COMMENTARY

Perirhinal and Postrhinal Cortices of the Rat: A Review of the Neuroanatomical Literature and Comparison With Findings From the Monkey Brain

Rebecca D. Burwell,[1] Menno P. Witter,[2] and David G. Amaral[1]

[1]*Center for Behavioral Neuroscience, SUNY at Stony Brook, Stony Brook, New York.* [2]*Department of Anatomy and Embryology, Research Institute of Neurosciences, Vrije Universiteit, Graduate School of Neurosciences Amsterdam, Amsterdam, The Netherlands*

INTRODUCTION

This review is prompted by recent findings that the perirhinal and parahippocampal cortices in the monkey brain are important components of the medial temporal lobe memory system. Given the potential importance of the comparable regions to memory function in the rat brain, it is surprising that so little is known about their neuroanatomy. In fact, there are no comprehensive studies of the borders, cytoarchitecture, or connections of the cortical regions surrounding the posterior portion of the rhinal sulcus in the rat. This review is meant to summarize the current state of our knowledge regarding these regions in the rat brain. Based on existing data and our own observations, a new terminology is introduced that retains the term *perirhinal cortex* for the rostral portion of the region and renames the caudal portion the *postrhinal cortex*. Issues of continuing uncertainty are highlighted, and information gleaned from the monkey literature is used to predict what anatomical traits the rat perirhinal region might demonstrate upon further examination. To the extent possible with available data, the similarities and differences of the rat and monkey perirhinal, postrhinal, and parahippocampal regions are evaluated.

WHAT'S IN A NAME?

Historically, Brodmann (1909) illustrated three distinct cytoarchitectonic regions near the rhinal sulcus in primates: area 28 (area *entorhinalis*), area 35 (area *perirhinalis*), and area 36 (area *ectorhinalis*). He did not dis-

tinguish the cortex situated caudal to these regions from the pre-striate cortex (areas 19 and 20). Von Bonin and Bailey (1947), however, noted that the cortex lying lateral to the hippocampus, in the parahippocampal gyrus, was distinct from prestriate cortex and designated two areas, TF and TH, in this region.

What are these regions called in the rodent? Rose (1929) applied Brodmann's terminology to the mouse brain and illustrated area 28, area 35, and area 36 (Fig. 1A). Rose did not further subdivide these cortical regions, nor did he indicate a region that might be homologous to areas TF and TH. Krieg (1946b) also used Brodmann's numerical terminology in his cortical map of the rat, although his boundaries differed substantially from Rose's, especially for areas 35 and 36 (Fig. 1B). The entire region was located more caudally than in Rose. This is because the rostrally adjacent area 13 (insular cortex) extended farther caudally, substantially beyond the caudal limit of the underlying claustrum. As in Rose's nomenclature, Krieg did not indicate a separate region homologous to TF and TH. More recently, Deacon et al. (1983) illustrated the perirhinal cortex in the rat essentially according to Krieg but noted that the cytoarchitectonic and connectional attributes differed along the rostrocaudal axis. This prompted them to subdivide the rostral portion of perirhinal cortex and to name the more posterior portion the postrhinal cortex (Fig. 1C). Deacon et al. (1983) also illustrated a distinct ectorhinal cortex located dorsal to the postrhinal cortex. Again, there was no explicit attempt on the part of Deacon et al. (1983) to homologize either the postrhinal cortex or the ectorhinal cortex with areas TF and TH in the monkey brain. Although these and other descriptions of the rat perirhinal region recognize distinct perirhinal and ectorhinal cortices (areas 35 and 36, respectively), there has been no mention of cortex in the

A Rose, 1929

B Krieg, 1946

C Deacon, et al., 1983

D Zilles and Wree, 1985

E Paxinos and Watson, 1986
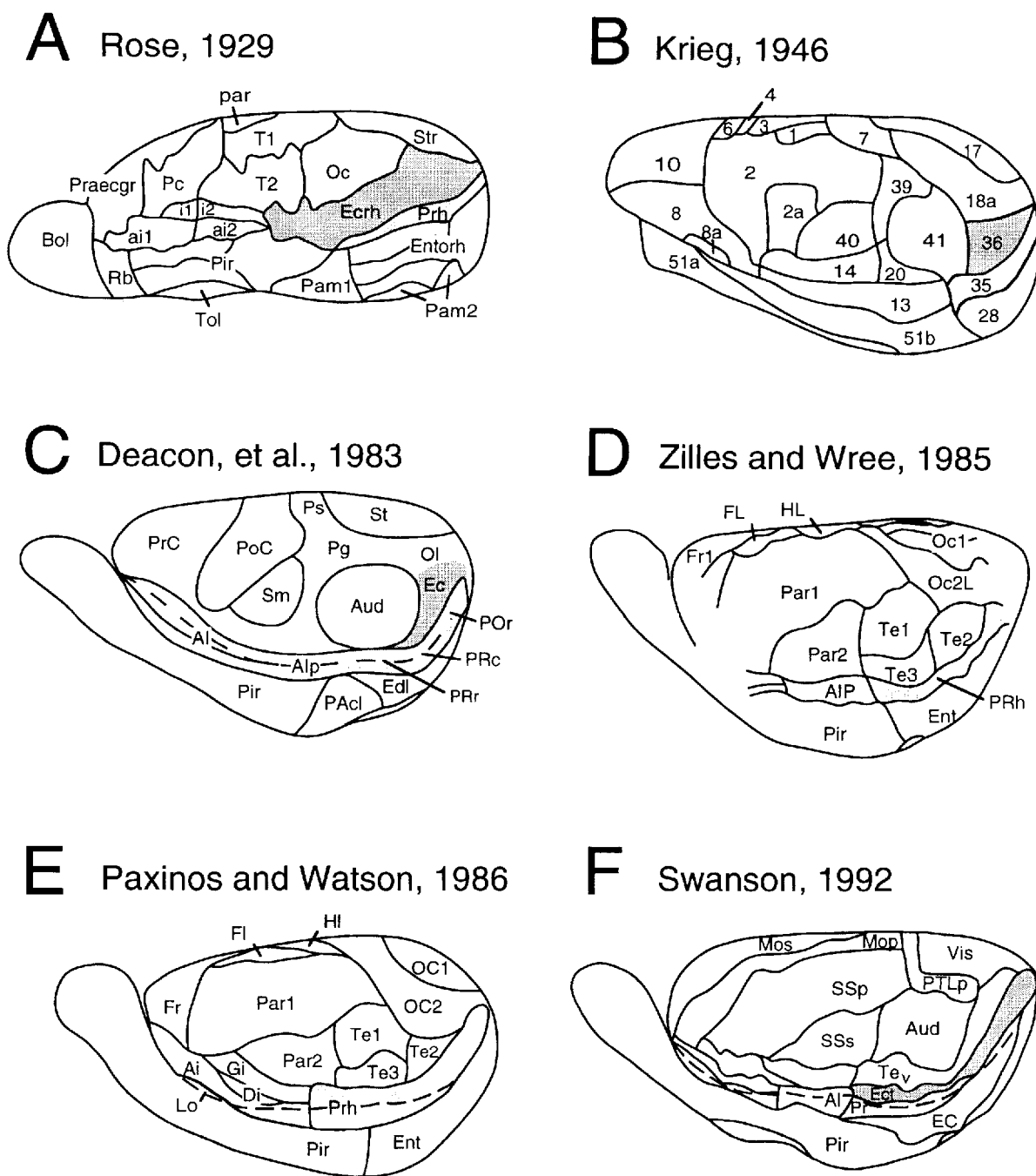
F Swanson, 1992

FIGURE 1.   A–F. Surface maps of the rodent cortex adapted from six neuroanatomical reports cited in this commentary. Except for A, which shows a surface map of the mouse brain, the maps show regional definitions of the cortical mantle for the rat brain. For each map, the region comparable to area 36 is shown in dark gray, and the region comparable to area 35 is shown in light gray. Note that no region comparable to area 36 is indicated in the surface maps in D and E. Essential abbreviations: Ecrh or Ec, ectorhinal cortex; Prh, perirhinal cortex; PRr and PRc, rostral and caudal perirhinal cortex; POr, postrhinal cortex.

rat brain similar to areas TF and TH in the monkey parahippocampal gyrus.

Before moving on to a more detailed description of the position and borders of the various perirhinal regions, some additional common usages of the terms perirhinal and parahippocampal should be addressed. In modern usage, the term perirhinal now refers to both perirhinal and ectorhinal cortices, and the term ectorhinal has largely been eliminated. Thus, Amaral et al. (1987) refer to the combination of areas 35 and 36 in the macaque monkey brain as the perirhinal cortex. The term parahippocampal has also had numerous usages. As noted above, parahippocampal refers to the gyrus in the macaque monkey that borders the hip-

pocampal formation. Amaral et al. (1987) have used the term parahippocampal cortex to encompass areas TF and TH, which make up the larger portion of the parahippocampal gyrus. Based on work carried out in the cat, but later applied to the rat and monkey brain, Witter et al. (1989a) used the term parahippocampal region as synonymous with retrohippocampal region and included the entorhinal and perirhinal cortices, the pre-subiculum and parasubiculum, and areas TF and TH. Van Hoesen (1982) used the term parahippocampal gyrus to represent essentially the same regions as in the parahippocampal region of Witter et al. (1989a) with the addition of primary olfactory cortex (area 51). According to this terminology, the entorhinal cortex makes up the major portion of the anterior parahippocampal gyrus, whereas areas TF and TH make up the major portion of the posterior parahippocampal gyrus. Finally, the term rhinal cortex was introduced by Murray and Mishkin (1986) to designate the region encompassing the entorhinal and perirhinal cortices in the monkey. This term has also been used for this region in the rat (Mumby and Pinel, 1994). While these inclusive terms may be useful shorthand designations in lesion and behavioral studies, they can be misleading if taken to imply neuroanatomical homogeneity. The entorhinal cortex, for example, is distinctly different from the neighboring perirhinal and parahippocampal cortices by virtue of its cytoarchitectonic, chemoarchitectonic, and connectional characteristics.

Our observations indicate that none of the existing terminologies for the cortical regions surrounding the posterior rhinal sulcus in the rat accurately delimit the full extent of the perirhinal cortex or capture the cytoarchitectonic, histochemical, and connectional heterogeneity of this region (see Table 1 for a summary of existing terminologies). We wish to encourage the use of the term perirhinal to encompass areas 35 and 36 in the monkey and rostral areas 35 and 36 in the rat and the terms parahippocampal to designate areas TF and TH of the monkey brain and postrhinal to designate a region that includes caudal areas 35 and 36 in the rat (Fig. 2).

WHERE ARE THE PERIRHINAL AND POSTRHINAL CORTICES?

As will become apparent, there is a remarkable lack of consensus regarding the boundaries and subdivisions of the regions surrounding the rhinal sulcus in the rat (Figure 1). The position and boundaries of the monkey perirhinal and parahippocampal cortices are first summarized before continuing to the more contentious rat literature.

