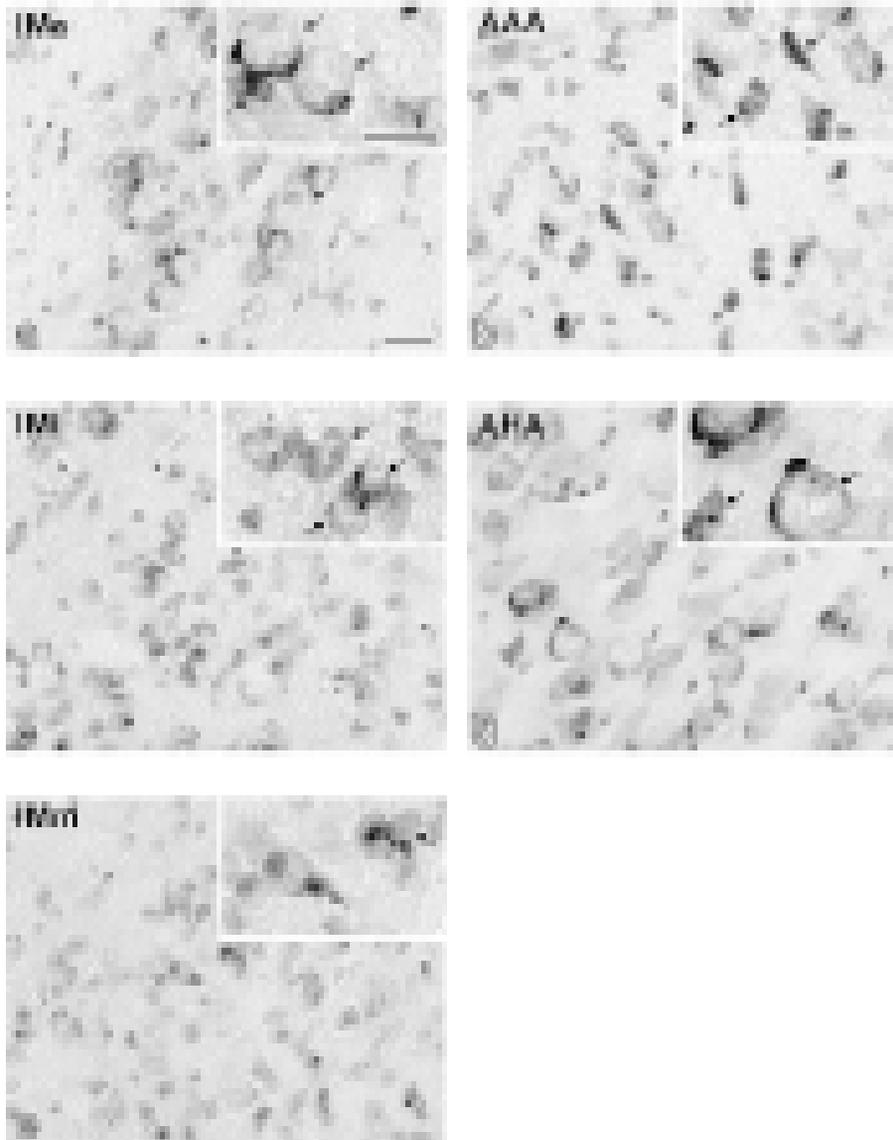
273

Figure 17. Photomicrographs of cells in some areas of the amygdaloid complex in the rabbit: **a)** the anterior group of intercalated masses (IMa) with large and small oval neurones (arrows); **b)** anterior amygdaloid area (AAA), arrows indicate fusiform and oval neurones; **c)** the longitudinal group of intercalated masses (IMl) with oval and round cells (arrows); **d)** amygdalohippocampal area (AHA) with small oval and large round neurones (arrows); **e)** the medial group of intercalated masses (IMm) with oval and round cells (arrows); cresyl violet; scale bar = 25 μm.

The basomedial nucleus (BM)

Among all nuclei of the basolateral complex, the basomedial nucleus is located the most medially and is composed of the smallest neurones. It is placed ventrolaterally to the terminal stria and lateral ventricle and medially — to the basolateral nucleus (Fig. 5–10). From the ventral aspect the basomedial nucleus is surrounded by the amygdalohippocampal area, the bed nucleus of the lateral olfactory tract, the posterior cortical nuclei and neighbouring periamygdaloid cortex; in the very caudal part the delineation between the basomedial nucleus and above mentioned areas is not sharp (Fig. 4–10).

