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ORIGINAL ARTICLE

Cytoarchitecture of mouse and rat cingulate cortex with human homologies

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Abstract A gulf exists between cingulate area designations in human neurocytology and those used in rodent brain atlases with a major underpinning of the former being midcingulate cortex (MCC). The present study used images extracted from the Franklin and Paxinos mouse atlas and Paxinos and Watson rat atlas to demonstrate areas comprising MCC and modifications of anterior cingulate (ACC) and retrosplenial cortices. The laminar architecture not available in the atlases is also provided for each cingulate area. Both mouse and rat have a MCC with neurons in all layers that are larger than in ACC and layer Va has particularly prominent neurons and reduced neuron densities. An undifferentiated ACC area 33 lies along the rostral callosal sulcus in rat but not in mouse and area 32 has dorsal and ventral subdivisions with the former having particularly large pyramidal neurons in layer Vb. Both mouse and rat have anterior and posterior divisions of retrosplenial areas 29c and 30, although their cytology is different in rat and mouse. Maps of the rodent cingulate cortices provide for direct comparisons with each region in the human including MCC and it is significant that rodents do not have a posterior cingulate region composed of areas 23 and 31 like the human. It is concluded that rodents and primates, including humans, possess a MCC and this homology along with those in ACC and retrosplenial cortices permit scientists inspired by human considerations to test hypotheses on rodent models of human diseases.

Keywords Anterior cingulate · Midcingulate cortex · Retrosplenial cortex

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Introduction

It is well established that Brodmann's (1909) designation of anterior cingulate cortex (ACC) does not represent a single structure/function entity and the human imaging community has sought to resolve this problem by applying spatial designations within ACC that do not reflect cytoarchitectural organization. Dorsal ACC, for example, is a term that is variably used to refer to area 24b above the genu of the corpus callosum (Mayberg et al. 2000), areas 24c′ and 32′ (Bush et al. 2002) or areas 24′ and 23 (Wager et al. 2004). We resolved the problem of cingulate, rostrocaudal transition and ACC heterogeneity in primates by introducing the midcingulate concept. The human midcingulate cortex (MCC) has been validated as a qualitatively unique structure/function region that differs from ACC based on cytological (Vogt et al. 1995), functional imaging (Vogt 2009), multireceptor binding (Palomero-Gallagher et al. 2009), and basal glucose metabolism (Vogt 2009).

Brodmann (1909) was actually the first to realize that ACC in many non-primates was not uniform and suggested that area 23 lies between areas 24 and 29 in the rabbit, squirrel, fox and hedgehog, while expressing concern that this region is agranular and not granular like area 23. This conundrum was resolved when the midcingulate concept

was proposed for the rabbit and monkey (Vogt 1993) based on its cytoarchitecture, projections to the pontine nuclei in rat (Wiesendanger and Wiesendanger 1982a, b), transient developmental expression of oxytocin receptors in rat (Tribollet et al. 1989) and regulation of muscarinic receptors during discriminative avoidance learning in rabbit (Vogt et al. 1991). Preliminary observations suggest that MCC is also present in the rat (Vogt et al. 2004).

There has been ongoing confusion in the rodent literature as to the organization of ACC. The mouse (Franklin and Paxinos 2007) and rat (Paxinos and Watson 2007) atlases employ an old scheme which posits "prelimbic" (PL), "infralimbic" (IL) and "limbic" (Cg1 and Cg2) areas (Brodmann 1909; Rose and Woolsey 1948). These designations, however, do not refer to limbic functions as "IL," for example, has the most prominent projections to the nucleus of the solitary tract (Gabbott et al. 2005) and does not lie below limbic cortex but is part thereof. In addition, these terms are not used for primate research and this has produced a gulf between human imaging studies and those in rodent and this is a particular problem because efforts to model aspects of human diseases with rodents are impeded.

As we are revising the mouse and rat atlases to include MCC, it is time to explain and justify these major changes in the rodent atlases along with new observations in ACC and retrosplenial cortex (RSC). Using images extracted from the atlases, we accomplished the following goals: (1) We tested the hypothesis based on connection and functional studies that area 32 can be divided into dorsal and ventral parts. (2) The MCC was identified in the mouse and rat and its lamination patterns provided which is not part of the atlases. (3) We show that areas 29c and 30 are composed of anterior and posterior divisions. (4) Maps of both species were constructed for direct comparison to a flat map of the human cingulate cortex. This systematic exercise revealed a MCC cytology for rodents that is present in most, if not, all mammalian species studied and removes any doubt that rodents can be used to model human diseases related to the MCC.