In the monkey brain, the perirhinal cortex is laterally adjacent to the full rostrocaudal extent of the rhinal sulcus (Fig. 2A). Area 35 is a narrow band of agranular cortex situated primarily in the fundus and lateral bank of the rhinal sulcus (Suzuki and Amaral, 1994a). Area 36 is a larger strip of granular cortex located lateral to area 35 and bordered laterally by the unimodal visual area TE of inferotemporal cortex. Based on cytoarchitectonic and connectional grounds, Suzuki and Amaral (1994a) extended area 36 rostrally and dorsally to include the medial half of the temporal pole (area TG according to von Bonin and Bailey, 1947). These authors also described the border between area 36 and area TE as occurring more laterally than was previously appreciated. The parahippocampal cortex is caudally adjacent to the perirhinal cortex (Fig. 2A). Area TH is a thin strip of cortex caudal to the parasubiculum and entorhinal cortex. Area TF is larger and is laterally adjacent to TH. The region's lateral border is with the caudal continuation of area TE, i.e., area TEO.

One obvious difference between the rat and monkey is that, in the rat, the perirhinal cortex occupies only caudal levels of the rhinal sulcus, whereas, in the monkey, the perirhinal cortex borders the full rostrocaudal extent of the rhinal sulcus (Fig. 2). Otherwise, the spatial relationships among these regions are similar for the two species. Entorhinal cortex, area 35, and area 36 lie adjacent to each other in the ventrodorsal plane in the rat and the mediolateral plane in the monkey. The postrhinal cortex in

TABLE 1.

Terminology for Cortical Regions Surrounding the Rhinal Sulcus*

Reference	Area 35		Area 36		Postrhinal	
	−2.50 to −4.50	−4.50 to −7.80	−2.50 to −4.50	−4.50 to −7.80	(Ventral)	(Dorsal)
Rose (1929)	Perirhinalis	Perirhinalis	Ectorhinalis	Ectorhinalis	Perirhinalis	Ectorhinalis
Kreig (1946a,b)	Caudal 13	Area 35	Caudal 14	20, Vent. 41	Area 35	Area 36
Deacon et al. (1983)	Caudal AIp	Perirhinal	Caudal AIp	Ectorhinal	Postrhinal	Ectorhinal
Zilles and Wree (1985)	Caudal AIp	Perirhinal	Caudal AIp	Vent. Te3/2	Perirhinal	Caudal Te2
Paxinos & Watson (1986)	Perirhinal	Perirhinal	Perirhinal	Vent. Te3/2	Perirhinal	Caudal Te2
Swanson (1992)	Perirhinal	Perirhinal	Ectorhinal	Ectorhinal, Vent. Te$_v$	Ectorhinal	Ventral Te$_v$

*Areas 35 and 36 are divided into anterior (−2.50 to −4.50 mm) and posterior (−4.50 to −7.80 mm) portions relative to bregma.

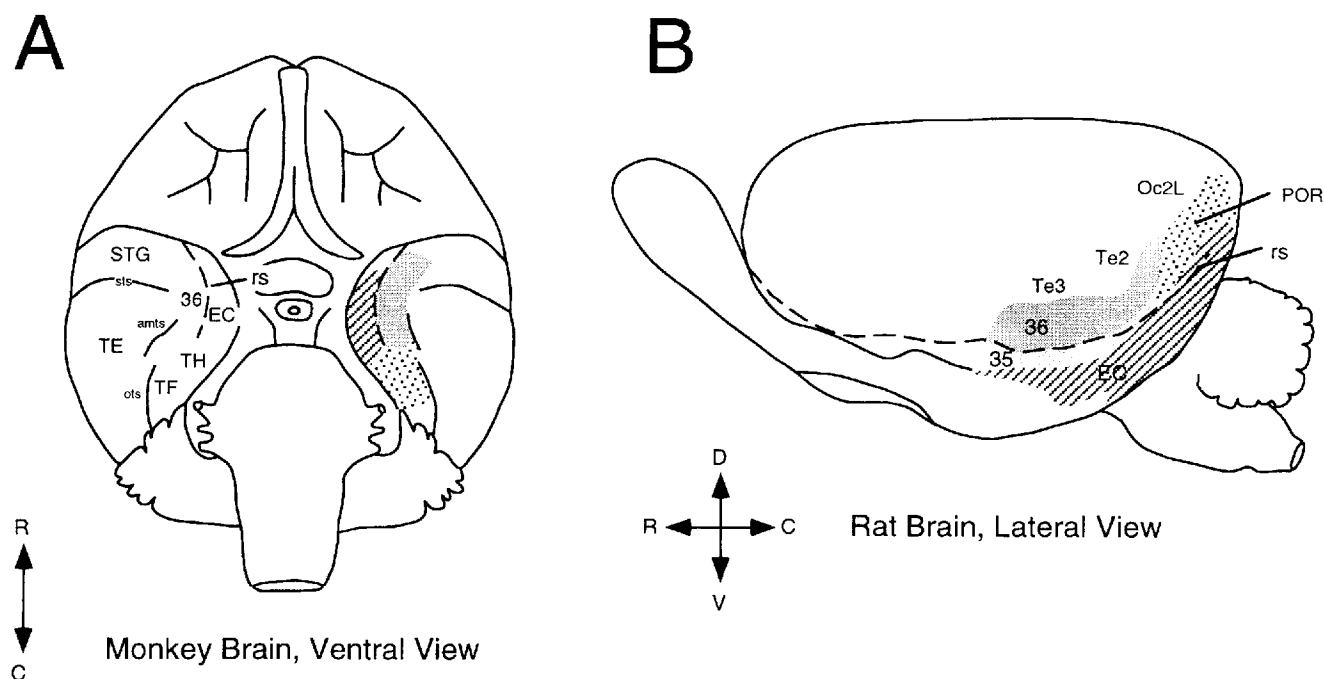**A** Monkey Brain, Ventral View

B Rat Brain, Lateral View

FIGURE 2.   A ventral surface view of the monkey brain adapted from Suzuki and Amaral (1994, A) and a lateral surface view of the rat brain (B) showing borders of the entorhinal, perirhinal, and parahippocampal/postrhinal cortices as described in this review. Perirhinal cortex is shown in gray (area 36 in dark gray and area 35 in light gray), parahippocampal/postrhinal cortices in mottled shading, and the entorhinal cortex (EC) in diagonal stripes. Note that area 35 in the monkey, which is buried in the depths of the rhinal sulcus, is not visible in this ventral view. Abbreviations: amts, anterior middle temporal sulcus; ots, occipitotemporal sulcus; rs, rhinal sulcus; STG, superior temporal gyrus; areas TH, TF, and TE of von Bonin and Bailey (1947); Te3 and Te2, temporal cortex; Oc2L, secondary visual cortex.

the rat and the parahippocampal cortex in the monkey are located caudal to the perirhinal and entorhinal cortices.

The perirhinal and postrhinal cortices in the rat have clearly proven difficult to demarcate based purely on cytoarchitectonic criteria. In fact, the two most widely cited historical resources for regional definitions of the cortex of the rat (Rose, 1929; Kreig, 1946a) differ substantially with regard to their placement of the boundaries of perirhinal cortex (Fig. 1A and B, respectively). According to Rose, the perirhinal cortex is a long but narrow strip of cortex extending along the posterior half of the rhinal sulcus. He also illustrated a fairly wide ectorhinal cortex that was situated just dorsal to the perirhinal area. As is evident in Figure 1B, Krieg's (1946a) area 35 and 36 occupy only the caudal portion of Rose's perirhinal and ectorhinal regions.

Modern workers continue to vary in their placement of the boundaries of these cortical areas. Zilles et al. (1980), employing quantitative cytoarchitectonic techniques, defined perirhinal cortex as a transitional area lying in the fundus of the rhinal sulcus (Fig. 1D). This relatively narrow region was interposed between entorhinal cortex, ventrally, and cortical area Te2, dorsally. Although Zilles did not illustrate a distinct area 36, his temporal regions Te2 and Te3 were said to include portions of areas 20, 41, and 36 of Krieg (Zilles, Wree, 1985). Paxinos and Watson (1986) illustrate the perirhinal cortex as occupying a band of cortex broader than that of Zilles and Wree (1985) lying within the

fundus and along the dorsal bank of the rhinal sulcus for approximately the caudal half of the rhinal sulcus (Fig. 1E). Swanson's (1992) designation of the perirhinal and ectorhinal cortices is much like that of Rose (Fig. 1F). Swanson, however, suggested that the dorsal part of Rose's ectorhinal cortex, where layer IV is more apparent, corresponds to temporal association cortex in humans, and should thus be separated from agranular ectorhinal cortex. This region was designated ventral temporal association cortex (Te$_v$) by Swanson (1992).

The regional delimitation of the perirhinal and ectorhinal cortex has varied largely because there is little agreement concerning the definition of the borders of these regions with adjacent cortical areas. In fact, the rostral border of the perirhinal cortex with the insular cortex varies by several millimeters along the rostrocaudal axis from author to author. This is due, in part, to differing definitions of the insular cortex. As classically defined by Rose (1928; Fig. 1A) in the human, monkey, and rodent, the insular cortex overlies the claustrum. Thus, a number of neuroanatomists have adopted the caudal limit of the claustrum as a convenient landmark for the boundary between the insular and perirhinal cortices. Of the maps shown in Figure 1, those by Paxinos and Watson, Zilles and Wree, and Swanson follow Rose's lead in this regard (see also Krettek, Price, 1977c; Cechetto and Saper, 1987). Krieg (1946a; Fig. 1B), in contrast, asserted that "regarding the insula as coextensive with the cortex which overlies the claustrum,

though a convenient criterion, is a specious one," and he placed the insular-perirhinal border more caudally than Rose. Deacon et al. (1983, Fig. 1C) adhered to Krieg's suggestion (see also Miller and Vogt, 1984; Turner and Zimmer, 1984). Regarding the ventral border of the perirhinal cortex and postrhinal cortex, there is again some difference of opinion. Some investigators show the entorhinal cortex as situated entirely ventral to the rhinal sulcus throughout its full rostrocaudal extent (Kreig, 1946a; Kosel, 1981; Deacon et al., 1983; Zilles and Wree, 1985; Paxinos, Watson, 1986). Others, however, indicate that the caudal entorhinal cortex not only occupies the fundus of the rhinal sulcus, but also encompasses its dorsal bank (Swanson, 1992; Dolorfo and Amaral, 1993). The dorsal borders of the perirhinal and postrhinal cortices are even more problematic. At one extreme, Zilles and Wree (1985) illustrate a very narrow perirhinal cortex bordered dorsally by areas Te3 and Te2. At the other extreme, Rose (1929) illustrates a very broad ectorhinal cortex dorsal to perirhinal cortex, which extends to primary auditory and visual areas. As noted above, Swanson (1992) divides the ectorhinal region of Rose into a ventral ectorhinal region and a dorsal "associational" cortex called ventral temporal association cortex. Again, the cytoarchitectonic characteristics of this region in the rat brain provide insufficient criteria for easily, or at least consistently, setting boundaries between cortical areas. The posteromedial border of the postrhinal cortex is generally not addressed in descriptions of the perirhinal and postrhinal cortex. Our own observations suggest that the retrosplenial region borders the postrhinal cortex.

