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Cytoarchitecture of the canine perirhinal and postrhinal cortex

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Abstract. The perirhinal cortex in the dog's brain is composed of two traditional Brodmann's areas: 35 and 36. Area 35 is situated along the entire rostro-caudal extent of the fundus of the posterior rhinal sulcus, whereas area 36 occupies its lateral bank. In this study, four subdivisions were distinguished in area 35 based on cytoarchitectonic differentiation. Area 36 is poorly developed in the dog's brain and was divided into two subdivisions. The most characteristic features of area 35 are: a wide layer I, scattered cell clusters in layer II, and a prominent layer V containing a distinct population of large multiform neurons. Area 36 can be recognized by the presence of numerous cell clusters in layer II and increasing radial arrangement of neurons in deep layers of the area. Two fields of the postrhinal cortex were identified in the additional postrhinal gyrus, which is found in the fundus of the most caudal extent of the posterior rhinal sulcus.

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INTRODUCTION

The perirhinal cortex, traditionally designated as Brodmann's (1909) cytoarchitectonic areas 35 and 36, is a narrow strip of cortex located along the posterior part of the rhinal sulcus. Recent findings in primates (Mishkin et al. 1997, Murray 1992, Squire and Zola-Morgan 1991, Suzuki et al. 1993, Zola-Morgan and Squire 1985, Zola-Morgan et al. 1989, 1994) indicated that the perirhinal cortex, like the entorhinal and parahippocampal cortical regions of the "medial temporal lobe", is an important component of the memory system. More recently it has been discovered that in the human brain this cortex undergoes severe neurodegenerative changes in Alzheimer's disease, schizophrenia or temporal lobe epilepsy, and interest in this cortical region has increased significantly (Arnold et al. 1991, Mishkin et al. 1982). Neuroanatomical studies in primates (Suzuki 1996a, Suzuki and Amaral 1994a,b) and subprimates (Burwell 2000, Burwell and Amaral 1998a,b, Deacon et al. 1983, Room and Witter 1985) have shown that the perirhinal cortex has numerous reciprocal connections with a number of cortical areas in the temporal, parietal, occipital and frontal cortex, both sensory and associative in function. Thus, it is a site of polymodal convergence where particular sensory systems can be introduced into memory processes. Lesion studies in monkeys (Meunier et al. 1993, Mishkin et al. 1997, Murray 1996, Suzuki et al. 1993, Zola-Morgan 1989) provided evidence that damage to the rhinal cortex causes deficits in recognition memory tasks. However, the deficits were found predominantly for stimuli presented in the visual and tactile modalities, whereas the effect of rhinal lesions on tasks involving auditory memory is not clear and is still being explored (Meunier et al. 1993, Saunders et al. 1998, Suzuki et al. 1993). A new DMS procedure (delayed matching-to-sample) like that used in the monkey was developed for dogs by Kowalska (1997) and was applied in auditory recognition tasks, providing an opportunity to compare the results in both species. However, rhinal lesions in dogs had no effect on performance in these tasks (Kowalska et al. 2001). This unexpected result prompted us to study the morphological background to the processing of auditory information throughout the areas of the temporal and perirhinal cortex. We need, however, to start with an examination of basic morphology of these cortical regions, which until now have not been studied in the canine brain.

According to current terminology, the perirhinal cortex in the monkey brain (Murray and Bussey 1999) includes cytoarchitectonic areas 35 and 36 in the rhinal sulcus. It is, however, extended laterally and caudally in comparison to earlier cytoarchitectonic maps of Brodmann (1909). Laterally, the perirhinal cortex reaches the anterior middle temporal sulcus. Caudally, two fields of the parahippocampal cortex (TF, TH), representing an extension to the perirhinal cortex, are now included into the functional cortical system. A comparable cortical region in the rat involves areas 35 and 36, located along the posterior part of the rhinal sulcus and postrhinal cortex, situated postero-dorsally (Burwell 2001). On account of the common cytoarchitectonic features and connectivity pattern in both species, the postrhinal cortex in the rat is considered to be a homologous region to the TF and TH fields in the monkey.

In the dog's brain, the posterior rhinal sulcus is substantially longer than in other species, with depth increasing in the caudal direction. The borders of these caudal cytoarchitectonic areas are difficult to delineate also because the caudal part of the rhinal sulcus ramifies into the retrosplenial and recurens sulci of the occipital lobe.

METHODS

Subjects

Observations of cellular structure were performed on three adult mongrel dogs weighing 8 to 15 kg. All procedures followed the guidelines established by the Ethical Committee on Animal Research of the Nencki Institute.

Processing of sections

The animals were given a lethal dose of Nembutal (35 mg/kg) and were perfused through the heart with normal saline (0.9% NaCl), followed by a fixative (4% formaldehyde in 0.1 M phosphate buffer, pH 7.4). Photographs of the ventral aspect of the brains were made after the brains were removed from the skulls but before they were cut into blocks. The blocks of brains were processed according to a standard combined celloidine-paraffin procedure. 20 μm thick coronal sections were obtained at 400 μm intervals and stained with cresyl violet using the standard Nissl method. Next, a digital image of the perirhinal and postrhinal cortex was obtained using a computer image processing system (Image Pro

Plus program, version 4.1), under magnification 10x of planachromat objective of Nikon (Optiphot 2) microscope, with fixed automatic stage.

Analysis of the cytoarchitectonic features concentrated on the arrangement of various types of neurons recognizable in Nissl staining, into cortical layers. Next, the coronal sections with marked cortical fields showing distinctive cytoarchitectonic features were used for preparing the ventral plan of the right hemisphere.

Figure preparation

Photographic images were scanned from photographic prints or directly from the coverslipped sections at a resolution of 2,400 dpi (Agfascan XY-15). Digitized images were processed using PhotoPaint (version 8.0) for contrast and brightness adjustment and then labeled using Corel DRAW (version 9.0). Except for these adjustments, the images were not altered in any way.