Neurones of the basomedial nucleus are pyramidal-like, oval and fusiform (Fig. 16b, c). On the basis of their size and density we have divided the basomedial nucleus into dorsal and ventral divisions (Fig. 7–10). The ventral division has less dense and larger cells (Fig. 16c), while the dorsal one consists of smaller and more densely packed cells (Fig.16b). In the most caudal part only the dorsal division appears.

274

The AChE activity is homogeneously low in the basomedial nucleus (Fig. 4b–10b) similarly to neighbouring structures (Fig. 8b–10b).

Other amygdaloid areas

The anterior amygdaloid area (AAA)

The anterior amygdaloid area builds a rostral extreme of the amygdala (Fig. 1). It is located dorsally to the anterior cortical nucleus and ventrally to the central nucleus (Fig. 2, 3). Caudally it is replaced by the basolateral complex (Fig. 4).

This is the area of scattered cells and fibres. Its neurones are a heterogeneous population of mainly oval and round but also pyramidal-like and fusiform cells (Fig. 17b). AChE activity in this area is negative (Fig. 1b–3b).

Intercalated masses (IM)

Intercalated masses are very well developed in the rabbit. On the basis of topographic, cytoarchitectonic and histochemical properties, three large groups of intercalated masses can be distinguished.

The first group — anterior (IMa) — precedes the lateral nucleus and constitutes a broad cellular band located along the external capsule from the level above the rhinal sulcus and infiltrating the dorsolateral division of the lateral nucleus (Fig. 1–7). It appears as dense cell clusters consisting of two neuronal populations of darkly stained large or small cells (Fig. 17a). Large neurones are in the majority. The boundary between the anterior group of intercalated masses and the dorsolateral division of the lateral nucleus is not clear.

The remaining groups of the intercalated masses — medial and longitudinal — differ only topographically. The medial group of intercalated masses (IMm) is located medially between the central and basal nuclei (Fig. 4–6), whereas the longitudinal one (IMl) — among the fibres separating the central nucleus from the basolateral complex (Fig. 5–7). Neurones of these intercalated masses are mainly small, darkly stained and oval or round in shape (Fig. 17c, e).

The activity of AChE varies among groups of intercalated masses, although the difference is minimal: medial and longitudinal groups are negative while the anterior one is weakly stained.

DISCUSSION

In the literature we cannot find any detailed report concerning the morphology of the amygdala in the rabbit, available data on the subject are fragmentary [19, 26, 45, 57, 66, 70]. Thus the aim of our study was an attempt at a precise delineation of nuclear boundaries and the settlement of the terminology in the amygdaloid complex.

According to Girgis et al. [19] the amygdaloid complex in the rabbit extends from +2.0 to –3.0 with reference to Bregma — so the length of the amygdala equals approximately 5 mm. According to our observations it is closer to 4.3 mm, but there is a considerable variability between individuals within the species [19].

Our results may suggest that although general divisions of the amygdaloid nuclear complex in the rabbit are comparable to that in the cat and rat, they differ reasonably. The rabbit is taxonomically different from rodents (it belongs to *Lagomorpha*) and consequently shows a peculiar aspect in the nuclear pattern. Besides that the pattern of the AChE activity seems to be comparable (with some exceptions) within different species [3, 58].

We present in this paper a revised anatomical division of the amygdaloid complex in the rabbit based on both conventional Nissl cytoarchitectural studies and the differential distribution of AChE activity. In the majority of amygdaloid nuclei cresyl violet staining was adequate for designating their limits, for those cases the demarcation made by AChE staining correlates strongly with Nissl cytoarchitectural boundaries. The boundaries of remaining nuclei (especially the central nucleus) were seen more clearly and additional subdivisions were more obvious in the histochemical preparations.

The highest enzymatic intensity is found in the basolateral nucleus and the nucleus of the lateral olfactory tract, low — in the basomedial nucleus, posterolateral cortical and medial nuclei; the posteromedial nucleus, amygdalohippocampal and anterior amygdaloid areas are negative in AChE staining. All these areas are characterised also by homogeneous distribution of the enzymatic activity. Lateral and central nuclei as well as intercalated masses show negative to moderate and heterogeneous intensity of AChE staining. Differences in AChE activity in different nuclei of the amygdaloid complex probably reflect differential innervation of these nuclei by cholinergic neurones of the basal forebrain [35].