There is obviously little consensus about the boundaries of the perirhinal and postrhinal cortices in the rat. Clearly, without concise demarcation of the borders and subdivisions of these regions in the rat, it will be difficult to accurately assess their contribution to memory. How does one define cortical boundaries? Classically, the definition of a cortical area was based almost exclusively on cytoarchitectonic criteria. Modern neuroanatomical approaches, however, rely on both cytoarchitectonic and connectional data as well as on chemical neuroanatomical information concerning the region of interest. When all of these neuroanatomical approaches are applied to the perirhinal and postrhinal cortices, a much clearer picture of its organization is produced. In the following sections, we review the available cytoarchitectonic, chemoarchitectonic, and connectional data of the perirhinal and postrhinal cortices in the rat.

WHAT ARE THE CYTOARCHITECTONIC CHARACTERISTICS OF THESE REGIONS?

A casual survey of photomicrographs through the perirhinal cortex in the macaque monkey (Fig. 3A) and the rat (Fig. 3B) is sufficient to appreciate that these cortices are substantially wider and more distinctly laminated in the monkey. In this section, the general cytoarchitectonic characteristics of the perirhinal and parahippocampal/postrhinal cortices in the monkey and rat are summarized and evaluated for areas of common features in the two species. For the rat, data are also surveyed from a variety of

histochemical or immunohistochemical preparations that lend additional confirmatory data concerning the proposed boundaries and subdivisions of these regions.

The Monkey Perirhinal Cortex

Area 35 of the macaque monkey perirhinal cortex is fairly homogeneous cytoarchitectonically (Suzuki and Amaral, 1994a). Layer III is poorly populated and forms a distinctive gap in cell stains. Another distinctive feature of this agranular cortex is layer V, which is populated by large, darkly stained, and densely packed cells that form an arc around the fundus of the rhinal sulcus (Fig. 3A). In contrast to the homogeneity of area 35, area 36 shows substantial regional variation in its cytoarchitectonic appearance. In general, it becomes more columnar and more differentiated as one moves either laterally or caudally (Suzuki and Amaral, 1994a). One of the most distinctive features of area 36 is layer II, which is prominent owing to the clusters of darkly stained spherical cells that populate it. At rostral levels of area 36, these cell clusters extend into layer I giving the layer I/II border an irregular appearance. Unlike area 35, area 36 has a distinct layer IV, although it tends to be very primitive in the medial portions of the area.

The Monkey Parahippocampal Cortex

Areas TH and TF of the parahippocampal cortex are clearly distinct from areas 35 and 36. Area TH, the more primitive of the two areas, is agranular and bilaminate in appearance at rostral levels, but is more laminar and contains a meager internal granular layer at caudal levels. Area TF is more highly granular with large, darkly stained cells in the infragranular layers. One of the distinctive features of area TF is the very prominent layer V, made up of large darkly stained pyramidal cells, that fuses with layer VI.

The Rat Perirhinal Cortex

Only very limited cytoarchitectonic descriptions of the rat perirhinal cortex are currently available in the literature (Kreig, 1946b; Turner and Zimmer, 1984). The following is thus heavily based on our own observations.

Area 35 in the rat is agranular cortex characterized by a broad layer I (Fig. 4B). This cortex can be distinguished from the nearby piriform and entorhinal cortices (Fig. 4A) by several features, e.g., the small round cells in layer II. Layer III is poorly populated as in the monkey. Also similar to the monkey, layer V of area 35 is distinguished by the occurrence of large, darkly stained pyramidal cells distributed throughout the layer. These darkly stained cells are organized in a gradient fashion with smaller cells located superficially and progressively larger cells located more deeply in the layer.

Area 36 has a distinctly different cytoarchitecture from area 35. As in the monkey, area 36 is characterized by a prominent layer II containing mostly round cells organized in distinctive patches (Fig. 4C,D). The layer II cells are larger and often darker than those seen in area 35. A very weak granular layer is present in which granule cells are intermixed with the cells that consti-
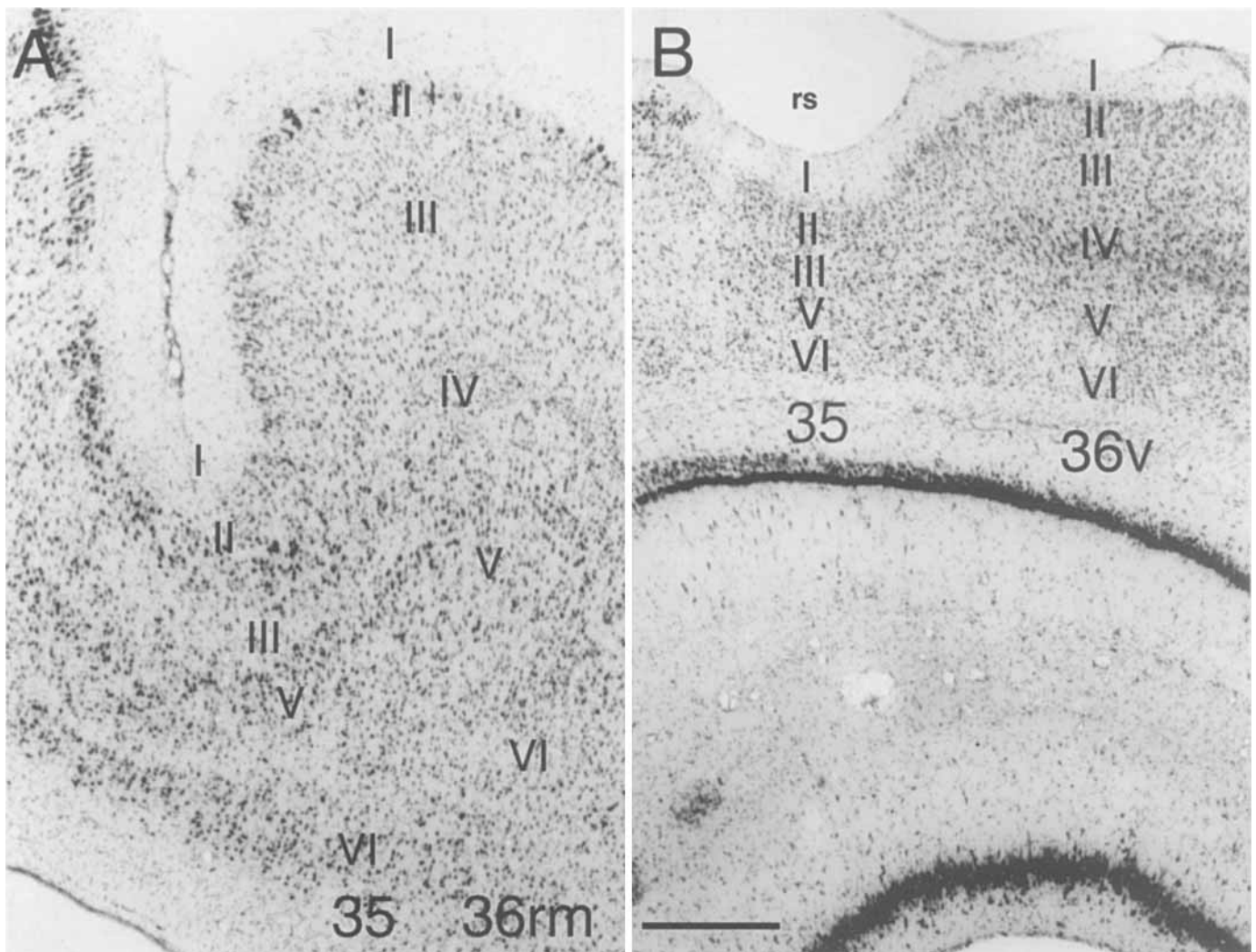
FIGURE 3.   Photomicrographs of Nissl-stained standard coronal sections through the perirhinal cortex of the macaque monkey (A) and the rat (B). Laminae are designated by Roman numerals. Area 35 for both species, area 36rm for the monkey, and the ventral portion of area 36 for the rat are shown. Scale bar = 500 μm.

tute layers III and V. In dorsal portions of area 36, layer II remains patchy, but is thinner than in ventral area 36 (Fig. 4D). Layer IV becomes more prominent in the dorsal portion of the field.

One useful histochemical preparation for defining cortical borders is the Timm's sulphide silver technique, which demonstrates the distribution of heavy metals (Timm, 1958; Haug, 1973; Slovitor, 1982). Although comprehensive studies of these regions in the monkey using Timm's staining methods are not available for comparison, this technique provides a useful marker for areas 35 and 36 in the rat. Figure 5B shows a coronal Timm-stained section of the rat brain that was cut in a plane oriented perpendicular to the rhinal sulcus. Area 35 is characterized by a single, densely stained band encompassing layers II through V (see also Turner and Zimmer, 1984). Area 36 is distinguished from the homogeneously stained area 35 by two dark bands separated by

a light band (Fig. 5B). Although the occurrence of these two bands clearly differentiates area 36 from area 35, the bands continue, albeit substantially more lightly, into the dorsally adjacent cortex. Thus, the Timm's staining pattern provides only a partial indication of the dorsal border of area 36.

What do the cytoarchitectonic and other characteristics of the rat perirhinal cortex described above contribute to the definition of borders with the surrounding cortical areas? Rostrally, the perirhinal cortex abuts the posterior insular cortex. Area 35 is easily distinguishable from the posterior insular cortex on purely cytoarchitectonic grounds. This most rostral portion of area 35 is distinctly bilaminate, whereas the posterior insular cortex has an isocortical or six-layered appearance. The differentiation of posterior insular cortex from area 36 is more problematic. Perhaps the main features of the posterior insular cortex that differentiate it from area 36 are the cell-sparse gaps between layers III and V,
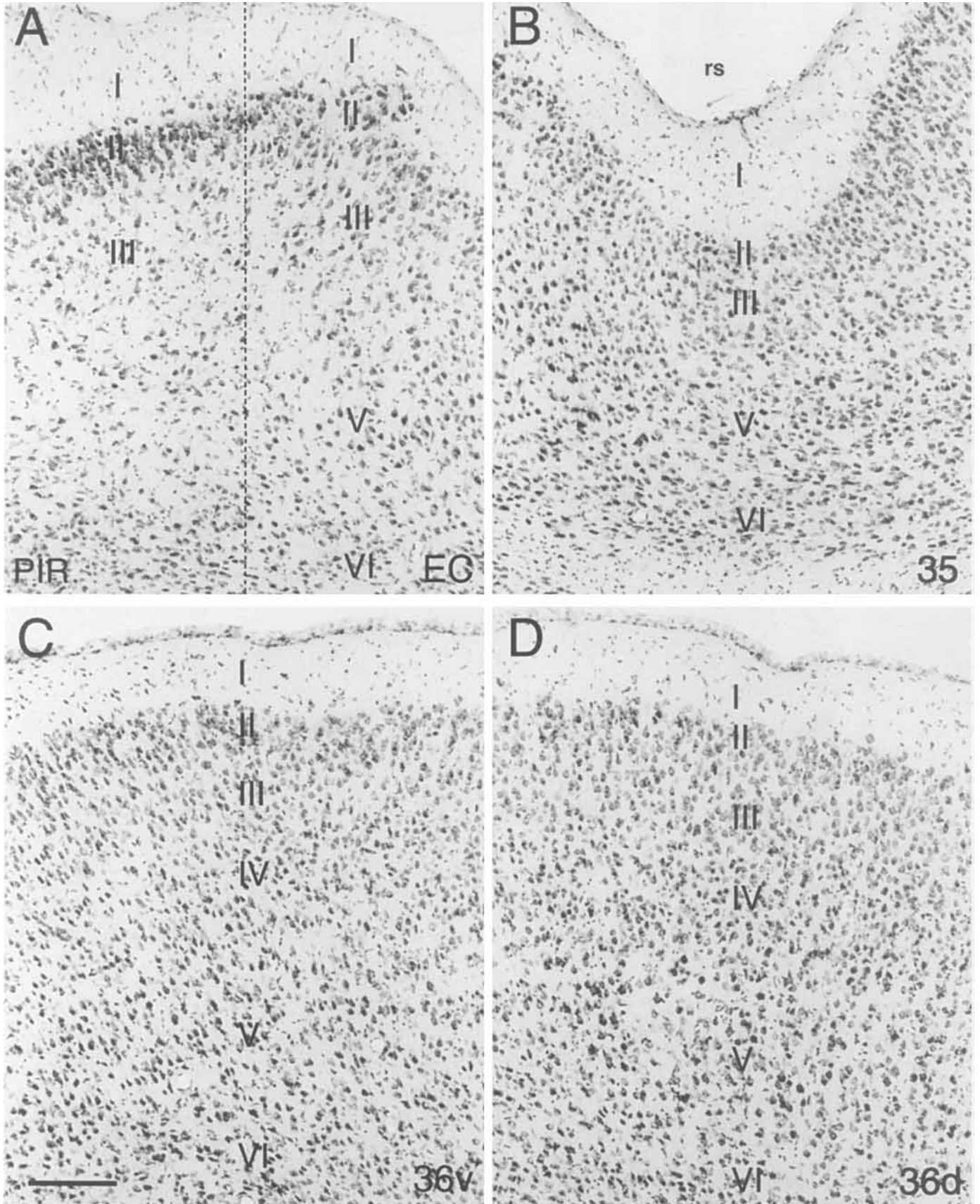
V and VI, and VI and the underlying claustrum (see also Krettek and Price, 1977c). The loss of these characteristic gaps coincides rostrocaudally with the caudal limit of the claustrum and the level where we place the rostral border of area 36.