RESULTS

Location and borders of the perirhinal cortex

The canine perirhinal cortex, like that in other investigated mammals (Burwell 2001, Krettek and Price 1977, Room and Witter 1985, Suzuki 1996b, Suzuki and Amaral 1994a, Witter et al.1989), is situated along the posterior rhinal sulcus on the lateral and medial aspect of the hemisphere. It corresponds to main cytoarchitectonic fields defined by Brodmann (1909) as area 35 (area perirhinalis) and area 36 (area ectorhinalis) and currently known under the common name of the perirhinal cortex. Additionally, the cytoarchitectonic fields composing the caudal extension of both areas are included into this cortex. In the rat's brain, it has been defined as the postrhinal cortex (Fig. 6A), corresponding to areas TF and TH of the parahippocampal gyrus in the monkey (Fig. 6C) (Burwell et al. 1995).

The anterior limit of the posterior rhinal sulcus (*rhp*) is formed in the dog by a very deep sylvian sulcus (*ss*) and partly covered by a convolution of a well-developed posterior composite gyrus (CP) of the temporal neocortex (Figs. 1 and 6B). The anterior border of the perirhinal cortex (PC), where its cytoarchitectonic features can be clearly recognized, is dived into the junction of the rhinal and sylvian sulci. It occupies the fundus of a shallow anterior part of the *rhp*, between the posterior composite and piriform (PirC) cortices (Fig. 2D), which together overlie the caudal extent of the claustrum (Cl).

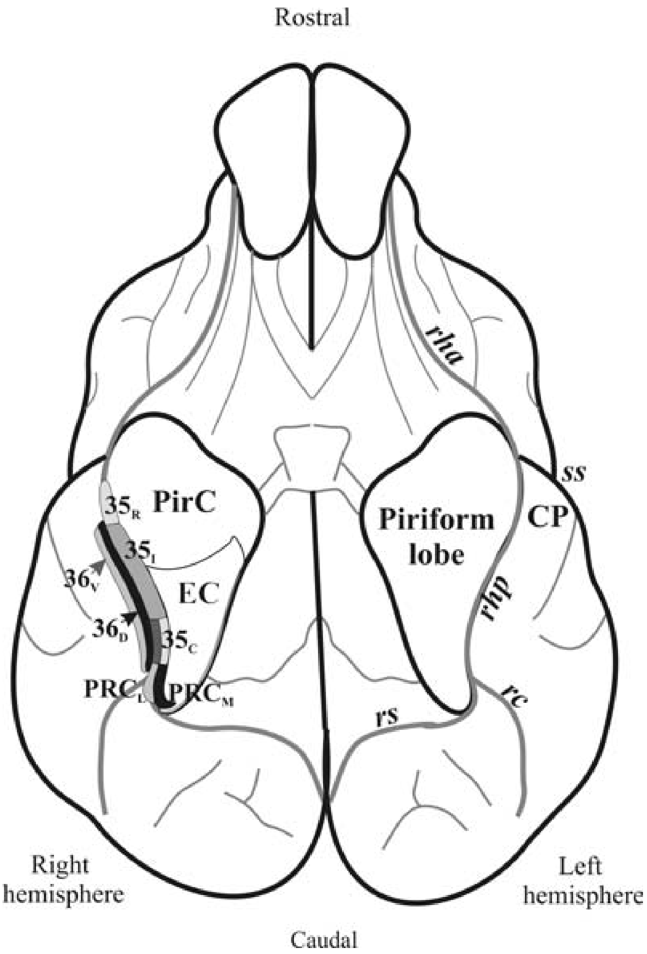

Fig. 1. Diagram of the ventral surface of the dog's brain illustrating general topography of the sulci and gyri and locations of subdivisions of the perirhinal and postrhinal cortex.

Ventrally, the anterior extent of the perirhinal cortex border PirC and more caudally, the entorhinal cortex (EC, see Fig. 2D,F). The junction of the perirhinal and piriform cortex is located on the surface of the hemisphere (Fig. 2A,D). However, the depth of the rhinal sulcus significantly increases caudally and the junction of the entorhinal and perirhinal cortex is displaced from the surface into the medial bank of this sulcus (Fig. 2B,F). Cytoarchitectonic borders between the perirhinal cortex (area 35) and both the piriform and entorhinal cortices are very clear. The border with the piriform cortex can be recognized by sharp changes in the pattern of cortical lamination, especially the dark, clustered appearance of layer II and the scarcity of cells in the inter-