We distinguished in the lateral nucleus two divisions: dorsolateral and ventromedial. Our dorsolateral and ventromedial divisions correspond to the pars anterior and posterior of the lateral nucleus, respectively, observed in the rabbit by Young [70], due to the fact that both dorsolateral and ventromedial divisions are situated in such a pattern along the rostrocaudal axis.

Our division of the lateral nucleus corresponds to the division of the lateral nucleus in the cat used by Krettek and Price [29], whereas the lateral nucleus in the rat has more divisions [51, 53]. Krettek and Price [29] distinguished the lateral shell and the main body of this nucleus (further subdivided) in the cat, while in the rat – the dorsolateral, medial and ventromedial divisions are visible [51].

According to our studies the activity of AChE is higher in the dorsolateral part than in the ventromedial one, although according to Nitecka [45] activity of AChE in the rabbit is exceptionally (in comparison with other species) uniform throughout the whole lateral nucleus. Activity of this enzyme in the lateral nucleus in the human varies from relatively high to low depending on the topography [46] or is weak [58], whereas in the cat it is medium [48]. According to de Olmos et al. [14] enzymatic activity in the rat varies through the lateral nucleus in a similar way as in the rabbit, which means that in the dorsolateral division of the lateral nucleus is moderate and in the ventromedial division of the lateral nucleus is weak. Also in other species two areas of slightly different activity, not very well distinguishable, were found in the lateral nucleus [35, 45].

The descriptions of the basal nucleus in the present paper are based on terminology used by Kapp et al. [26], Nitecka [45] and Young [70] in the rabbit. The same terms were used by Krettek and Price [29] in the cat and by Price et al. [55] in the rat. Totally different terminology of the basolateral amygdaloid complex (also of the other parts of the amygdala) was used by Japanese scientists (e.g. Uchida [66]). Uchida [66] named the basolateral nuclear complex as amygdala propria and subdivided it into lateral, intermediate and medial parts. Only the two latter terms can correspond to the basolateral nucleus.

In our data, the basolateral nucleus is a homogeneous mass of large cells in cresyl violet staining. It agrees with the previous findings [26], whereas Young [70] has realised that the rabbit basolateral nucleus might be subdivided, but into lateral and medial parts. Posterior and anterior parts of the basolateral nucleus were delineated both in the rat [14, 35] and in the cat [29].

Also in the histochemical staining the basolateral nucleus shows uniformly strong positive reaction for AChE. This finding is supported in the rabbit [45], and in the rat [14, 45, 48]. According to de Olmos et al. [14] the rat basolateral nucleus appears as a sharply delineated homogeneously densely stained structure throughout its whole extent.

In the cat and man two areas of different intensity of AChE activity have been found [45, 46, 48, 58]. In the human the basolateral nucleus splits into superior and inferior parts; the former shows stronger AChE reaction, while the latter — moderate or low [46]. Similarly — in the cat — this nucleus is also an area of the strongest but variable enzymatic activity [48].

The rabbit basomedial nucleus splits into two divisions: dorsal and ventral, which are easily distinguishable only in the middle part of the nucleus. Kapp et al. [26] and Young [70] did not partition this nucleus in the rabbit, however the topographic relations and the localisation described by them are similar to ours.

In all studied species the basomedial nucleus shows much lower AChE activity than the basolateral nucleus [14, 46, 58]. In the rabbit AChE activity within this nucleus is homogeneously low, which is supported by others [45].

The localisation and extent of the central nucleus in the rabbit are described in a similar way [26, 70]. Although Young [70] did not divide this nucleus in the rabbit, Kapp [26] has treated it as being built of only two groups of cells (medial and lateral), but he used cresyl violet as well as retrograde axonal transport methods. Nevertheless according to our results the central nucleus in the rabbit is composed in the same way as in the rat — we delineated four subdivisions, which closely correspond to those in the rat and are better visible in AChE preparations.

According to Pitkänen et al. [27,53] and McDonald [34] in the rat there are four divisions (capsular, lateral, intermediate and medial). Their topographical interrelations correspond to those observed in the rabbit, but their extent differs.