Methods

The medial surface from each atlas was imported into Photoshop CS2; thirty Nissl and adjacent acetylcholinesterase (AChE) sections were extracted from the mouse (Franklin and Paxinos 2007) and 60 from the rat (Paxinos and Watson 2007) atlases. Every section was evaluated through the entire cingulate cortex and sections selected for photography. The planes of section are shown on the medial surface map and numbers in each figure refer to the plate numbers in the atlases. The histological sections were co-registered at the same magnification to the medial surface and the exposures adjusted so that all sections were the same because staining intensity and exposures in the atlas were often not equivalent. In some instances, such as Plates 6–14 in the rat, only Nissl sections were available. Finally, the horizontal sections in both atlases were too ventral to assess the histological ACC/MCC border.

The maps are not equivalent to any sagittal section from the atlases as warping was required. The layer II/III border was used to strike the location of area borders and the rostrocaudal extent of each area was held constant to the atlas coordinates so the maps are consistent with the coordinates along the corpus callosum. Since area 30 extends onto the dorsal surface particularly in the rat, it was extended dorsally to reflect this fact. Additionally, areas 29a and 29b overlie the superior colliculi and they were extended ventrally beyond the borders of the rat atlas parasagittal sections. Finally, the distribution of areas was smoothed to account for minor variations in co-registration of <100 μm in any plane. As is always the case, the maps are a schematic generalization.

Results

Anterior cingulate areas 32 and 33

Subcortical and corticospinal projections from area 32 differentiate dorsal and ventral subdivisions of area 32 (Gabbott et al. 2005; Fig. 1c. "Rat Projections"; red arrow indicates the potential division for subcortical projections). Since corticospinal projection neurons are particularly large and are located mainly in layer Vb of dorsal rather than ventral area 32 (d32 and v32, respectively), we explored the hypothesis that large neurons in the former might assist in differentiating two divisions of area 32. There were groups of large neurons in layer Vb of both species (red asterisks in Fig. 1b, Plate 13; Fig. 1c, "Area 32") and they were most prominent in area d32. The mouse also had an AChE-rich plexus in layer Va of area v32 that tapers off in area d32 (Fig. 1b, Plate 14; red arrow). A feature unique to the mouse is the particularly large neurons in layer III of area v32 that are not present in d32 (Fig. 1b, Plate 13; compare layer III above and below the red line). Other morphological details in both species distinguishing area d32 from v32 included clumps of neurons in layer II (3 black arrowheads) and a more neuron-dense layer III in d32 than in v32. Although layer VI in the mouse appears as a single layer, the rat has three divisions of this layer (Fig. 1c, right panel). Neurons in layers VIa and VIb are small but those in the latter are more sparsely packed. Layer VIc is composed of larger neurons and it is just a few neurons thick in area v32 but thicker and more prominent in area d32.