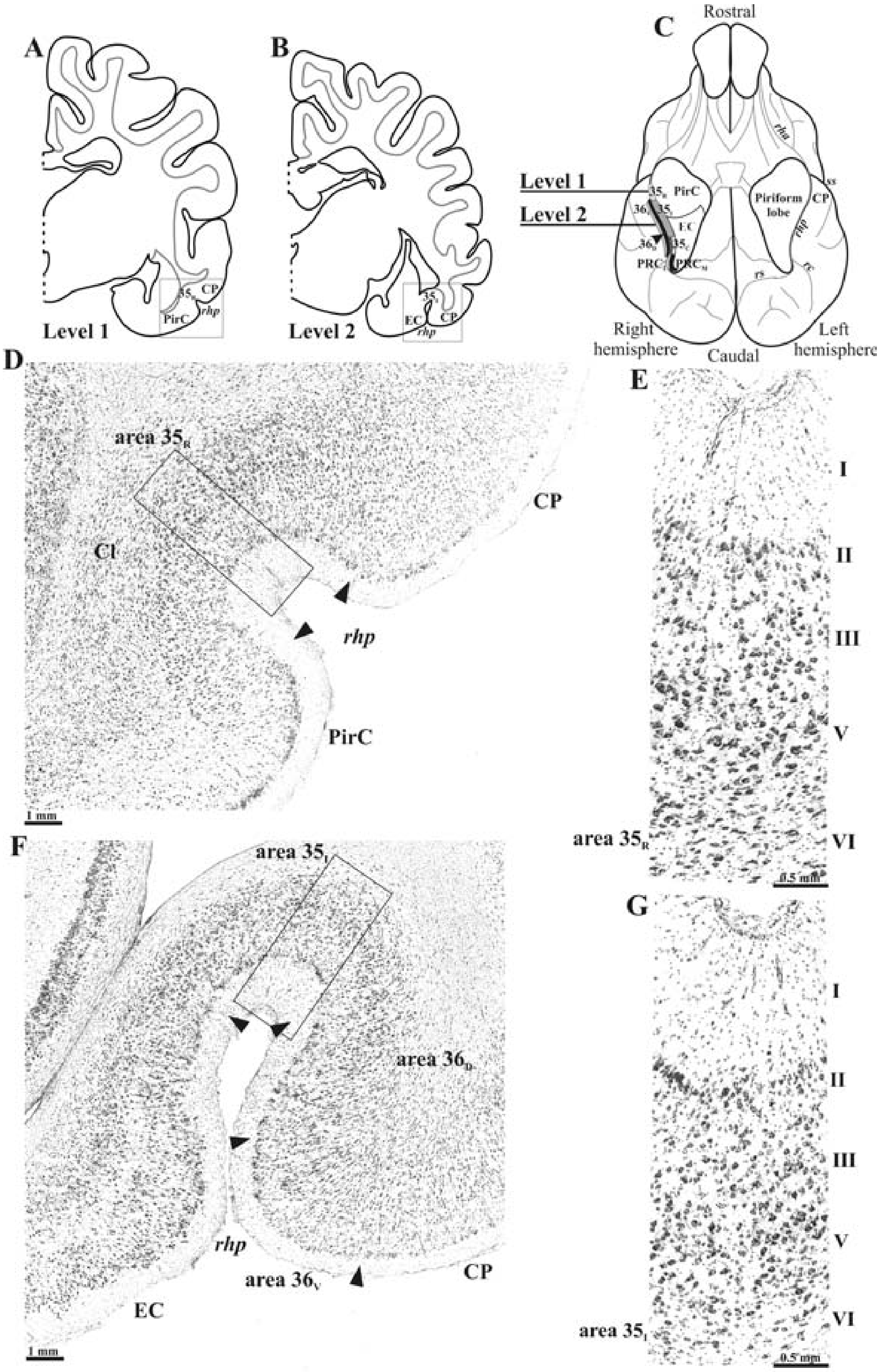

Fig. 2. Cytoarchitecture of the rostral (35_R) and intermediate (35_I) subdivisions of area 35 of the perirhinal cortex. A, B, two diagrams of the frontal sections showing location of areas 35_R and 35_I at the antero-posterior level 1 and 2, marked on the diagram of the ventral view of the brain in C. D, digital image of Nissl-stained coronal section showing location of area 35R and neighboring structures. Fragment of section is taken from part of tissue in square frame in diagram A. E, enlarged fragment of digital image delineated by frame in D, showing cytoarchitectonic features of area 35_R. F, digital image of Nissl-stained coronal section showing location of area 35_I and neighboring structures. Fragment of section is taken from part of tissue in square frame in diagram B. G, enlarged fragment of digital image delineated by frame in F, showing cytoarchitectonic features of area 35_I.

nal layers of the piriform cortex (Fig. 2D; see arrow). The border with the entorhinal cortex is marked by a cell-free gap corresponding to layer IV (lamina dissecans) of the entorhinal cortex and the lack of large neurons in layer V, characteristic of area 35 of the perirhinal cortex (Fig. 2F; see arrow).

More problematic is the lateral border between area 36 and the temporal and occipital lobes. In Nissl-stained sections, cytoarchitectonic features at the border between the perirhinal and neocortex change gradually through the gyral convolutions (Figs. 2F, 3C, 4C and 5C; see arrows). The posterior border of the perirhinal area is located at the caudal limit of the posterior rhinal sulcus, where it ramifies into the medially directed retrosplenial (*rs*) and laterally directed recurens (*rc*) sulci (Fig. 1).

In the depth of this most caudal limit of the rhinal sulcus, between area 35 and the entorhinal cortex, there is an additional small, so far unnamed gyrus which is occupied by the postrhinal cortex and can be named the postrhinal gyrus (PRG, see Fig. 5A,C). Caudally, the postrhinal cortex adjoins the retrosplenial cortex (Kreiner 1966) of the medial aspect of the hemisphere (RSC, see Fig. 5A).

Subdivisions of the perirhinal cortex and their cytoarchitectonic features

Area 35 is agranular cortex, which occupies mainly the fundus of the posterior rhinal sulcus and some parts of both walls of the rhinal sulcus. Common cytoarchitectonic features of area 35 are: a broad layer I, layer II with small, densely packed neurons, a narrow layer III consisting of medium-size, lightly stained cells, and a distinct layer V of large, darkly stained neurons. The number of these large, dark neurons decreases gradually along the antero-posterior axis of the posterior rhinal sulcus. Differentiation in cellular arrangement along this axis and additionally between its lateral and medial regions was the basis for subdivision of the area 35 into four subfields: rostral (35_R), intermediate (35_I) as well as caudal-medial (35_{CM}) and caudal-lateral (35_{CL}) (Fig. 1)

Area 35_R

The most anterior part of area 35_R occupies the whole depth of the posterior rhinal sulcus (Fig. 2A,D). This subdivision is bordered medially by the piriform cortex, and overlies the posterior claustrum. Laterally, 35_R is adjacent to the temporal sylvian cortex. Its posterior part extends into the medial bank of *rhp* and laterally adjoins 35_I. Area 35_R is distinguished by a wide layer I (Fig. 2E). Layer II is arranged into separate, densely packed clusters of small, darkly stained multiform and pyramidal neurons. Cells of the layer II extend into the layer III. Layer III is narrow and made up of medium-sized, sparsely distributed multiform, pyramidal and round cells. A very distinct layer V contains large, darkly stained multiform neurons. Small round and medium-sized multiform neurons of layer VI merge with the cells of the claustrum (Fig. 2D).

Area 35_I

This subdivision lies in the fundus of *rhp* and forms a distinct arc around this sulcus. Laterally, this area abuts area 36_D, and medially joins to 35_R. The most caudal portion of 35_I borders laterally on the entorhinal cortex (Fig. 2B,F). As in area 35_R, layer I of area 35_I is also wide (Fig. 2G). Layer II is well separated from layer III and contains two different populations of neurons. The medium-sized, darkly stained multiform neurons are arranged into distinct groups. Among these multiform cells, less numerous, smaller, lightly stained round neurons are seen. A well-differentiated layer III is slightly wider than in area 35_R. It contains medium-sized, dark, multiform and scattered pyramidal cells. Layer V is the most distinct in that area, being mainly composed of large and medium sized dark multiform neurons and single pyramidal cells. Layer VI is narrow but better differentiated than in area 35_R. There is no clear border with the white matter. Variously shaped neurons of this layer are smaller than in layer V, and oriented in different directions. Some of them, located in the deepest part of the layer, are oriented along the passing fibers.