The ventral border of the perirhinal cortex is formed by the entorhinal cortex. In Nissl-stained material, the border can be distinguished by several characteristics. For example, layer II of the entorhinal cortex contains medium-to-large, darkly stained stellate cells organized in clusters, whereas in area 35, layer II cells are smaller and lighter and are primarily round with a few pyramids. The presence of the cell-sparse lamina dissecans in the entorhinal cortex also distinguishes it from area 35. In Timm's material, the perirhinal cortex is heavily stained, whereas the entorhinal cortex is much more lightly stained. Immunoreactivity for the calcium-binding protein parvalbumin also demonstrates a definite border (Fig. 5C, see also Dolorfo and Amaral, 1993). Here, the entorhinal cortex is heavily labeled, whereas area 35 shows little or no labeling. Parvalbumin immunoreactivity in superficial layers also clearly distinguishes entorhinal cortex from perirhinal cortex in the monkey (Pitkanen and Amaral, 1993).

By most accounts, the dorsal border of the perirhinal cortex is formed by association cortex of some type, either multimodal association cortex or auditory association cortex. There are bands of cortex lying dorsal to what is clearly area 36 that can be distinguished from it on the basis of cytoarchitectonic features. Whether these bands should be grouped within area 36 or within the dorsal association cortex is not presently clear. This distinc-

tion will likely be made on the basis of connectional, rather than cytoarchitectonic, criteria. In the monkey, for example, area 36 can be differentiated from area TE (unimodal visual association cortex) because area 36 projects heavily to the entorhinal cortex and area TE does not. We would predict that a projection to the rat entorhinal cortex may also be a defining feature of the rat perirhinal cortex.

The Rat Postrhinal Cortex

As noted above, Deacon et al.'s (1983) original definition of the postrhinal cortex has been expanded into a somewhat larger region. In the present report, the term postrhinal includes the caudal levels of area 35 (as in Deacon et al.'s original usage) as well as the caudal portion of area 36 (or ectorhinal cortex as in Deacon et al.'s map). The ventral portion of postrhinal cortex is agranular and bilaminate in appearance (Fig. 6A). A distinguishing feature is the presence of small ectopic layer II cells near the border with the entorhinal cortex. The larger, dorsal portion of the postrhinal cortex is more laminar and has a distinct layer IV (Fig. 6B).

The postrhinal cortex can be differentiated from the rostrally adjacent perirhinal cortex by the occurrence of the ectopic layer II cells. These outpouchings of cells into layer 1, give layer II a distinctively irregular appearance in the ventral portion of the region. The dorsal postrhinal cortex can be differentiated from rostral levels of area 36 in that layer II is more densely packed and therefore not as patchy as in area 36. Finally, the deep layers of the postrhinal cortex contain elongated cells that are radially oriented, whereas layer VI of the perirhinal cortex contains elongated cells that are horizontally oriented.

The postrhinal cortex is bordered medially by agranular retrosplenial cortex (Vogt, 1985). Agranular retrosplenial cortex, area
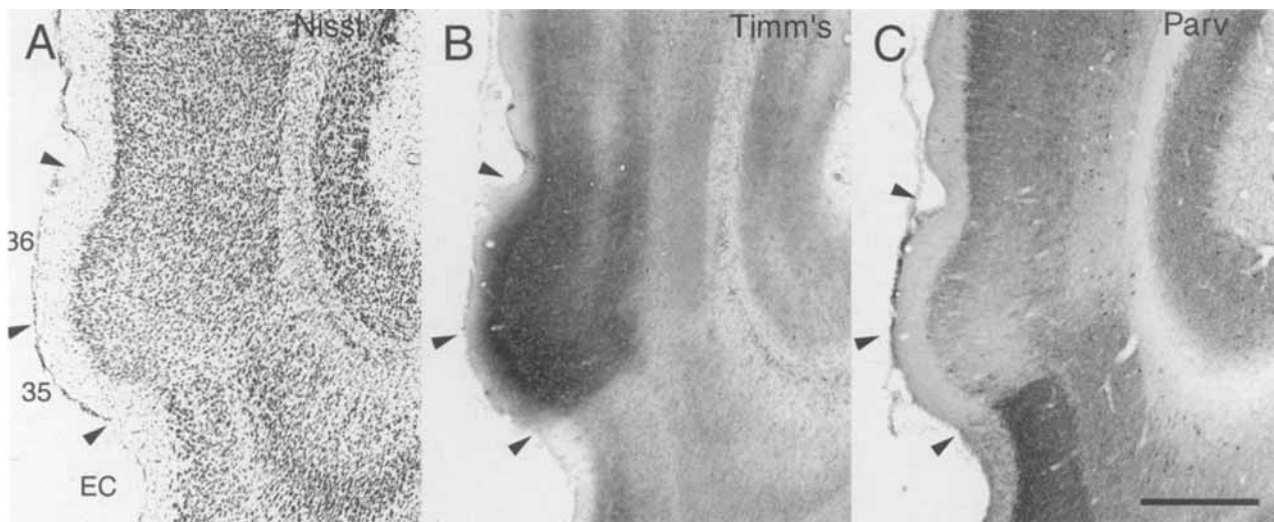

FIGURE 5.   Photomicrographs of coronal sections of the rat brain cut obliquely so that the plane of section is perpendicular to the rhinal sulcus. Adjacent sections are stained for Nissl (A), heavy metals by the Timm's method (B), and the calcium-binding protein parvalbumin (Parv, C). The boundaries of areas 35 and 36 are demarcated by arrows. In the Timm's-stained material, area 36 is characterized by two darkly labeled bands that coalesce in area 35, but the entorhinal cortex (EC) is lightly labeled. In contrast, the middle layers of the entorhinal cortex stain heavily for parvalbumin, but the perirhinal cortex is only lightly stained. Scale bar = 500μm.
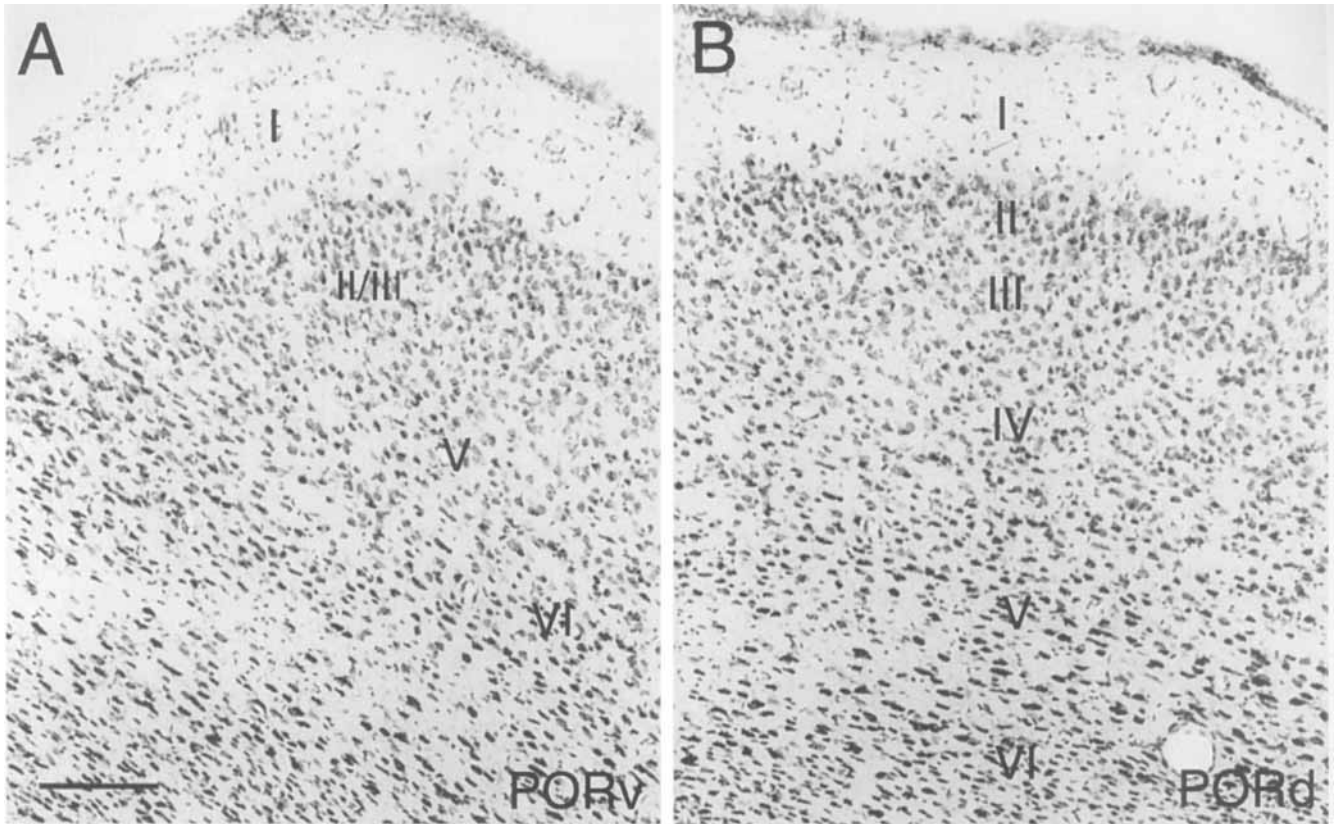
FIGURE 6.   Photomicrographs of Nissl-stained standard coronal sections through the ventral portion (A) and the dorsal portion (B) of the postrhinal cortex of the rat. Laminae are designated by Roman numerals. Scale bar = 200 μm.
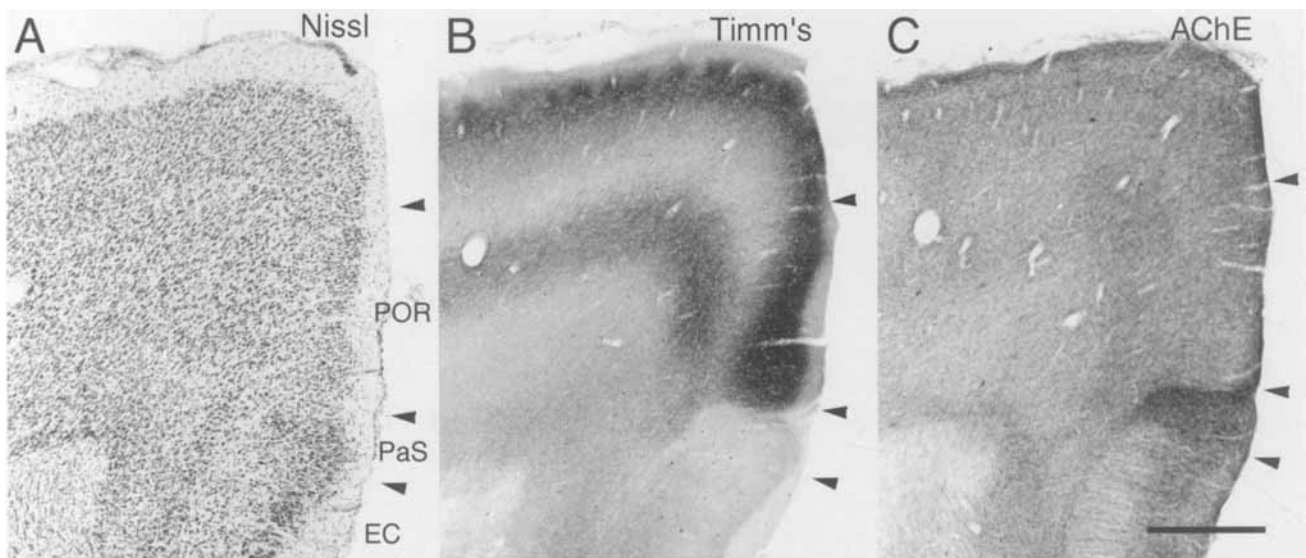