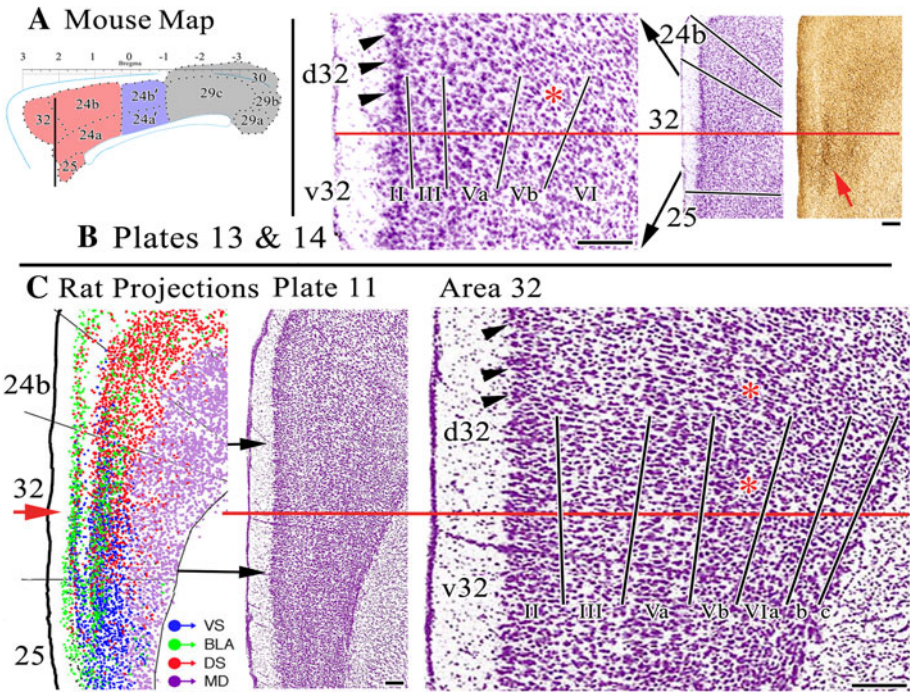

Fig. 1 Differentiation of area 32 into dorsal and ventral divisions. **a** Mouse map showing the level of the sections taken for Plates 13 (Nissl) and 14 (AChE; *right panel*). **b** The *red line* demarcates the two divisions and *arrowheads* emphasize neuron islands in layer II of area d32. The AChE plate on the *right* shows a layer Va plexus in area v32 (*red arrow*) that is not present in area d32. **c** A summary illustration from Gabbott et al. (2005) showing projection neurons from the ventral striatum (VS), basolateral nucleus of the amygdala (BLA), dorsal striatum (DS) and mediodorsal thalamic nucleus (MD). This summary suggests there is a distinction between dorsal and ventral area 32 in the rat and the *red arrow* shows the hypothesized split point. The *red line* is extended from the arrow in Plate 11 and its magnification labeled area 32 and the *black lines* were drawn along the layer borders of each part of area 32. The three *black arrowheads* identify neuronal islands as for the mouse. The *two red asterisks* note two groups of large neurons in layer Vb that we speculate may be examples of large corticospinal projection neurons. *Scale bars* 100 μm

Anterior cingulate in the rat has a small and relatively undifferentiated area just above the indusium griseum (Fig. 2). Swanson (1999) referred to this area as "ILA" and the human brain has a poorly differentiated area 33 in a similar position (Vogt and Palomero-Gallagher 2012). It appears that the rat has a similar area 33 that is not detectable in the mouse. There are minor differences between area 33 in ACC and MCC with a slightly more neuron-dense layer II in the latter; nevertheless, the deep layers in particular are difficult to delimit. Because this area is small and does not appear to include the entire MCC, we include it as part of ACC where it is most prominent.

Midcingulate area 24′

The composition of MCC area 24′ in the mouse is demonstrated in Fig. 3. The breadth of layers II and III and sizes of neurons in Plate 35 emphasize that this is not area 29c (Fig. 3d, #41) but rather area 24′ as area 29c has more dense layers II and III and a layer IV. Neurons in all layers of ACC area 24 are smaller than that in area 24′ and this is emphasized in the figure with red arrows in layer Va (Fig. 3b) and the higher magnification photographs in Fig. 3d. The latter microphotographs also show that neurons in layers II–V are prominently larger and neuron packing in layer V is less dense, as expected with neurons that have larger dendritic fields, in all layers. The AChE preparations (Fig. 3c) emphasize differences between areas 24b and 24b′. The former has dense plexi in layers I, III and Vb (Plate #24) that are substantially reduced in MCC (Plates #30 and #36). Although there is always a gradation in cytoarchitectural features within any cingulate area, it is clear that MCC can be identified in the mouse based on neuron sizes, packing densities and AChE staining.

Sections were selected from each cingulate region to evaluate progressive changes in the cytoarchitecture of rat cingulate cortex (Fig. 2). As is the case for the mouse, the rat MCC has substantially larger neurons in all layers compared to ACC. The large layer Va neurons are particularly prominent and comparison of areas 24b and 24b′ in the magnified sections emphasizes this fact (Fig. 2c). In particular, note that layer Va from Plates 42 and 46 has very large neurons, although some variations occur between sections. The net result of generally smaller neurons in ACC is that the cortical lamination in these areas is