Area 35_{CM}

Area 35_{CM} extends around a very deep fundus and medial bank of the most caudal part of *rhp*. This subdivision is situated laterally to the entorhinal cortex, and medially to the area 35_{CL} (Fig. 3A,C). The cortical thickness of area 35_{CM} tends to be narrow, and cells become smaller as one proceeds caudally (Fig. 3D). The cortical layers are not so clearly separated as in areas 35_I and 35_R. Area 35_{CM} has a very wide layer I. Layer II is rather thin and contains scattered, small clusters of darkly

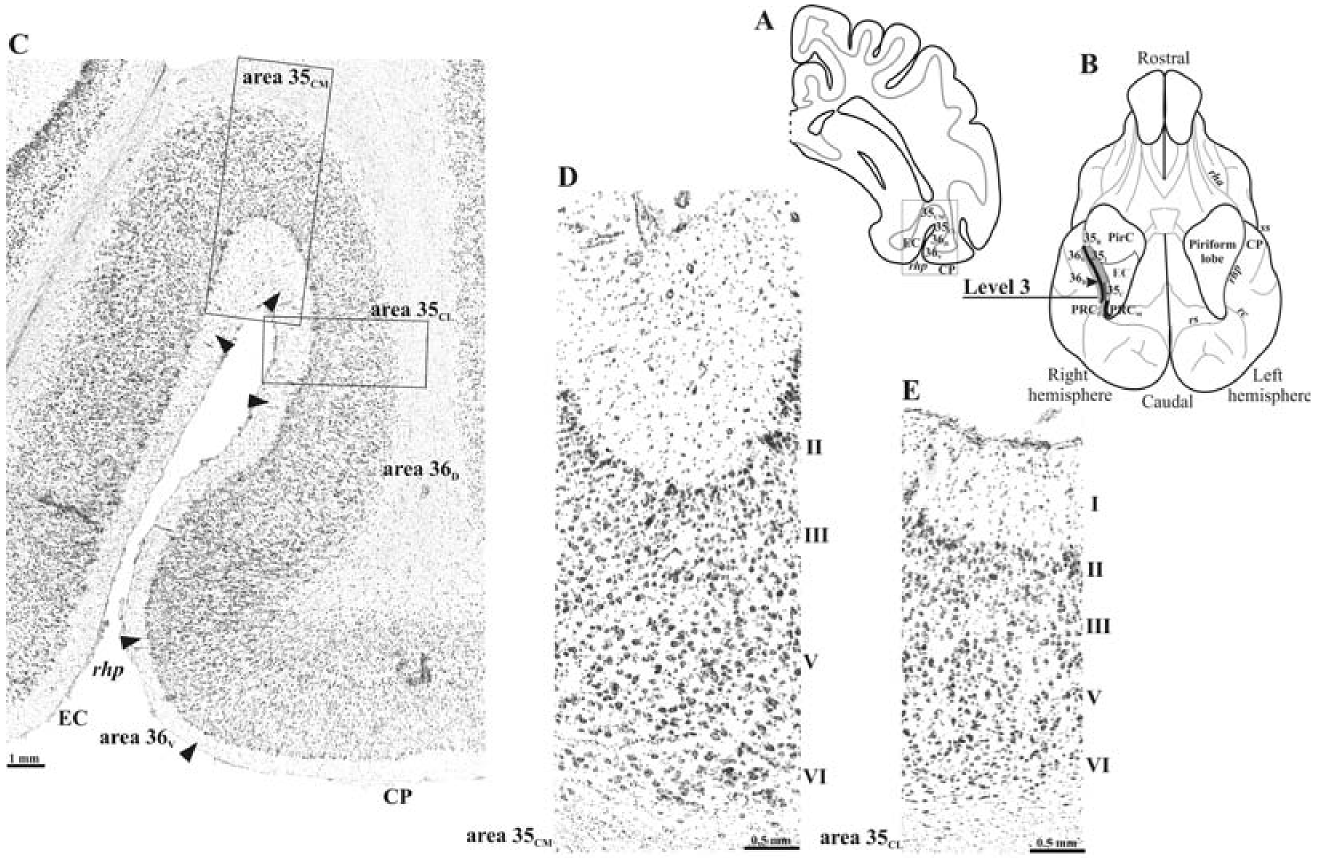

Fig. 3. Cytoarchitecture of the caudal-medial (35_{CM}) and caudal-lateral (35_{CL}) subdivisions of area 35 of the perirhinal cortex. A, diagram of the frontal section showing location of areas 35_{CM} and 35_{CL} at the antero-posterior level 3, marked on the diagram of the ventral view of brain in B. C, digital image of Nissl-stained coronal section showing location of areas 35_{CM} and 35_{CL} located in the fundus of the *rhp* and in the lateral bank of the sulcus, respectively. Fragment of section is taken from part of tissue in square frame in diagram A. D, enlarged fragment of digital image delineated by frame in C, in the fundus of *rhp*, showing cytoarchitectonic features of area 35_{CM}. E, enlarged fragment of digital image, delineated by frame in C in lateral bank of *rhp*, showing cytoarchitectonic features of area 35_{CL}.

stained, small, round and multiform cells. Both layers II and III are fused. Layer III is distinguished by the presence of small, fairly densely arranged round and multiform neurons. The border between layers III and V is unclear. Layer V is made up of predominantly multiform neurons, smaller than in area 35_I. Moreover, medium-sized round and single pyramidal neurons were observed in this layer. Layer VI is also fused with layer V and forms a sharp border with the white matter. It contains neurons of various shape and size, more densely packed than in area 35_I.