Two parts of the central nucleus (medial and lateral) were distinguished in the cat by Hall [20] and Krettek and Price [29], and — on the basis of physiological properties — in the guinea-pig [33]. Also de Olmos [14] in the rat distinguished two main parts of the central nucleus, but he further subdivided them into the anterodorsal, anteroventral, posteroventral, central and capsular subdivisions.

Our studies show heterogeneous low to moderate AChE activity in the central nucleus, while other data [45] suggest heterogeneous but strong reaction in this nucleus in the rabbit. The heterogeneity of AChE activity was also observed in the human amygdaloid body (with the almost negatively stained the lateral subdivision and slightly more intense — the medial subdivision [58]), however in the cat the AChE activity is homogeneously high throughout the whole central nucleus [48].

276

The localisation of the medial nucleus in the rabbit corresponds to its position in other species [26, 29, 53, 62], but its shape (bow-like) on coronal sections in the rabbit is very characteristic. Previously the rabbit medial nucleus was treated in cresyl violet staining as a homogeneous mass of densely packed small neurones [15] (this was also supported by other authors [26]) also characterised by a nearly complete lack of AChE activity [45]. According to our new data, the rabbit medial nucleus might be divided into two parts: dorsal and ventral, but the boundary between them is not clear. In the cat two subdivisions of the medial nucleus: anterior and posterodorsal, were found [29], whereas in the rat Pitkänen et al. [53] distinguish its three main subdivisions: rostral, central, and caudal.

This area performs heterogeneous light to poor AChE activity in the rabbit, all studied species of animals [14, 45, 48] and in man [58].

Cortical nuclei are divided in our study into the following distinct well differentiated areas, named the anterior, posteromedial and posterolateral nuclei. This division closely corresponds to that used by Kapp et al. [26], although our previous data (Dziewiątkowski [15]) suggest the presence of anterior and posterior parts. Young [70] and Girgis et al. [19] did not divide the cortical nuclei at all.

The morphology and topography of the cortical nuclei in the rabbit correspond to those observed in the rat and cat [29, 50, 53], although in the rabbit the posterior cortical nuclei appear medially to the anterior cortical nucleus, in contrast to the rat where they are located laterally to the anterior cortical nucleus [50].

Also the laminar pattern of the cortical nuclei in the rabbit is very similar to that in the cat and rat; the distribution of cells' types constituting the layers is close, too [20, 29].

In our investigations AChE activity in the cortical nuclei is heterogeneous and low. Similarly — both in the cat and rat there is almost negative enzymatic reaction for AChE [14, 48], but in the human the cortical nuclei have rather moderate intensity [58]. According to our data there is only a slight difference of staining between three cortical nuclei, but it is very helpful in delineating boundaries.

According to our data the periamygdaloid cortex is an easily distinguishable structure lying medially to the piriform cortex, although it was not described in previous findings of the amygdala in the rabbit [19, 26, 70]. In the cat [50, 53] a similar homogeneous structure, of almost identical topography but larger size, was delineated [29]. The periamygdaloid cortex was only divided by Kemppainen and Pitkanen [27] into sulcal and medial parts, although de Olmos [48] did not find them. However, such topographic areas might be delineated in our material, too.

In the corticomedial amygdaloid complex there are two superficial, cortical-like nuclei related to the olfactory system [12, 14]: the nucleus of the lateral olfactory tract and the bed nucleus of the accessory olfactory tract. In the rabbit they were not described.

Within species the nucleus of the lateral olfactory tract presents a very close laminar arrangement as well as high AChE activity [3, 20, 50]. Also the morphology of the bed nucleus of the accessory olfactory tract, although characterised by the lack of a layered structure, seems not to differ inter species [15, 29].

The anterior amygdaloid area is, among the remaining amygdaloid nuclei, the one with poorly distinguishable borders. Moreover, some authors consider that the term "anterior amygdaloid area" is proper only in a topographical sense, because taking into account its connections it does not belong to the amygdala [31]. Its localisation in the rabbit corresponds to that in other species [14, 29, 46]: similarly to the rat it is characterised by the lack of any laminar cells' arrangement present in the neighbouring cortical nuclei [14].

The AChE activity in the anterior amygdaloid area is negative. Also in man this area has little AChE activity [46, 58], while in the cat — it gives weakly positive reaction [48]. Our observations suggest the homogeneity of the anterior amygdaloid area, some authors suppose the presence of areas of various activity within this field [45]. Characteristically in the rat the anterior amygdaloid area shows a light to moderate "patchy" staining reaction [14].