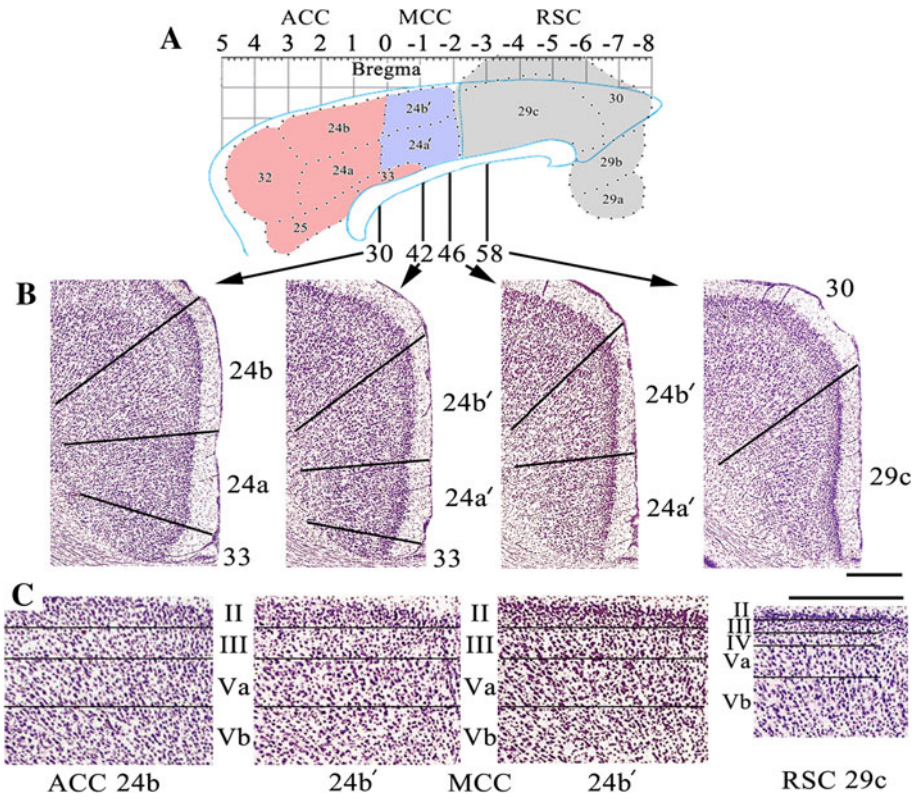

Fig. 2 Localization of MCC in the rat. **a** Rat map with selected levels. **b** Macrophotographs of each level with area borders marked. **c** Microphotographs showing each layer of ACC area 24b, MCC area 24b′ and area 29c. *Scale bars* 0.5 mm