Area 35_{CL}

Area 35_{CL} is the most narrow among all subdivisions of area 35. This subfield is located in the lateral bank of the *rhp*, between area 35_{CL} and area 36_D (Fig. 3A,C). In comparison to the other subdivisions, it has a narrower layer I and less differentiated cortical layers containing small neurons of similar size (Fig. 3E). Clusters of darkly-stained cells are seen in layer II less frequently than in area 35_{CM}. There are no clear-cut borders between layers III, V and VI. Layer V can only be distinguished by the presence of slightly larger and darker cells in comparison to layers III and VI. Layer VI is very narrow and made up of similarly distributed but generally smaller neurons than in 35_{CM}.

Area 36

Area 36 adjoins the area 35 in the lateral bank on the posterior rhinal sulcus (Fig. 1). It appears more caudally

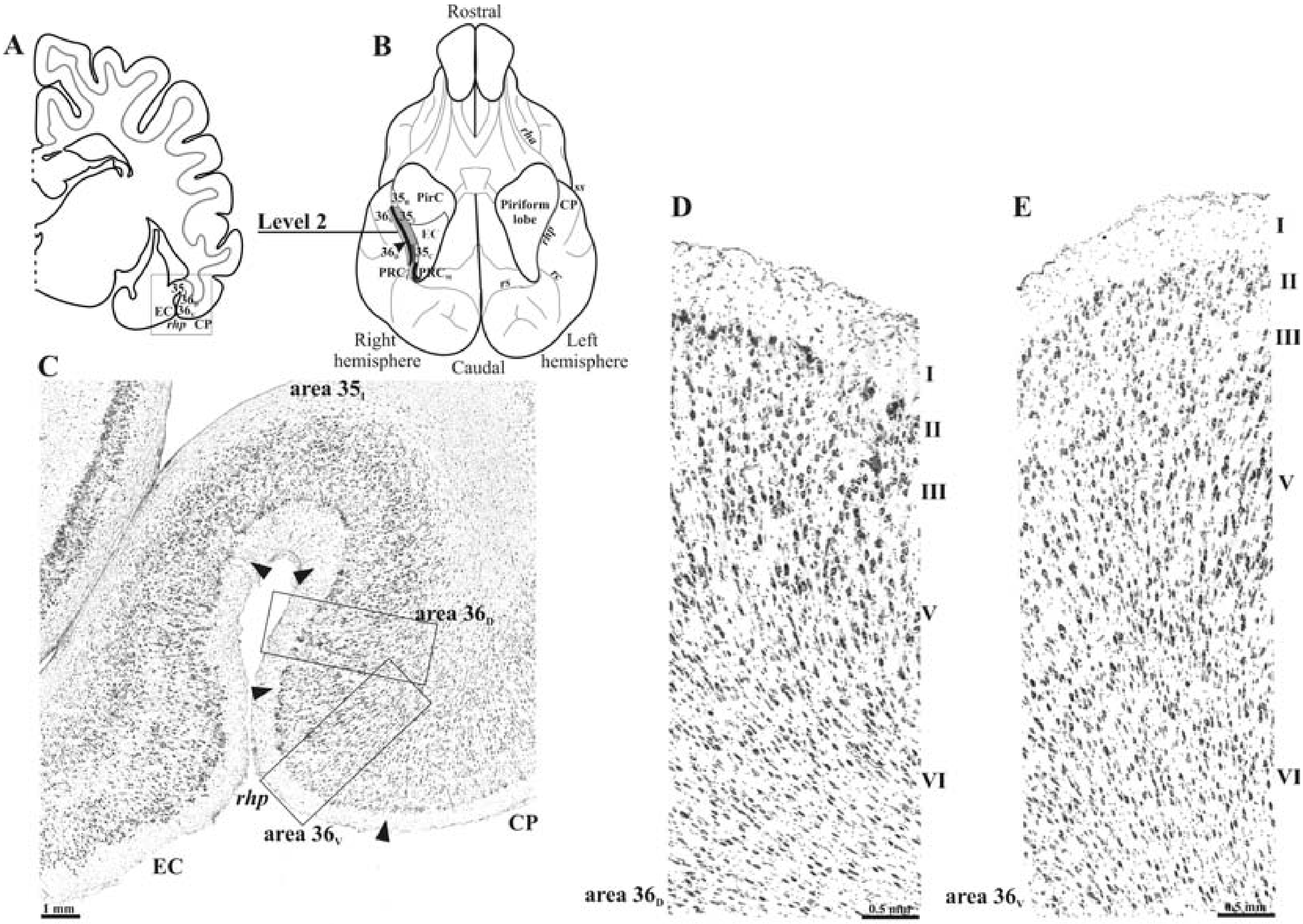

Fig. 4. Cytoarchitecture of the dorsal (36_D) and ventral (35_V) subdivisions of area 36 of the perirhinal cortex. A, diagram of the frontal section showing location of areas 36_D and 36_V at the antero-posterior level 2, marked on the diagram of the ventral view of brain in B. C, digital image of Nissl-stained coronal section showing location of areas 36_D and 36_V situated in the lateral bank of the *rhp*. Fragment of section is taken from part of tissue in square frame in diagram A. D, enlarged fragment of digital image delineated by upper frame in C, in lateral bank of *rhp*, showing cytoarchitectonic features of area 36_D. E, enlarged fragment of digital image, delineated by lower frame in C, in lateral bank of *rhp*, showing cytoarchitectonic features of area 36_V.

in comparison to area 35 and seems to be poorly developed in the dog's brain. Its border with area 35 is unclear in Nissl-stained sections, although it can be identified by increased total cortical thickness, due to the increased number of neurons in layers III and V. The border of area 36 with the temporal cortex of the posterior composite gyrus is also difficult to identify on account of cytoarchitectonic features. In general, the total thickness of the cortex and cell numbers in layers III and V keep increasing gradually in the temporal cortex and cortical layers are better differentiated. Area 36 can be divided into the dorsal (36_D) and ventral (36_V) cytoarchitectonic subdivisions.