As a "transitional" area, the amygdalohippocampal transition area occupies a similar localisation in all studied species [14, 46, 53, 70], although Kapp et al. [26] did not distinguish this field. Differences in the localisation between species are connected with the growing size of a brain and changes of interrelations between these structures. Pitkänen et al. [53] delineated lateral and medial divisions of amygdalohippocampal transition area in the rat, corresponding to anterolateral and posteromedial divisions by de Olmos [14]. In the rat the medial division is characterised by small darkly stained and densely packed neurones that resemble the small cells of the subiculum, while the ventral division contains

277

also darkly stained but bigger and less densely packed neurones, which are slightly similar to the neighbouring basal nucleus cells [14]. In our study we also found two populations of cells but the boundary between them is not clear and we were not able to delineate two different areas in the amygdalohippocampal area.

The AChE activity of the amygdalohippocampal transition area shows a slight interspecies variability; it is moderate in the rat [14], negative in the cat [48] and rabbit.

In the comparison with other species, intercalated masses in the adult rabbit differ significantly. In the rabbit we found three main groups of intercalated masses: anterior, medial and longitudinal; their morphology and topography were never described. The localisation of intercalated masses is similar in studied species [14, 40, 49].

According to Pare and Smith [49] in the cat neurones of intercalated masses are mainly GABAergic small cells, but there is also a small population of larger ovoid neurones which are immunonegative. Also in the rat intercalated masses consist of two cell types: most of them are small and round, a minority (about 5%) — are large [40]. A similar distribution of cell types characterises, according to our data, medial and longitudinal groups of intercalated masses. The anterior group is mainly build of large neurones and small cells are in the minority, moreover this group appears very rostrally, and its cells reach the level of the rhinal sulcus Such an anterior and dorsal location of this group of intercalated masses was not observed in other species [40, 49, 63].

In contrast to the strong AChE reaction of intercalated masses in man [58] but similarly to the weak enzymatic activity in the rat [40], the intensity of AChE reaction in the rabbit varies from negative (medial and longitudinal groups) to weak (anterior group).

To summarise our findings we can conclude that, although the general scheme of the topography as well as division of the amygdaloid complex in the rabbit resembles those in the rat and cat, it reveals a peculiar morphology pattern. Especially the arrangement of the nuclei of the basolateral complex is characteristic in the rabbit. The basolateral nucleus changes its position on coronal sections into the ventral direction and is replaced from above by the ventrolateral division of the lateral nucleus. In the cat this nucleus changes its position into more dorsal and the ventrolateral division of the lateral nucleus covers it from the lateral side. Within the baso-

lateral complex the ventromedial division of the lateral nucleus occupies the biggest area, while its dorsolateral division is the smallest.

The similar arrangement of the corticomedial complex in the rabbit, rat and cat supports their phylogenetic older origin. Within the corticomedial complex the central nucleus is the largest and the most differentiated area.

Differentiation of the amygdaloid nuclei — easy for large nuclear complexes, or specific nuclei in cresyl violet method — should be revised by immuno-histochemical (e.g. calcium binding proteins) or histochemical methods (e.g. AChE activity) for their detailed description. Although each species is characterised by its own pattern of reactivity within the nuclear subdivisions, the general scheme is very similar, reflecting their physiological properties.

ACKNOWLEDGEMENTS

REFERENCES

1. Aggleton JP (1985) A description of intra-amygdaloid connections in old world monkey. Exp Brain Res, 57: 390–399.
2. Aggleton JP (1986) A description of the amygdalo-hippocampal interconnections in the macaque monkey. Exp Brain Res, 64: 515–526.
3. Ben-Ari Y, Zigmond RE, Shute CCD, Lewis PR (1977) Regional distribution of choline acetyltransferase and acetylcholinesterase within the amygdaloid complex and stria terminalis system. Brain Res, 120: 435–445.
4. Berdel B, Morys J, Maciejewska B, Narkiewicz O (1996) Acetylcholinesterase activity as a marker of maturation of the basolateral complex of the amygdaloid body in the rat. Int J Dev Neurosci, 14: 543–549.
5. Brashear HR, Godec MS, Carlsen J (1988) The distribution of neuritic plaques and acetylcholinesterase staining in the amygdala in Alzheimer's disease. Neurology, 38: 1694–1699.
6. Cahill L, Haier RJ, White NS, Fallon J, Kilpatrick L, Lawrence C, Potkin SG, Alkire MT (2001) Sex-related difference in amygdala activity during emotionally influenced memory storage. Neurobiol Learn Mem, 75: 1–9.
7. Cahill L, Vazdarjanova A, Setlow B (2000) The basolateral amygdala complex is involved with, but is not necessary for, rapid acquisition of Pavlovian 'fear conditioning'. Eur J Neurosci, 12: 3044–3050.
8. Cahill L, Weinberger NM (1999) Is the amygdala a locus of "conditional fear"? Some questions and caveats. Neuron, 23: 227–228.
9. Camps P, Cusack B, Mallender WD, El Achab R, Morral J, Munoz-Torrero D, Rosenberry TL (2000) Huprine X is