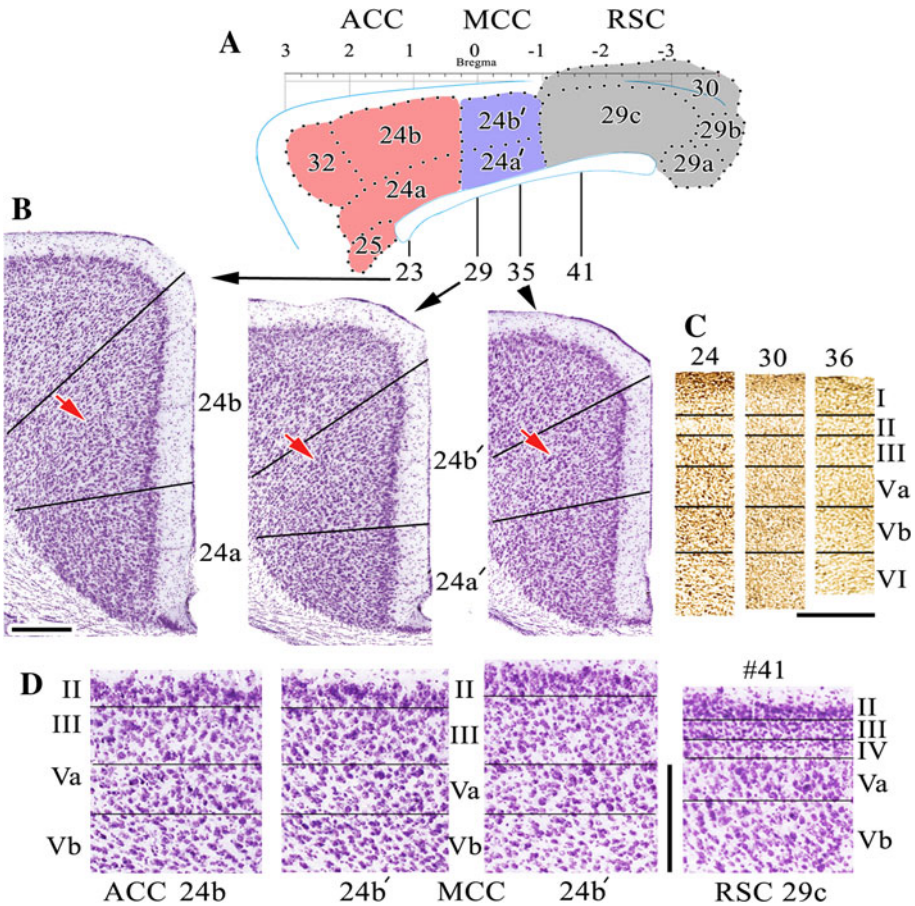

Fig. 3 Characterization of midcingulate cortex in the mouse. **a** Mouse map with four levels identified for microphotographs. **b** Three macrophotographs of coronal Nissl sections with borders noted for each area. The *red arrows* point to the largest neurons in layer Va to emphasize the differences in size in ACC and MCC. **c** Adjacent AChE shows that ACC (Plate 24) has prominent reactivity in layers Ia/b and III–Vb that are substantially reduced in MCC (Plates 30 and 36). **d** Magnifications of each area to show differences in neuron sizes; layer II in Plate 29 has the largest neurons in this layer, while the largest neurons in layer Vb are in Plate 35. In general, neurons in all layers of ACC are larger than those in MCC. Area 29c has greatly reduced neuron sizes and densities (Plate #41) that differentiates it from MCC. *Scale bars* 1 mm

less pronounced and the overall laminar cytoarchitecture appears less differentiated (Fig. 2b, c; Plate 30).

Retrosplenial areas 29 and 30

Retrosplenial connection patterns reviewed in the "Discussion" show differences in the intracingulate connections of rat anterior and posterior parts of areas 29c and 30 and we considered the hypothesis that this was reflected in their cytoarchitectural organization. Figure 4 shows anterior and posterior levels of RSC. The posterior areas 29c and 30 (p29c and p30, respectively) have a layer VIc with neurons that are larger than those in layers VIa and VIb (Fig. 4c, d; red arrows) and which are not present in the anterior areas. In addition, note that layer VIb is relatively neuron sparse in posterior levels, although the anterior section has an even lower neuron density without a layer VIc. Other differences between these areas include a thicker layer III in area p29c and thicker layers II–III in area p30. Finally, neurons in layer Vb are somewhat larger in the posterior than in anterior levels of these areas (Fig. 4c, d; red arrows).

The mouse also has anterior and posterior divisions of areas 29 and 30; however, their cytoarchitecture differs from the rat. Figure 5 shows two levels of these areas from the mouse atlas and the macrophotographs (Fig. 5b, c) show that both posterior areas are significantly thicker. Interestingly, the large neurons in rat layer VIc of areas p29c and p30 are not present in the mouse. Instead, layer VI is composed of small neurons that intermingle with those in layer Vb (Fig. 5c; parentheses for emphasis). Layer Vb itself in area p29c is more robust than that in area p30 with larger and more densely packed neurons. Finally, although there is a layer IV in area a30, it is incipient (almost undetectable), while that in area p30 is dysgranular (variable thickness but more clearly defined).