Area 36_D

Area 36_D dorsally adjoins the area 35_I and ventrally borders with area 36_V (Fig. 4A,C). Its layer I is much more narrow than in all subdivisions of area 35 (Fig. 4D). A distinctive feature of 36_D is the presence of a clearly differentiated layer II. The dominant population in the layer consists of large, darkly stained multiform neurons grouped into well-separated clusters. Layer III is narrow and made up of sparsely arranged, medium-sized, lightly-stained pyramidal cells. Layer V contains slightly larger predominantly pyramidal cells than layer III. Between fused layers III and V a single, small, lightly-stained

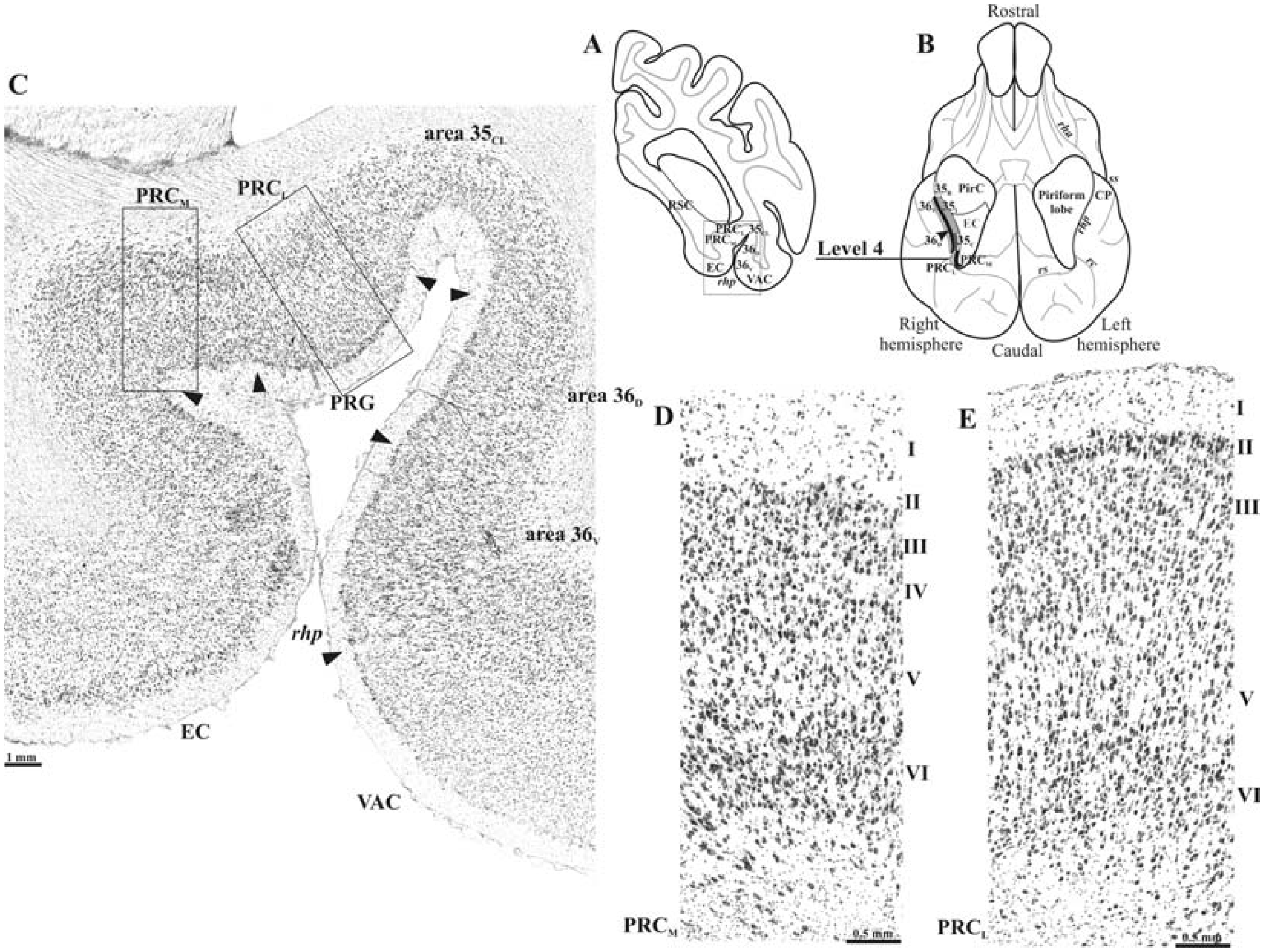

Fig. 5. Cytoarchitecture of the medial (PRC_M) and lateral (PRC_L) subdivisions of the postrhinal cortex. A, diagram of the frontal section showing location of areas PRC_M and PRC_L at the antero-posterior level 4, marked on the diagram of the ventral view of brain in B. C, digital image of Nissl-stained coronal section showing location of areas PRC_M and PRC_L situated in the additional postrhinal gyrus. Fragment of section is taken from part of tissue in square frame in diagram A. D, enlarged fragment of digital image delineated by frame in C, showing cytoarchitectonic features of area PRC_M. E, enlarged fragment of digital image, delineated by frame in C showing cytoarchitectonic features of area PRC_L.

nonpyramidal neurons are seen, but do not constitute a separate layer IV. A heterogeneous population of elongated neurons is present in layer VI with cells invading into the white matter deeper inside this layer. Neurons composing layers V and VI are arranged into oblique rows, parallel to passing fibers.

Area 36_V

Area 36_V is the ventral continuation of area 36_D, located on the convolution of the composite posterior gyrus (CP, see Fig. 4A,C). The main cytoarchitectonic peculiarity of area 36_V is a decreased number of neurons in layer II (Fig. 4E). Their density and size diminish significantly in the ventral direction. Multiform neurons of layer II are small, lightly stained and not well-separated from cells of layer III. Pyramidal neurons composing layer III are small and more sparsely distributed than in area 36_D. Layer IV is not clearly differentiated, but nonpyramidal cells are sparsely distributed between the pyramidal cells of lower layer III and upper layer V. Both layers V and VI are not clearly separated. They are composed of medium-sized pyramidal cells in layer V and smaller, elongated cells in layer VI. These cells show clear radial arrangement throughout the deeper cortical layers. Cells of layer VI invade deeply into the white matter.

Postrhinal cortex

The postrhinal cortex (PRC) is located between the most caudal extent of area 35_{CL} and the entorhinal cortex (Fig. 5A,C). Two subdivisions: the medial (PRC_M) and lateral (PRC_L) can be distinguished within the postrhinal cortex.