a novel high-affinity inhibitor of acetylcholinesterase that is of interest for treatment of Alzheimer's disease. Mol Pharmacol, 57: 409–417.

10. Carlsen J (1989) New perspectives on the functional anatomical organization of the basolateral amygdala. Acta Neurol Scand Suppl, 122: 1–27.

11. Coleman-Mesches K, McGaugh JL (1995) Muscimol injected into the right or left amygdaloid complex differentially affects retention performance following aversively motivated training. Brain Res, 676: 183–188.

12. Crosby EC, Humphrey T (1941) Studies of the vertebrate telencephalon. II. The nuclear pattern of the anterior olfactory nucleus, tuberculum olfactorium and the amygdaloid complex in adult man. J Comp Neurol, 74: 309–352.

13. Davis M (2000) The role of the amygdala in conditioned and unconditioned fear and anxiety. In: Aggleton JP (ed.). The amygdala, Vol. 2. Oxford University Press, Oxford, UK, pp. 213–287.

14. de Olmos J, Alheid GF, Beltramino CA (1985) Amygdala. In: Paxinos G (ed.). The rat nervous system. Academic Press, Sydney, pp. 223–334.

15. Dziewiatkowski J, Berdel B, Kowianski P, Kubasik-Juraniec J, Bobek-Billewicz B, Morys J (1998) The amygdaloid body of the rabbit — a morphometric study using image analyser. Folia Morphol (Warszawa), 57: 93–103.

16. Emre M, Heckers S, Mash DC, Geula C, Mesulam M-M (1993) Cholinergic innervation of the amygdaloid complex in the human brain and its alterations in old age and Alzheimer's disease. J Comp Neurol, 336: 117–134.

17. Ferry B, Roozendaal B, McGaugh JL (1999) Role of norepinephrine in demiating stress hormone regulation of long-term memory storage: A critical involvement of the amygdala. Biol Psychiatry, 46: 1140–1152.

18. Gerebtzoff MA (1953) Recherches histochimiques sur les acetylcholine et choline esterases. Acta Anat, 19: 366–379.

19. Girgis M, Shih-Chang W (1981) Stereotaxic atlas of the rabbit brain, Warren H. Green, Inc., St Louis, Mi. pp. 1–70.

20. Hall E (1972) The amygdala of the cat: A Golgi study. Z Zellforsch, 134: 439–458.

21. Hall E, Geneser-Jensen FA (1971) Distribution of acetycholinesterase and monoamine oxidase in the amygdala of the guinea pig. Z Zellforsch, 120: 204–221.

22. Howard MA, Cowell PE, Boucher J, Broks P, Mayes A, Farrant A, Roberts N (2000) Convergent neuroanatomical and behavioural evidence of an amygdala hypothesis of autism. Neuroreport, 11: 2931–2935.

23. Humphrey T (1968) The development of the human amygdala during early embryonic life. J Comp Neurol, 132: 135–166.

24. Humphrey T (1972) The development of the human amygdaloid complex. In: Eleftherion BE (ed.). The neurobiology of the amygdala. Plenum Press, New York, pp. 21–77.

25. Johnston JB (1923) Further contributions to the study of the evolution of the forebrain. J Comp Neurol, 35: 337–481.

26. Kapp BS, Schwaber JS, Driscoll PA (1985) Frontal cortex projections to the amygdaloid central nucleus in the rabbit. Neuroscience, 15: 327–346.