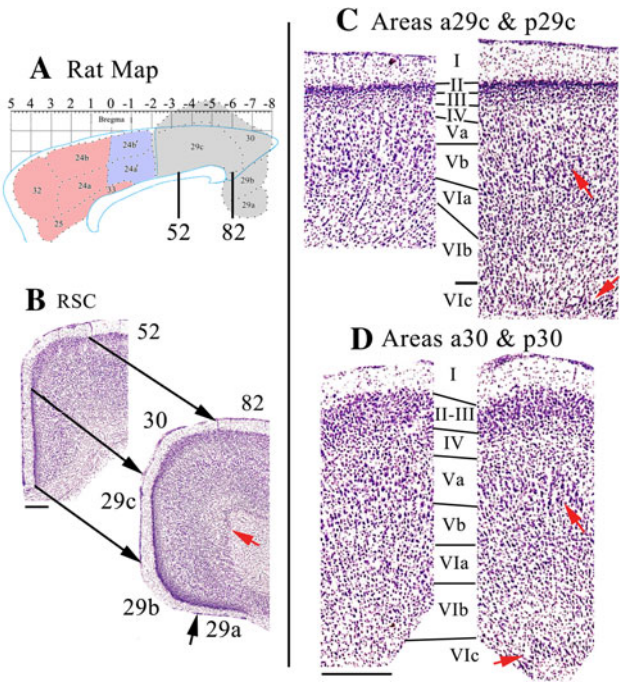

Fig. 4 Differentiation of anterior and posterior retrosplenial areas 29c and 30 in the rat. **a** Rat map showing levels of two sections shown as macrophotographs (**b**) and microphotographs (**c**, **d**). Of particular note in making the differentiation of a29c/p29c and a30/p30 are the large neurons in layer Vb (*red arrows*) and the presence of a layer VIc (*red arrows*) in both posterior areas. Also note that layer IV is more difficult to identify in the anterior than in posterior divisions. *Scale bars* 200 μm

Discussion

This study is a major revision of our first rat cytoarchitectural study (Vogt and Peters 1981) and the first time the mouse cingulate cortex has been subjected to an equivalent analysis. It demonstrates that mouse and rat brains have a MCC and neurons in all if its layers are larger than in ACC with layer Va having particularly prominent neurons. Although MCC has some variability, there are not adequate laminar differences to declare subregions, i.e., no anterior or posterior subdivisions as in monkey (Vogt et al. 2005) or human (Vogt et al. 2003). The ACC area 32 has dorsal and ventral subdivisions that appear to equate to the differential projections of these areas to the brainstem and spinal cord. Finally, RSC areas 29c and 30 are not uniform but have anterior and posterior divisions that may partially reflect differences in intracingulate, visual cortical and thalamic afferents. These findings will be incorporated into future editions of the widely used mouse and rat atlases.

We explored the hypothesis that area 32 is composed of cytoarchitectural dorsal and ventral subareas based on the work of Gabbott et al. (2005; Fig. 1c) and concluded that both mouse and rat have areas d32 and v32. Moreover, the clumps of large neurons in layer Vb of area d32 may reflect the fact that many of these large neurons have corticospinal projections (Gabbott et al. 2005). The concept of this dichotomy was considered in the larger context of medial prefrontal cortex by Heidbredera and Groenewegen (2003) who proposed a dorsal component composed of FR2, dorsal ACC, and dorsal prelimbic cortex and a ventral component including ventral prelimbic, infralimbic and medial orbital areas. Functionally, they proposed that the dorsal part is involved in the temporal shifting of behavioral sequences, while the ventral part is responsible for a flexible shifting to new strategies related to spatial cues. Connection differences were also noted with the dorsal areas heavily connected with sensorimotor and association neocortical areas, while the ventral areas virtually lacked such connections but had extensive connections with the