PRC_M

The medial subdivision of the postrhinal cortex is placed between PRC_L and the most posterior part of the entorhinal cortex (Fig. 5C). A distinctive feature of PRC_M is the laminar appearance of its densely packed, generally medium-size neurons in the layer VI (Fig. 5D). Layer I is wide because of an additional sulcus. Layer II is made up of small, mainly round neurons, less densely packed than in the neighboring subdivisions. A few pyramidal cells can be seen among the round cells. Layer II is not clearly separated from layer III. Layer III contains small pyramidal neurons, comparable in size to neurons of layer II. Layer IV is seen as a gap between layers II and V, and is made up of lightly-stained nonpyramidal neurons and dark, less numerous pyramidal cells. Layer V is well-developed and has a distinct bilaminate appearance. Its upper part is made up of small and medium-size, densely packed pyramidal cells. The lower part contains more sparsely distributed, similar in size pyramidal cells, which seem to be slightly larger in the deepest part of the layer. The most distinct feature of PRC_M is the structure of the prominent layer VI. It can be distinguished by the presence of a heterogeneous population of densely packed, medium-size neurons of various shape. Cells in the deepest part of the layer invade into the white matter.

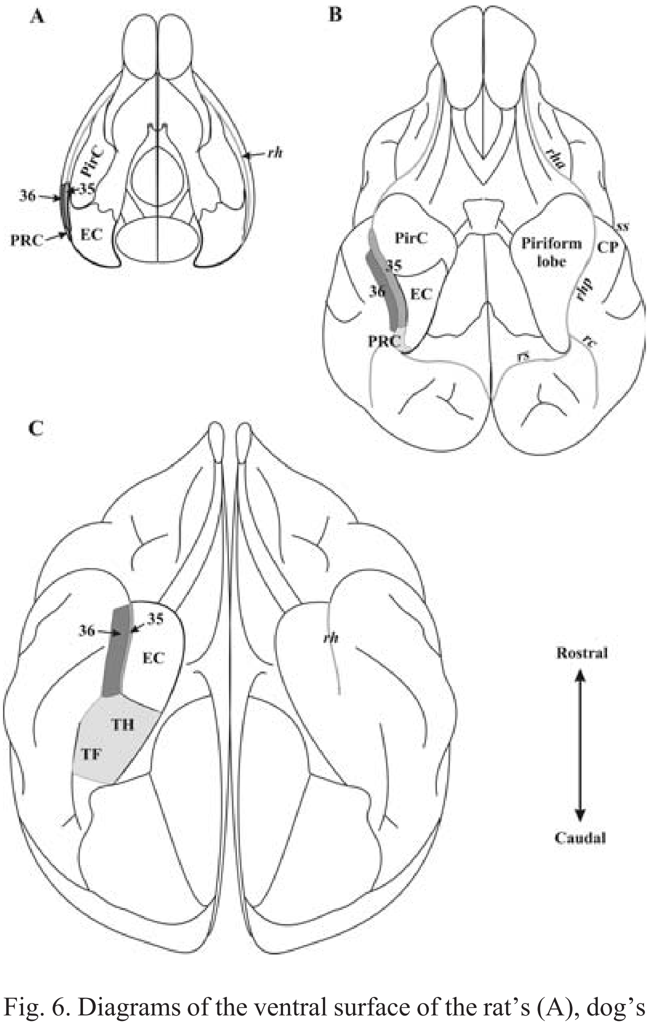

Fig. 6. Diagrams of the ventral surface of the rat's (A), dog's (B) and monkey's (C) brains illustrating placement of the perirhinal, postrhinal and parahippocampal cortices.

PRC_L

The lateral subdivision of the postrhinal cortex borders on area 35_{CL} and medially adjoins PRC_M (Fig. 5A,C). This subfield has a distinct radial pattern and laminar organization of cortical layers. Layer I is narrow (Fig. 5E). The only distinct part is the layer II with densely packed, homogeneously distributed darkly-stain, medium-size multiform and pyramidal neurons. Smaller, lightly stained cells are scattered among them. Layer III is wider and clearly separated from layer II in comparison to PRC_M. It is composed of homogeneously arranged, small pyramidal cells. The border between layers III and V is not clear, as the neurons are similar in size and arrangement. In lower part of layer V neurons are slightly more scattered. At the border with layer VI, slightly larger pyramidal cells are observed. Layer VI is fused with layer V. However, it can be distinguished on account of a more heterogeneous population of neurons. The cells of layer VI, diversified in shape and size, are oriented in various directions. Some of them invade into the white matter.

DISCUSSION

Cytoarchitectonic features of the canine perirhinal cortex have not been examined until now, except for a brief description of its general division in Kowalska et al. (2001). Detailed observations of the perirhinal cortex in Nissl-stained sections revealed its remarkable cellular differentiation along the antero-posterior axis of the posterior rhinal sulcus. In keeping with a recent division in the other species (Burwell 2001, Burwell et al. 1995, Deacon et al. 1983, Room and Witter 1985, Suzuki 1996a,b, Suzuki and Amaral 1994a,b) it has been roughly divided into Brodmann's (1909) areas 35 and 36 and the postrhinal cortex. The name "postrhinal cortex" is adopted by us by analogy with the rat's brain (Burwell et al. 1995, Deacon et al. 1983), and it corresponds to areas TH and TF of the monkey's parahippocampal cortex (Murray and Bussey 1999). Area 35 occupies the entire rostro-caudal extent of the posterior rhinal sulcus. The anterior border of area 36 is seen slightly more caudally in relation to area 35. The postrhinal cortex, like in other species, is located in the most posterior part of the perirhinal cortex. However, it seems to be placed more medially in comparison to other species. This is associated with a distinct pattern of sulci in this most caudal part of the canine brain. Based on the differentiation of cellular arrangement within the two areas, further subdivisions can be distinguished. Area 35 has four cytoarchitectonic subdivisions. Area 36 seems to be much less developed than area 35 and only two subdivisions were identified.