27. Kemppainen S, Pitkänen A (2000) Distribution of parvalbumin, calretinin, and calbindin-D_{28k} immunoreactivity in the rat amygdaloid complex and colocalization with gamma-aminobutyric acid. J Comp Neurol, 426: 441–467.

28. Kosmal A, Malinowska M, Woznicka A (1997) Diversity of connections of the temporal neocortex with amygdaloid nucli in the dog (*Canis familiaris*). Acta Neurobiol Exp, 57: 289–314.

29. Krettek JE, Price JL (1978) A description of the amygdaloid complex in the rat and cat with observations on intra-amygdaloid axonal connections. J Comp Neurol, 178: 255–280.

30. LeDoux JE (2000) Emotion circuits in the brain. Ann Rev Neurosci, 23: 155–184.

31. Magnus O, Lammers HJ (1956) The amygdaloid-nuclear complex. Folia Psychiat Neurol Neurochir Neerl, 59: 555–582.

32. Maren S (1999) Long-term potentiation in the amygdala — a mechanism for emotional learning and memory. Trends Neurosci, 22: 561–567.

33. Martina M, Royer S, Paré D (1999) Physiological properties of central medial and central lateral amygdala neurons. J Neurophysiol, 82: 1843–1854.

34. McDonald AJ (1982) Cytoarchitecture of the central amygdaloid nucleus in the rat. J Comp Neurol, 208: 401–418.

35. McDonald AJ (1984) Neuronal organization of the lateral and basolateral amygdaloid nuclei in the rat. J Comp Neurol, 222: 589–606.

36. Mesulam M-M, Geula C (1988) Nucleus basalis (Ch4) and cortical cholinergic innervation in the human brain: observations based on the distribution of acetylcholinesterase and choline acetyltransferase. J Comp Neurol, 275: 216–240.

37. Mesulam M-M, Geula C (1991) Acetylcholinesterase-rich neurons of the human cerebral cortex: cytoarchitectonic and ontogenetic patterns of distribution. J Comp Neurol, 306: 193–220.

38. Mesulam M-M, Geula C, Moran MA (1987) Anatomy of cholinesterase inhibition in Alzheimer's disease: Effect of physostigmine and tetrahydroaminoacridine on plaques and tangles. Ann Neurol, 22: 683–691.

39. Mesulam M-M, Mufsom EJ, Levey AI, Wainer BH (1984) Atlas of cholinergic neurons in the forebrain and upper brainstem of the macaque based on monoclonal choline acetyltransferase immunohistochemistry and acetylcholinesterase histochemistry. Neuroscience, 12: 669–686.

40. Millhouse OE (1986) The intercalated cells of the amygdala. J Comp Neurol, 247: 246–271.

41. Millhouse OE, DeOlmos J (1983) Neuronal configurations in lateral and basolateral amygdala. Neuroscience, 10: 1269–1300.

42. Morys J (1996) The limbic system and emotions. Post Psychiat Neurol, 5: 1–13.

43. Morys J, Berdel B, Jagalska-Majewska H, Luczynska A (1999) The basolateral amygdaloid complex — its de-

velopment, morphology and functions. Folia Morphol (Warszawa), 58: 29–46.

44. Murray EA (1991) Contributions of the amygdalar complex to behavior in macaque monkeys. Prog Brain Res, 87: 167–180.

45. Nitecka L (1975) Comparative anatomic aspects of localization of acetylcholinesterase activity in the amygdaloid body. Folia Morphol (Warszawa), 34: 167–185.

46. Nitecka L, Narkiewicz O (1976) Localization of acetylcholinesterase activity in the amygdaloid body of man. Acta Neurobiol Exp, 36: 333–352.

47. Nitecka L, Narkiewicz O, Zawistowska H (1971) Acetylcholinesterase activity in the nuclei of the amygdaloid complex in the rat. Acta Neurobiol Exp, 31: 383–388.

48. Nitecka L, Zawistowska H, Bialowas J (1973) Nuclei of the amygdaloid body in cats - structure and acetylcholinesterase activity. Folia Morphol (Warszawa), 23: 40–49.

49. Pare D, Smith Y (1993) The intercalated cell masses project to the central and medial nuclei of the amygdala in cats. Neuroscience, 57: 1077–1090.

50. Paxinos G, Watson C (1986) The rat brain in stereotaxic coordinates. Second Edition, Academic Press Inc., San Diego, CA, pp. 1–262.