FIGURE 7.   Photomicrographs of sagittal sections stained for Nissl (A), heavy metals by the Timm's method (B), and AChE (C). These images show the most caudodorsal aspect of the section where the parasubiculum (PaS) is identified by light staining for heavy metal and dark staining for AChE. Postrhinal cortex (POR) is identified by two bands of staining in Timm's material with a broader, darker outer band. The entorhinal cortex (EC) is situated below PaS, and secondary visual cortex is located above POR. Scale bar = 500 μm.

29d of Vogt and Peters (1981), has a distinctly different cytoar-chitectonic appearance from postrhinal cortex. It has a broad fused layer II/III and a weak layer IV made up of distinctive, larger cells. Our observations indicate that the postrhinal cortex extends far-ther posteromedially than indicated by previous descriptions of the perirhinal or ectorhinal cortices. In the caudomedial portion of the postrhinal cortex its ventral border is not with the en-torhinal cortex. Rather, a thin band of the parasubiculum insin-uates between the entorhinal and postrhinal cortices. This can be appreciated in sagittal sections stained for acetylcholinesterase (AChE) or by Timm's method (Fig. 7). The parasubiculum stains intensely for AChE and forms a thin band just above entorhinal cortex (Fig. 7C); in Timm's-stained material this area is pale (Fig. 7B). The postrhinal cortex stains lightly for AChE, but very densely in the Timm's preparations. The region can be clearly seen to form a narrow band above the parasubiculum.

As with the perirhinal cortex, the dorsal border of postrhinal cortex is formed by association cortex of some type, but in this case it is either visual association cortex (Kreig, 1946b; Zilles et al., 1980; Miller and Vogt, 1984; Zilles, Wree, 1985) or poly-modal association cortex (Swanson, 1992). In cell-stained mate-rial, visual cortex is distinguished from the ventrally adjacent cor-tex by a more prominent layer IV and a bilaminate layer VI. In Timm's-stained material, visual association cortex demonstrates clumps of dark precipitate associated primarily with layer II and the deep portion of layer I. Based on the information available, it is not clear whether postrhinal cortex abuts visual association cortex or whether a band of polymodal association cortex is in-terposed. As with the perirhinal cortex, this distinction will likely be made on the basis of connectional criteria, and again, we pre-dict that a projection to the rat entorhinal cortex will be a defin-ing feature of the rat postrhinal cortex. A delimitation of the cor-tical boundaries of the rat perirhinal and postrhinal cortices that reflects all available neuroanatomical information is illustrated in Figure 8.

Cross-Species Similarities and Differences

In addition to the specific cross-species comparisons already noted, there are a number of similarities in the general organiza-tional features in the rat and monkey perirhinal and postrhi-nal/parahippocampal cortices. For example, there is a common gradient of increasing cytoarchitectonic differentiation along the rostrocaudal and ventrodorsal axes (mediolateral in the monkey). Area 36 becomes more radially organized at caudal levels in both species, and area 36 is thicker with more distinct cellular layers than area 35. These same principles are observed in the postrhi-nal and parahippocampal cortices. Dorsal postrhinal cortex is more highly laminated than ventral postrhinal cortex in the rat, and area TF is more highly laminated than area TH of the parahippocampal cortex in the monkey.

One question of importance is whether postrhinal cortex in the rat shares cytoarchitectonic characteristics with parahip-pocampal cortex in the monkey. The available data suggest that the ventral portion of the postrhinal cortex may share some fea-tures with area TH, i.e., a combined layer II/III composed pri-

marily of round cells and deeper layers of larger, darkly stained cells. Nevertheless, the homology of postrhinal cortex with parahippocampal cortex will rely heavily on more detailed infor-mation concerning the connectivity of these regions.

WHAT ARE THE CONNECTIONS OF THESE REGIONS?

The Connections of the Monkey Perirhinal and Parahippocampal Cortices

Arguably, the most compelling feature of the connectivity of perirhinal and parahippocampal cortices in the monkey is the con-nectivity with the hippocampal formation. In fact, Insausti et al. (1987) defined an enlarged area of the primate mediotemporal lobe as belonging to the perirhinal or parahippocampal cortices on the basis that cells throughout this region project directly to the entorhinal cortex. In the monkey, these cortical regions pro-vide almost two-thirds of the neocortical input to the entorhinal cortex (Insausti et al., 1987), which, in turn, provides the pre-dominant cortical input to the dentate gyrus and hippocampus via the perforant pathway (Van Hoesen and Pandya, 1975c; Witter et al., 1989b; Witter and Amaral, 1991). The topography of the entorhinal interconnections with the perirhinal and parahippocampal cortices has been described in detail by Suzuki and Amaral (1994b). The perirhinal cortex projects most heavily to the rostrolateral two-thirds of entorhinal cortex, and the parahippocampal cortex projects most heavily to the caudal two-thirds.

The functional significance of the perirhinal and parahip-pocampal projections to the entorhinal cortex of the hippocam-pal formation is augmented by the information that these cor-tices are themselves the focus of converging input from unimodal and polymodal associational cortices (Jones and Powell, 1970; Van Hoesen and Pandya, 1975a,b). Suzuki and Amaral (1994a) provided evidence that unimodal associational inputs arise from somatosensory, auditory, and visual association cortices. While the majority of the input to these cortices is from visual areas, different types of visual information reach the perirhinal and parahippocampal cortices. Visual object information from area TE predominantly reaches the perirhinal cortex, whereas visuo-spatial information is more heavily directed to the parahip-pocampal cortex. Cortices identified with somatosensory proc-essing, primarily granular and agranular insular cortices, project to both perirhinal and parahippocampal cortices. Auditory asso-ciation cortex only projects to the parahippocampal cortex.