Comparison of the location of the perirhinal and postrhinal cortex

There are substantial differences in the location of the perirhinal cortex in relation to the rhinal sulcus between subprimates and primates. In subprimates the perirhinal cortex occupies only the posterior part of the sulcus (Fig. 6A,B), whereas in primates it occupies the entire rostro-caudal extent of a much reduced rhinal sulcus (Fig. 6C). In the rat, the continuous rhinal sulcus is not divided into the anterior and posterior parts. The anterior is occupied by the insular cortex and was defined as overlying the claustrum, whereas the posterior part of the rhinal sulcus contains the perirhinal cortex (Burwell et al. 1995, Deacon et al. 1983, Krieg 1946, Rose 1929, Swanson 1992). As the sulcus is continuous, the border between insular and perirhinal cortex has been variously designated by authors in the rostro-caudal extent of the sulcus. In general, the insular cortex in various species has been defined as overlying the claustrum (Rose 1928). Accordingly, the anterior border of the perirhinal cortex corresponded to the caudal limit of the claustrum. In the cat and dog, the anterior and posterior parts of the rhinal cortex are approximately separated by the sylvian sulcus (*ss*, see Fig. 1). Well-developed insular cortex occupies both the anterior and sylvian cortices (Clascá et al. 1997), whereas, the perirhinal cortex occupies its caudal part. In the dog, this anterior border of the perirhinal cortex is somewhat different, overlapping the most caudal part of the claustrum (Fig. 2D) and additionally covered by a well-developed operculum of the temporal neocortex (not illustrated).

Some peculiarity of location of the perirhinal and postrhinal areas in the dog's brain is related to the unique pattern of the rhinal sulcus. The spatial arrangement of anterior areas of the canine perirhinal cortex resembles that observed in the rat (Fig. 6A,B). The canine anterior perirhinal cortex, like that in the rat (Burwell 2001), is situated on the lateral surface of the brain, and its subdivisions are arranged one over another (ventro-dorsally) (Fig. 2C). On the other hand, the caudal part of the canine rhinal sulcus is located on the ventral aspect of the brain, with individual subdivisions related latero-medially like in monkey (Murray and Bussey 1999). The most complicated are spatial relations in the most caudal part of the sulcus, where the postrhinal cortex was distinguished. The postrhinal cortex is dived in the rhinal sulcus and was recognized within the additional postrhinal gyrus forming in the depth of this sulcus.

The lateral border of the perirhinal cortex is situated on the convolution of the composite posterior gyrus and unclear from the cytoarchitectonic point of view. Generally, there is gradual change in the cellular arrangement from the area 36_V to the temporal neocortex. This border can be recognized by the more clearly differentiated laminar organization in the neocortex. The most distinct is the medial border of the perirhinal area 35_I with the entorhinal cortex. It is marked by disappearance of the prominent layer V characteristic of area 35 and a well visible lamina dissecans of the entorhinal cortex. The border was especially clear in the Timm (Woźnicka et al. 2001) and parvalbumin immunostaining (Woźnicka and Kosmal 2003).

Cytoarchitectonic characteristics of the perirhinal and postrhinal cortex

Area 35 in the dog's brain shows some remarkable similarities in general cellular organization in comparison to that in the rat and monkey (Burwell et al. 1995). Among them are broad layer I, sparsely distributed cells of layer II and especially prominent layer V. In spite of these similarities, there are specific species-related differences. Layer II in the dog is composed of at least two populations of neurons. One consists of large, darkly stained multiform cells, while the other has smaller, round cells, some of which appear pyramidal-shaped. The number of these large dark cells increases gradually along the antero-posterior axis of area 35. These large, dark multiform cells gradually increase in number in the caudal direction to form distinct clusters in area 35_{I}. These clusters are, however, less sparsely distributed than in area 36. A prominent layer V forms an arc around the fundus of *rhp*, similar to that found in other species. A specific canine feature is a clear decrease in the size of cells composing layer V, from anterior to posterior end. Immunostaining for parvalbumin reveals the predominant population of cells in layer V to be multiform but not pyramidal type (Woźnicka and Kosmal 2003).

Within canine area 36 a cytoarchitectonic feature common to other species is the dense distribution of cell clusters in layer II and more prominent radial organization of the cortex. However, the appearance of layer II is mainly seen in area 36_{D}, because in 36_{V} a reduction in the number of these clusters towards the temporal neocortex was observed. However, the radial pattern in cortical layers is more pronounced in area 36_{V}. In addition, as area 36_{V} is located on the convolution of the gyrus, neurons of layer VI deeply invade into the white matter.

The postrhinal cortex in the dog identified between the most posterior extents of area 35_{CL} and entorhinal cortex, like that in the monkey brain, can be differentiated into two subdivisions. A common cytoarchitectonic feature showing some correspondence of area TH (Van Hoesen 1982) and the postrhinal cortex in the dog is the special appearance of layers II/III. As in the monkey, layer II is made up of a fairly homogeneous population of round cells (Burwell et al. 1995). The other common features are prominent deep layers of PRC_{M} with darkly stained neurons and numerous granular cells within this part of the cortex. However, in contrast to that, in the monkey's brain more granular cells are situated within the more laterally localized area TF. In the dog, the division of cytoarchitectonic features of the postrhinal cortex into two subdivisions is mainly related to the appearance of the additional postrhinal gyrus. For further comparison between species, the cytoarchitectonic division of the canine postrhinal cortex needs to be supported with data on the distribution of specific connections characteristic of individual subdivisions.

ABBREVIATIONS

35_{R} - rostral area 35 of the perirhinal cortex
35_{I} - intermediate area 35 of the perirhinal cortex
35_{CM} - caudal-medial area 35 of the perirhinal cortex
35_{CL} - caudal-lateral area 35 of the perirhinal cortex
36_{D} - dorsal area 36 of the perirhinal cortex
36_{V} - ventral area 36 of the perirhinal cortex
Cl - claustrum
CP - posterior composite gyrus
EC - entorhinal cortex
PC - perirhinal cortex
PirC - piriform cortex
PRG - postrhinal gyrus
rc - recurens sulcus
rh - rhinal sulcus
rha - anterior rhinal sulcus
rhp - posterior rhinal sulcus
rs - retrosplenial sulcus
RSC - retrosplenial cortex
ss - sylvian sulcus
TF - subdivision of the parahippocampal cortex
TH - subdivision of the parahippocampal cortex
PRC - postrhinal cortex
VAC - visual association cortex
PRC_{L} - lateral postrhinal cortex

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