51. Pikkarainen M, Rönkkö S, Savander V, Insausti R, Pitkänen A (1999) Projections from the lateral, basal, and accessory basal nuclei of the amygdala to the hippocampal formation in rat. J Comp Neurol, 403: 229–260.

52. Pitkänen A, Amaral DG (1993) Distribution of calbindin-D(28K) immunoreactivity in the monkey temporal lobe: The amygdaloid complex. J Comp Neurol, 331: 199–224.

53. Pitkänen A, Jolkkonen E, Kemppainen S (2000) Anatomic heterogeneity of the rat amygdaloid complex. Folia Morphol, 59: 1–23.

54. Pitkänen A, Tuunanen J, Kälviäinen R, Partanen K, Salmenperä T (1998) Amygdala damage in experimental and human temporal lobe epilepsy. Epilepsy Res, 32: 233–253.

55. Price JL, Russchen FT, Amaral DG (1987) Integrated systems of the CNS. The limbic region. II. The amygdaloid complex. In: Björklund A, Hokfelt T, Swanson LW (eds.). Handbook of chemical neuroanatomy. Elsevier, Amsterdam, pp. 279–388.

56. Salomé N, Viltart O, Leman S, Sequeira H (2001) Activation of ventrolateral medullary neurons projecting to spinal autonomic areas after chemical stimulation of the central nucleus of amygdala: a neuroanatomical study in the rat. Brain Res, 890: 287–295.

57. Shek JW, Wen GY, Wisniewski HM (1986) Atlas of the rabbit brain and spinal cord. Karger, Basel, pp. 1–235.

58. Sims KS, Williams RS (1990) The human amygdaloid complex: a cytologic and histochemical atlas using Nissl, myelin, acetylcholinesterase and nicotinamide adenine dinucleotide phosphate diaphorase staining. Neuroscience, 36: 449–472.

59. Smiley JF, Mesulam MM (1898) Cholinergic neurons of the nucleus basalis of Meynert receive cholinergic, catecholaminergic and GABAergic synapses: An electron microscopic investigation in the monkey. Neuroscience, 88: 241–255.

60. Stoop R, Pralong E (2000) Functional connections and epileptic spread between hippocampus, entorhinal cortex and amygdala in a modified horizontal slice preparation of the rat brain. Eur J Neurosci, 12: 3651–3663.

61. Svendsen CN, Bird ED (1985) Acetylcholinesterase staining of the human amygdala. Neurosci Lett, 54: 313–318.

62. ten Donkelaar HJ, Lammers GJ, Gribnau AAM (1979) Neurogenesis in the amygdaloid nuclear complex in a rodent (the Chinese hamster). Brain Res, 165: 348–353.

63. Tombol T, Szafranska-Kosmal A (1972) A Golgi study of the amygdaloid complex in the cat. Acta Neurobiol Exp, 32: 825–843.

64. Turner BH (1981) The cortical sequence and terminal distribution of sensory related afferents to the amygdaloid complex of the rat and monkey. In: Ben-Ari Y (ed.). The amygdaloid complex. Elsevier/North-Holland Biomedical Press, Amsterdam, pp. 51–62.

65. Uchida Y (1950) A contribution to the comparative anatomy of the amygdaloid nuclei in mammals, especially in rodents. Part I: rat and mouse. Folia Psychiat Neurol Jap, 4: 25–42.

66. Uchida Y (1950) A contribution to the comparative anatomy of the amygdaloid nuclei in mammals, especially in rodents. Part II: guinea pig, rabbit and squirrel. Folia Psychiat Neurol Jap, 4: 91–107.

67. Urban I, Richard P (1972) A stereotaxic atlas of the New Zealand rabbit's brain, Charles C. Thomas Publisher. Springfield pp. 1–86.

68. Van Elst LT, Woermann FG, Lemieux L, Trimble MR (1999) Amygdala enlargement in dysthymia — A volumetric study of patients with temporal lobe epilepsy. Biol Psychiatry, 46: 1614–1623.

69. Vazdarjanova A, McGaugh JL (1999) Basolateral amygdala is involved in modulating consolidation of memory for classical fear conditioning. J Neurosci, 19: 6615–6622.

70. Young MW (1936) The nuclear pattern and fiber connections of the non-cortical centers of the telencephalon of the rabbit (Lepus cuniculus). J Comp Neurol, 65: 295–401.