The perirhinal and parahippocampal cortices receive polysen-sory information from ventrolateral and orbitofrontal cortices, cingulate and retrosplenial cortices, posterior parietal cortex, and the polymodal region of the dorsal bank of the superior tempo-ral sulcus (Suzuki and Amaral, 1994a). All of these cortices pro-ject to parahippocampal cortex, but the predominant polymodal associational input to perirhinal cortex arises from the parahip-pocampal cortex and the superior temporal sulcus. Interestingly, while the parahippocampal cortex projects heavily to the perirhi-
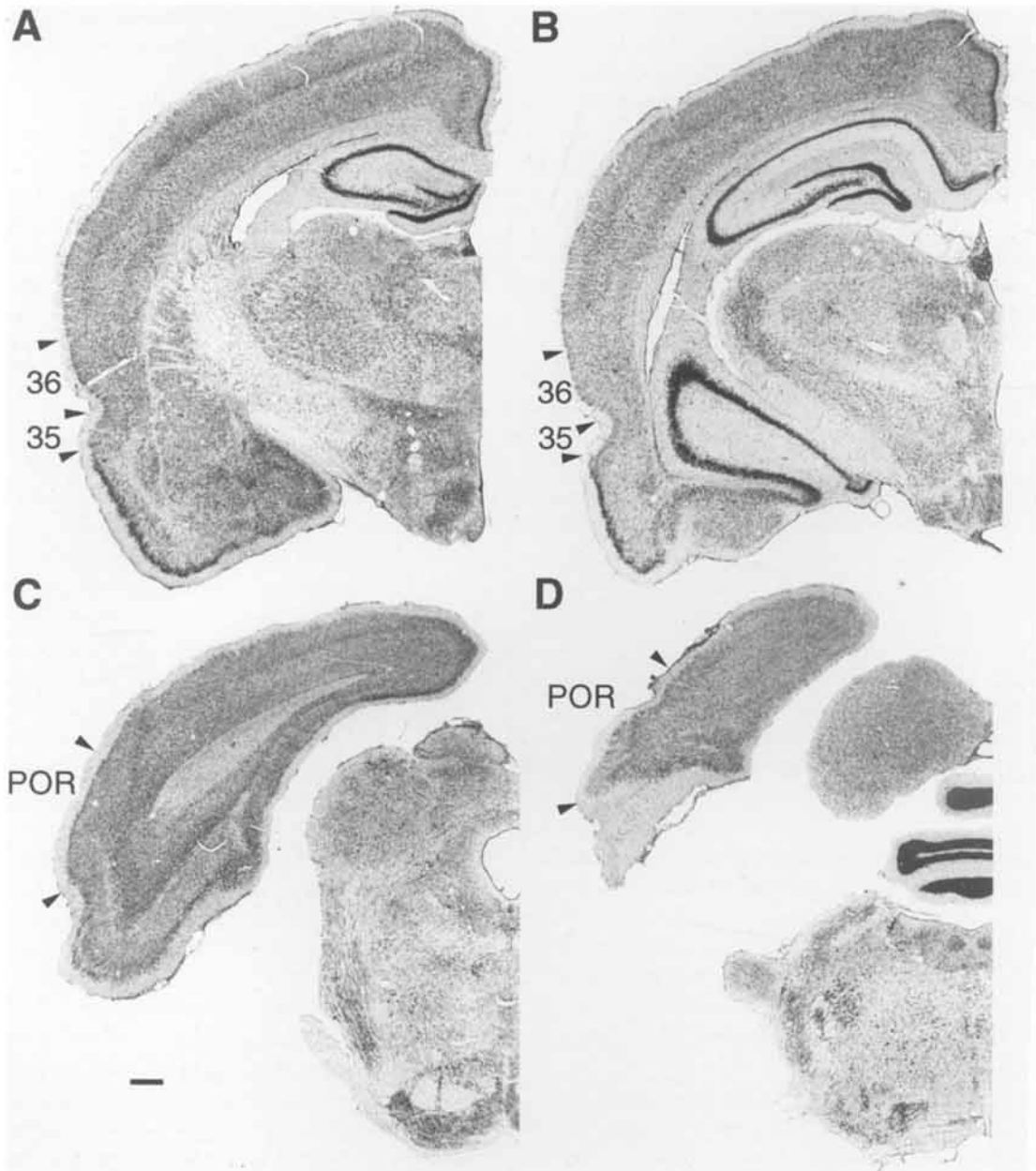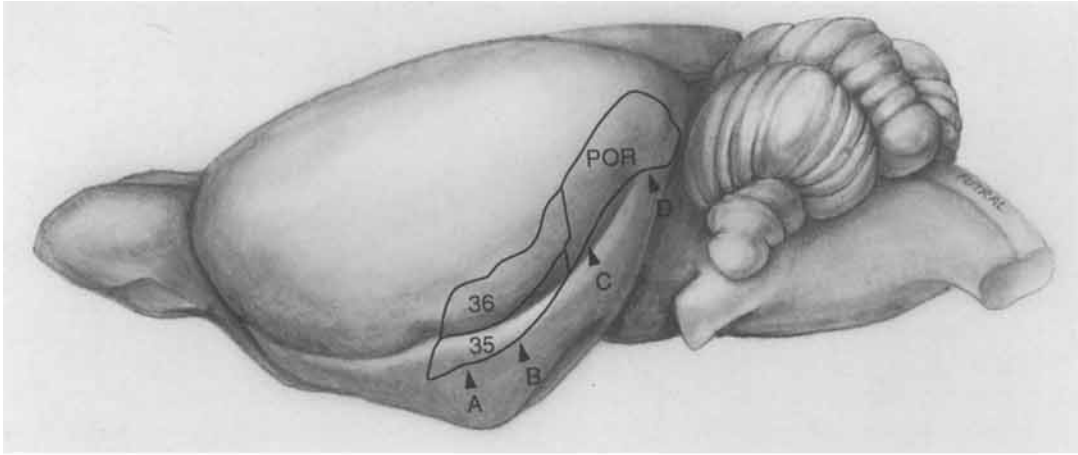
nal cortex, the perirhinal cortex projection to the parahippocampal cortex is rather meager. Thus, the monkey perirhinal and parahippocampal cortices appear to be the primary intermediaries between the neocortex and the hippocampal formation.

In addition to their connectivity with the neocortex and the hippocampal formation, the perirhinal and parahippocampal cortices are also interconnected with the amygdala, the basal ganglia, and the thalamus. The perirhinal and parahippocampal cortices project to the lateral, basal, and accessory basal nuclei of the amygdaloid complex (Van Hoesen, 1981; Stefanacci et al., 1994). The amygdaloid projections arise more from the perirhinal cortex than from the parahippocampal cortex. The return projections originate primarily from the same nuclei.

Available information indicates that the perirhinal and parahippocampal cortices provide substantial input to portions of the striatum including the caudate nucleus, putamen, and nucleus accumbens (Yeterian and Van Hoesen, 1978). The temporal polar portion of perirhinal cortex projects to ventromedial portions of the caudate nucleus and the putamen (Van Hoesen et al., 1981). There is some evidence that the remaining regions of the perirhinal cortex project sparsely to ventral regions of the head and prominently to lateral portions of the tail of the caudate nucleus (Saint-Cyr et al., 1990). The perirhinal cortex also projects to the nucleus accumbens (Hemphill et al., 1981). The parahippocampal cortex projects more prominently to the head of the caudate nucleus than does perirhinal cortex, but with a patchy terminal distribution (Saint-Cyr et al., 1990). The parahippocampal cortex also projects heavily to the tail of the caudate nucleus, especially to dorsal portions (Van Hoesen et al., 1981).

There is limited information available about the interconnectivity of the thalamus with the perirhinal and parahippocampal cortices in the monkey (reviewed in Witter et al., 1989a). The perirhinal cortex clearly projects to the medial division of the pulvinar (Yeterian and Pandya, 1988), and there is also evidence that the perirhinal cortex projects at least lightly to the mediodorsal thalamus (Aggleton et al., 1986; Russchen et al., 1987). The parahippocampal cortex projects to the medial pulvinar, the medial dorsal nucleus, and the lateral dorsal nucleus (Baleydier and Mauguiere, 1985; Russchen et al., 1987; Yeterian and Pandya, 1988).

The Connections of the Rat Perirhinal and Postrhinal Cortices

While there has thus far been no comprehensive analysis of the perirhinal projection to the entorhinal cortex in the rat, our own findings indicate that the perirhinal and postrhinal cortices give rise to robust projections to the entorhinal cortex, which are stronger to lateral regions than to medial regions. Projections from

different regions of the perirhinal cortex are largely overlapping in the entorhinal cortex, but there is a rough rostrocaudal topography. Rostral perirhinal cortex projects more strongly to rostral and lateral regions of entorhinal cortex, and caudal perirhinal cortex preferentially projects more caudally in entorhinal cortex. Postrhinal cortex projects more heavily to the caudal entorhinal cortex than does the caudal perirhinal cortex. Projections from the postrhinal cortex innervate both lateral and medial regions of the entorhinal cortex, although the labeling in lateral regions is heavier.

Although there have been reports that the entorhinal cortex gives rise to a return projection to the perirhinal and postrhinal cortices (Deacon et al., 1983; Kohler, 1988), the topography and laminar pattern of these projections have not been extensively examined. Our findings indicate that the rostral entorhinal cortex projects preferentially to the perirhinal cortex, whereas the caudal entorhinal cortex projects both to perirhinal and postrhinal cortices. Preliminary data suggest that layers III through V of rostral entorhinal cortex near the rhinal sulcus give rise to the projections to the perirhinal cortex, although the labeling is heavier from the deep layers. Layer V of the caudal regions of the entorhinal cortex projects to the perirhinal and postrhinal cortices.

The available literature suggests that widespread neocortical areas project extensively to the perirhinal and postrhinal cortices. Table 2 presents a compilation of references for neocortical inputs to perirhinal cortex. Owing to the pronounced differences in how the perirhinal borders are defined in these studies and the often incidental manner with which projections to the perirhinal cortex are presented, the data summarized in this table should be considered tentative and in need of confirmation. Miller and Vogt (1984) reported that area 35 receives input from primary visual area 17 (which was also reported to project to sensory, motor, and association cortices!) as well as from visual association area 18a (see also Deacon et al., 1983; Vaudano et al., 1990; Paperna and Malach, 1991). Area 36 was also reported to receive input from areas 18a and 18b. Primary auditory cortex does not project to perirhinal cortex, but a thin strip of auditory association cortex, located ventrally and caudally to the primary region, does project to rostral perirhinal cortex (Vaudano et al., 1990; Romanski and LeDoux, 1993; Mascagni et al., 1993). Regarding somatosensory input, Deacon et al. (1983) reported input from rostral, ventral, and posterior regions of insular cortex to area 35 (see also Saper, 1982; Guldin and Markowitsch, 1983). Olfactory input to the perirhinal cortex arises from the periamygdaloid region (Krettek and Price, 1977a; Deacon et al., 1983) and piriform cortex (Guldin and Markowitsch, 1983; Luskin and Price, 1983). Our preliminary retrograde tracing findings confirm that the perirhinal cortex receives substantial input from somatosensory and auditory associational cortices and olfactory areas. The postrhinal cortex, in contrast, receives strong input from visual association cortex, weak input from somatosensory association cortex, and little or no input from auditory and olfactory regions.

The polymodal associational cortices that provide input to perirhinal cortex include the medial prefrontal (Beckstead, 1979; Deacon et al., 1983; Guldin and Markowitsch, 1983; Cornwall and Phillipson, 1988; Sesack et al., 1989; Reep et al., 1990;

TABLE 2.

Cortical Input to Perirhinal Cortex

Frontal regions	
Frontal area 2	Deacon et al. (1983); Reep, et al. (1990); Guldin and Markowitsch (1983)
Anterior cingulate	Deacon et al. (1983); Beckstead (1979); Takagishi and Chiba (1991); Conde et al. (1995)
Prelimbic	Deacon et al. (1983); Sesack et al. (1989); Beckstead (1979); Hurley et al. (1991); Conde et al. (1995)
Infralimbic	Hurley et al. (1991); Conde et al. (1995)
Lateral orbital	Deacon et al. (1983)
Retrosplenial cortex	Deacon et al. (1983); Arnault and Roger (1990); Wyss and Van Groen (1992)
Olfactory cortex	
Piriform	Luskin and Price (1983); Guldin and Markowitsch (1983)
Periamygdaloid	Deacon et al. (1983); Luskin and Price (1983); Krettek and Price, 1977a–c
Insular cortex	Deacon et al. (1983); Guldin and Markowitsch (1983); Saper (1982)
Parietal cortex	Deacon et al. (1983); Guldin and Markowitsch (1983)
Temporal cortex	
TE1v, TE2	Romanski and LeDoux (1993); Mascagni et al. (1993); Paperna and Malach (1991); Vaudano et al. (1990)
TE3	Deacon et al. (1983); Romanski and LeDoux (1993); Mascagni et al. (1993)
Occipital cortex	Deacon et al. (1983); Miller and Vogt (1984); Paperna and Malach (1991); Vaudano et al. (1990)

Hurley et al., 1991; Conde et al., 1995), ventrolateral prefrontal (Deacon et al., 1983), and anterior cingulate (Beckstead, 1979; Deacon et al., 1983; Takagishi and Chiba, 1991; Conde et al., 1995) cortices (Table 2). Projections from ventral temporal cortices also are well documented (Deacon et al., 1983; Mascagni et al., 1993; Romanski and LeDoux, 1993). These cortices are likely to be polymodal associational regions rather than auditory association cortices (Mascagni et al., 1993). Our observations also indicate that the perirhinal cortex receives polymodal input from the postrhinal cortex. While the retrosplenial cortex is reported to project to the perirhinal cortex (Deacon et al., 1983; Arnault and Roger, 1990; Wyss and van Groen, 1992), there is no published information on the strength or topography of this projection. Our preliminary data provide evidence that the anterior cingulate, retrosplenial, and posterior parietal cortices project strongly to the postrhinal cortex but not to the perirhinal cortex.

The primary subcortical connections of the perirhinal cortex include strong projections to the amygdala, the striatum and the thalamus. The postrhinal cortex also projects to the striatum and the thalamus but has few or no connections with the amygdaloid complex. Postrhinal cortex, but not perirhinal cortex, is interconnected with the claustrum (Burwell and Amaral, unpublished findings).

Several amygdaloid nuclei are interconnected with the rat perirhinal cortex. Our own findings indicate that the perirhinal cortex is interconnected with the lateral, basal, and accessory basal nuclei of the amygdala (see also Krettek and Price, 1974, 1977b; Ottersen, 1982; McDonald and Jackson, 1987; Vaudano et al., 1990; Romanski and LeDoux, 1993) as well as the capsular region of the central nucleus. The heaviest projections terminate in the lateral nucleus and the capsule of the central nucleus and arise from all portions of perirhinal cortex. Area 36 projects more strongly to these nuclei than does area 35. Both areas 36 and 35

receive input from the lateral nucleus, but the area 35 projection is somewhat more substantial. Area 36 is reciprocally connected with the magnocellular division of the basal nucleus and area 35 with the parvicellular division of the basal nucleus. There is a minor reciprocal connection with the accessory basal nucleus.

There is little published information on the connections of the perirhinal and postrhinal cortices with the striatum. Our studies indicate that the perirhinal cortex projects substantially to the striatum, particularly to medial regions of the body and tail of the caudate nucleus (see also McGeorge and Faull, 1989; Vaudano et al., 1990). Area 35 projects moderately to the nucleus accumbens and to the tail of the caudate nucleus. Area 36 exhibits strong projections to the nucleus accumbens, the most medial portion of the body, and tail of the caudate nucleus. The postrhinal cortex projects heavily only to the most caudal and dorsal margin of the body and the tail of the caudate nucleus.

We examined the patterns of the perirhinal and postrhinal projections to the thalamus and found regional differences (Burwell et al., 1994). For the perirhinal cortex, the projection from area 36 is more robust than that from area 35. While all portions of the perirhinal cortex project to midline thalamic nuclei (see also Herkenham, 1978; Cornwall and Phillipson, 1988), subregions of areas 35 and 36 can be distinguished by the pattern of efferent connectivity with other thalamic regions. For example, rostral but not caudal area 36 projects to posterior nuclei (see also Deacon et al., 1983). Only the rostral portion of area 35 projects to the mediodorsal thalamic nucleus. Our own preliminary studies indicate that the perirhinal and postrhinal cortices are also distinguished by their thalamic projections. Unlike the perirhinal cortex, the postrhinal cortex projects to the anterior and lateral nuclear groups. The perirhinal and postrhinal cortices are further distinguished by their thalamic input. While both regions receive input from midline thalamic nuclei, the projections are heavier
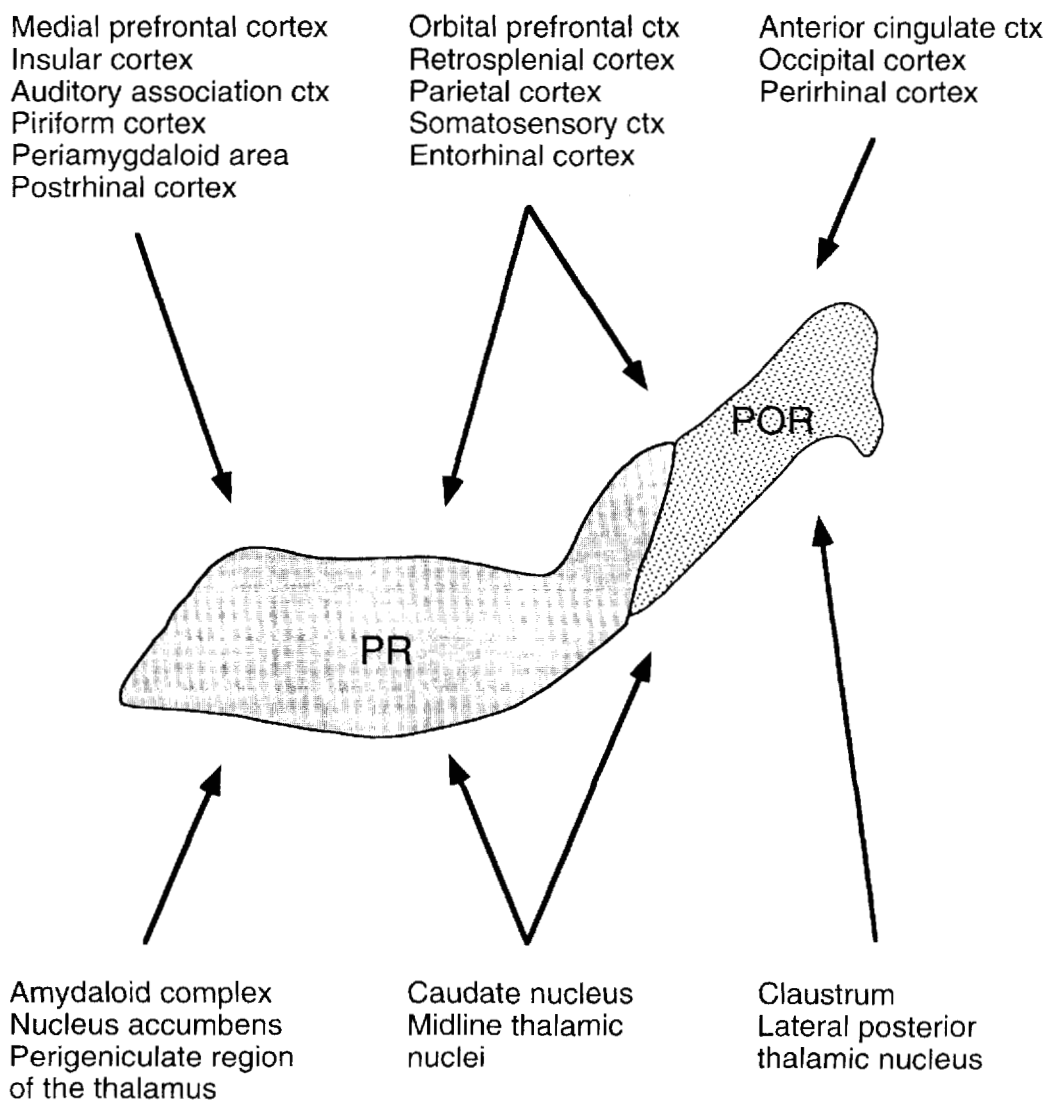
to perirhinal than to postrhinal cortex. Only the perirhinal cortex receives input from the auditory thalamus, and only the postrhinal cortex receives input from the lateral posterior thalamus. Both regions receive input from the perigeniculate region, but from different portions. A summary of the cortical and subcortical connections reviewed here is presented in Figure 9.

Cross-Species Similarities and Differences

A review of the connectivity of the perirhinal and parahippocampal cortices in the monkey and the perirhinal and postrhinal cortices in the rat suggests that two broad principles of cortical connectivity are exhibited in both species. First, as in the monkey, the rat perirhinal and postrhinal cortices give rise to strong projections to the hippocampal formation via the entorhinal cortex. Moreover, the projections exhibit similar topographics in the two species. The second principle common to both the rat and the monkey is that unimodal and polymodal association areas project extensively to the perirhinal and postrhinal/parahippocampal cortices. In both species these regions receive extensive unimodal associational input; however, the topography and relative contributions of this input differ. In the monkey, the perirhinal and

Cortical Connections

Medial prefrontal cortex
Insular cortex
Auditory association ctx
Piriform cortex
Periamygdaloid area
Postrhinal cortex

Orbital prefrontal ctx
Retrosplenial cortex
Parietal cortex
Somatosensory ctx
Entorhinal cortex

Anterior cingulate ctx
Occipital cortex
Perirhinal cortex

POR

PR

Amydaloid complex
Nucleus accumbens
Perigeniculate region
of the thalamus

Caudate nucleus
Midline thalamic
nuclei

Claustrum
Lateral posterior
thalamic nucleus

Subcortical Connections

FIGURE 9.   Summary diagram of the cortical and subcortical connections of the perirhinal and postrhinal cortices. ctx, cortex.

parahippocampal cortices receive a preponderance of visual inputs, with the parahippocampal cortex also receiving a small complement of auditory and somatosensory associational input. For the rat, the magnitude and distribution of sensory information appears to be more evenly weighted in the perirhinal and postrhinal cortices. The perirhinal cortex receives primarily somatosensory, auditory, and olfactory input, and the postrhinal cortex receives primarily visual and some somatosensory input. In both species, these regions receive polymodal associational input, but the parahippocampal cortex in the monkey and the postrhinal cortex in the rat receive the most widespread and extensive input. Moreoever, the parahippocampal cortex in the monkey and the postrhinal cortex in the rat provide a major source of polymodal associational input to the perirhinal cortex.

In addition to the shared attributes already described, the regions surrounding the rhinal sulcus in both species also project importantly to several subcortical structures. While available data are so limited as to make direct comparisons between the rat and monkey difficult, the rat and monkey perirhinal and postrhinal/parahippocampal cortices appear to make connections with the same subcortical structures and even the same subnuclei of these structures.

THE PERIRHINAL AND POSTRHINAL CORTICES AS A REFLECTION OF SPECIES-SPECIFIC SENSORY PROCESSING

The monkey perirhinal and parahippocampal cortices preferentially receive visual input, whereas the rat perirhinal and postrhinal cortices receive unimodal sensory input that is more evenly weighted across sensory modalities. It might be useful to consider species differences in unimodal sensory input to these regions within the framework of the relative amounts of the cortical surface areas dedicated to the various sensory modalities in the two species (Table 3). While almost half of the monkey neocortex is involved in unimodal visual processing (Felleman and Van Essen, 1991), only one-sixth of the rat neocortex is visual (extracted from Swanson, 1992). The relative cortical area dedicated to processing auditory stimuli is about the same in the two species, but the somatosensory regions are relatively larger in the rat. Thus, if the monkey perirhinal and parahippocampal cortices reflect the types of sensory processing that are carried out by the remainder of the neocortex, it follows that these cortices would be overwhelmingly visual. Because the amounts of cortical area dedicated to visual, auditory, and somatosensory processing are more equivalent in the rat, it also follows that these sensory systems should have a more evenly distributed input to the perirhinal and postrhinal cortices. The differences in unimodal input to the perirhinal parahippocampal/postrhinal cortices in the monkey and the rat should not imply that they play different roles in memory function. Rather, these cortices may carry out the same memory-related computations albeit on different types of sensory information. A search for the fundamental operation of these regions awaits sophisticated behavioral/electrophysiological analy-

TABLE 3.

Surface Area of Sensory Cortical Regions

Sensory Cortical Areas[1]	% of Neocortex	
	Monkey	Rat
Total visual areas[2]	48.2	17.9
Occipital	34.0	11.9
Parietal	4.8	3.5
Temporal	8.4	2.5
Auditory areas	3.4	4.0
Somatosensory areas[3]	11.5	25.9
Olfactory areas[4]	1.2	14.4

[1]Surface areas for the monkey are taken from Felleman and Van Essen (1991); however, we exclude some areas known to be polymodal from the list of visual areas (i.e., areas STP, TF/TH, 7a, and 46). Surface areas for the rat are taken from Swanson (1992).
[2]For the rat we include posterior parietal cortex (Swanson, 1992) and the visual portions of area 36 (Miller and Vogt, 1984).
[3]Somatosensory areas for the rat include the barrel fields which account for over one-quarter of the total area.
[4]Olfactory areas (piriform and periamygdaloid cortices) constitute an area equivalent to the indicated percentages of neocortex.

ses similar to those used in monkeys to explore these brain regions (e.g., Miller and Desimone, 1994).

FINAL COMPARISONS

Unfolded maps of the regions surrounding the rhinal sulcus for the monkey (Fig. 10A) and the rat (Fig. 10B) reveal that the combined area of the perirhinal and parahippocampal cortices in the monkey is about four times the area of the entorhinal cortex, whereas in the rat, the perirhinal and postrhinal cortices are about the same size as the entorhinal cortex. In contrast, the perirhinal/parahippocampal cortices in the monkey and the perirhinal/postrhinal cortices in the rat account for roughly similar percentages of the entire neocortical surface area, about 5% (data from (Felleman and Van Essen, 1991, for the monkey and Swanson, 1992, for the rat). Why would the entorhinal cortex be relatively smaller in the monkey? One possible explanation is that, as proposed above, the area of the perirhinal and parahippocampal/postrhinal cortices simply scales linearly with the total surface area of the remainder of the neocortex. The size of the entorhinal cortex, however, may not scale with the neocortex, but with the size of the olfactory system. Remember, the perirhinal and parahippocampal/postrhinal cortices in the monkey and rat actually receive little direct olfactory input. In contrast, the entorhinal cortex receives a direct input from the olfactory bulb. In the rat virtually all of the surface area of the entorhinal cortex receives a direct olfactory input. Although earlier studies reported that only the lateral entorhinal cortex received olfactory input
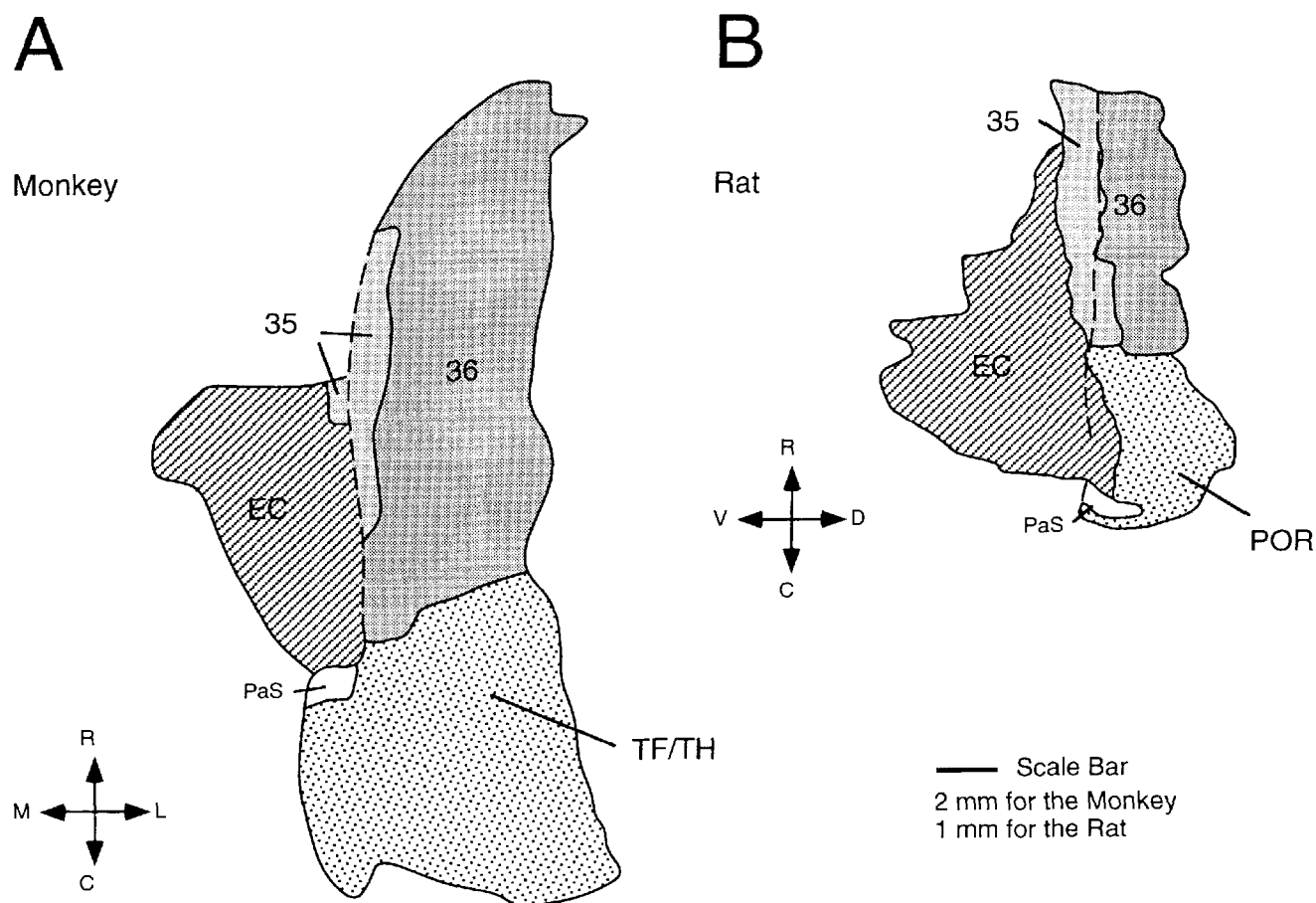
FIGURE 10.   Representative unfolded two-dimensional maps of the monkey (A, adapted from Suzuki, Amaral, 1994a) and the rat (B, Burwell and Amaral, unpublished findings) entorhinal, perirhinal and parahippocampal/postrhinal cortices. Layer IV was unfolded in the monkey and either layer IV or a line between layers III and V unfolded in the rat. These unfolded maps can be related to the surface views in Figure 8 and in Figure 2 where the same shading patterns are used to indicate areas of interest.

(Heimer, 1968; Price and Powell, 1971), later studies confirmed that these projections extend to the medial entorhinal cortex (Heimer, 1978; Kosel et al., 1981). In the monkey, only about 12% of the entorhinal cortex receives a direct olfactory input (Amaral et al., 1987). Thus, the entorhinal cortex may be relatively larger in the rat because of its greater contribution to olfactory information processing.

Defining the Borders

In the rat, the rostral, ventral, and posteromedial borders of the perirhinal cortex are clearly identified by a variety of connectional, histochemical, and immunohistochemical data. The dorsal border of the perirhinal and postrhinal cortices, however, cannot be resolved conclusively based on existing cytoarchitectonic and chemoarchitectonic data. One of the defining characteristics of the perirhinal and parahippocampal cortices in the monkey is the projection to the entorhinal cortex (Suzuki and Amaral, 1994a). If the monkey situation is taken as a guide, it follows that the dorsal border of these regions may also be indicated as the

transition from cortex that gives rise to prominent projections to the entorhinal cortex to that which gives rise to little or no projections to the entorhinal cortex. Unfortunately, there is no currently published data to answer this question for the rat, and thus a comprehensive analysis of the inputs to the entorhinal cortex using retrograde tracing techniques is needed.

The Issue of Parahippocampal Cortex

We have suggested that the postrhinal cortex in the rat may be homologous to the parahippocampal cortex in the monkey. This suggestion is based primarily on topological, histochemical, and connectional criteria (for discussions of homology and comparative neuroanatomy, see Campbell and Hodos, 1970; Rosene and Van Hoesen, 1987). Because a resolution of the question of homology between these structures is important for studies attempting to use rodent and primate models for the analysis of human memory, it will be critical to generate the connectional information most useful in making this determination. Some connectional characteristics of the parahippocampal cortex in the

monkey that might be useful in establishing homology include the origins of the polymodal associational input, the pattern of connectivity with the perirhinal cortex, and the patterns of downstream connections including those with the entorhinal cortex and subcortical structures. Even with the relatively meager connectional data that are available, it appears that a preliminary case can be made for homology between the monkey and rat perirhinal areas on the one hand, and the parahippocampal cortex in the monkey and the postrhinal cortex in the rat on the other. To give a few examples, the monkey parahippocampal cortex receives input from more multimodal associational areas than does the perirhinal cortex; it receives a prominent input from the retrosplenial cortex, whereas the perirhinal cortex does not. As indicated earlier, the postrhinal cortex of the rat receives a retrosplenial input but the perirhinal cortex does not. The monkey parahippocampal cortex projects heavily to the perirhinal cortex but not vice versa. Again the same appears to be true for the postrhinal and perirhinal cortex in the rat. Finally, the monkey parahippocampal cortex is less strongly connected with the amygdala than the perirhinal cortex, and the same relationship holds for the rat postrhinal and perirhinal cortices. Clearly, more connectional information about these regions in the rat will help to establish the validity of this neuroanatomical homology and will lead to a better framework for the analysis of the functional homology of these regions.

CONCLUSIONS

The evidence that the perirhinal and parahippocampal cortices contribute importantly to normal memory processing in the monkey has fostered an increasingly intense interest in the comparable regions of the rat brain. Behavioral studies in the rat have been hampered, however, by the lack of comprehensive neuroanatomical information. At this time only a few experimental lesion studies of the rat perirhinal cortex have been attempted. Some have addressed the contribution of the perirhinal cortex to spatial learning (Wiig and Bilkey, 1994a), exploratory behavior (Wiig and Bilkey, 1994b), and fear conditioning (Rosen et al., 1992; Romanski and LeDoux, 1992). Other studies have employed paradigms more similar to those used for the monkey such as the delayed non-matching to sample (DNMS) task. Rats with combined lesions of the entorhinal and the perirhinal cortices were impaired on DNMS using junk objects (Mumby and Pinel, 1994) and on a continuous DNMS task using olfactory cues (Otto and Eichenbaum, 1992). Only one study has assessed the effects of lesions of the perirhinal cortex alone on a DNMS task. Wiig and Bilkey (1994c) tested rats with bilateral electrolytic lesions of the perirhinal cortex on a spatial version of DNMS and found that lesioned subjects were normal in acquisition, but showed a delay-dependent performance deficit. The magnitude of the deficit was substantially less than that observed with the perirhinal-entorhinal lesions on DNMS tasks (Otto and Eichenbaum, 1992; Mumby and Pinel, 1994). This difference may be attributable to an incomplete perirhinal/postrhinal lesion, or alternatively, to the

absence of entorhinal damage. More studies exploring the effects of complete, selective lesions of the perirhinal and postrhinal cortices on memory tasks are needed to determine the role of these cortices in recognition and other forms of memory.

Investigators have made an important beginning in understanding the function of the cortical regions surrounding the rhinal sulcus in the rat and in developing appropriate rat models of human memory, but many questions remain. What is the fundamental operation performed on the sensory information received by the perirhinal and postrhinal cortices? Do these regions contribute preferentially to only certain forms of memory? Other than memory, to what cognitive processes might they contribute? How does the function of the postrhinal cortex differ from that of the perirhinal cortex? We have summarized the available neuroanatomical information about the perirhinal and postrhinal cortices in the rat and highlighted some of the remaining issues to be resolved in the hopes of providing a firmer ground for researchers addressing these questions and others in the endeavor to identify the functional role of the cortical regions surrounding the posterior rhinal sulcus in the rat.

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