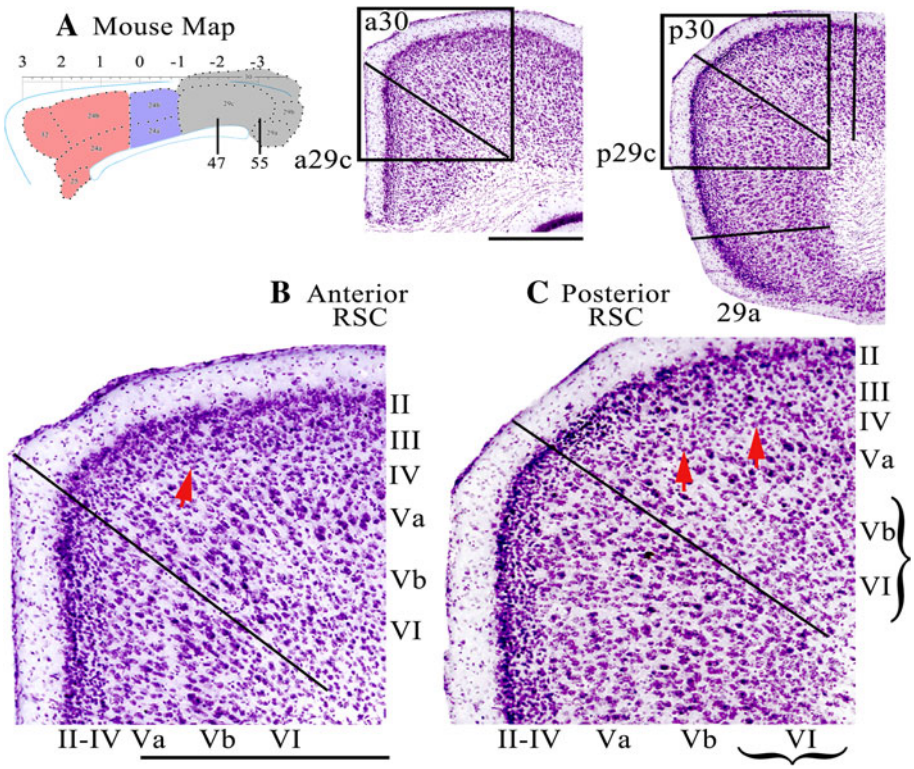

Fig. 5 Differentiation of anterior and posterior retrosplenial areas 29c and 30 in the mouse. **a** Mouse map showing levels for the anterior (**b**) and posterior (**c**) divisions of each area. The macrophotographs show the border between areas 29c and 30 and a box from which the microphotographs were taken. Layer IV in a30 is incipient (virtually undetectable, *red arrow*), while in area p30 it is dysgranular (variable in thickness). Also note that layers Va and Vb have larger neurons in the anterior than in posterior divisions and that layer VI is quite dense in the posterior divisions and these small neurons appear to intermingle with neurons in layer Vb (*parentheses* emphasize this latter point). *Scale bars* 0.5 mm

amygdala and temporal, limbic association cortices. The ventral cortices also project to the septum, and medial preoptic and hypothalamic areas, while dorsal projections to these areas are limited. Finally, projections to brainstem monoaminergic cell groups are stronger from the ventral compared to the dorsal areas.

The distribution of ACC and MCC is validated by rat studies of intracingulate, visual cortical and thalamic connections and these connections are thoroughly reviewed in the context of the new map of cingulate regions and areas (Vogt 2013). Intracingulate studies (Vogt and Miller 1983; van Groen and Wyss 2003; Jones et al. 2005) show a number of topographies that include the following: (a) area 32 projects mainly to MCC but not to RSC; (b) area 24a has a prominent projection to area 32 and lightly to areas 29a/b, while area 24b projects to MCC and areas p29c and 30; (c) area 24a′ projects lightly to areas 24a/b, throughout much of area 30 and rostral areas 29a/b, while area 24a′ projects mainly to area 24b, along the ventral edge of area 29c and includes a moderate but widespread projection to the remainder of areas 29 and 30; (d) area a29c projects mainly to area 24b′, less so to areas 24b and 24a′, and moderately throughout areas 30 and 29a/b; (e) area 29b projects mainly to area 29c and only moderately to area 30 and MCC and also projects heavily to area 33 emphasizing that this latter area is not part of area 24a; (f) area 30 projections have a distinct topography with area a30 projecting mainly to MCC and area 24b, heavily throughout all of area 30 and moderately to areas 29a/b, while area p30 projects mainly to areas 24a, dorsal area a29c, and 29b and has moderate projections to MCC. In summary, area 32 has distinctly limited projections to area 24 and light projections to MCC with virtually none to RSC. Area 24 projections are mainly to areas 24 and 24′ and modest projections to caudal and ventral areas 30, 29c, and 29a/b. Area a29c has a robust projection to area 24b and moderate projections to areas 24a′/b′ and virtually none to ACC. Area 29b has projections mainly in area 33 and RSC. Finally, in spite of the topography within area 30 projections, the main projections are within RSC and MCC with only a small projection to area 24a.

The first report of direct, robust, and reciprocal interactions between cingulate and visual cortices was made in a study of retrogradely labeled neurons and anterogradely labeled terminals (Vogt and Miller 1983) and it was later validated and extended by Paperna and Malach (1991). Some of the key findings of these studies are substantial projections of area 18b to MCC, and areas a30, p30, 29b and 29a. While area 30 has massive projections into visual areas 17 and 18b, area 29c does not. Area 17 has major projections into MCC and areas p30 and 29b. These studies show that ACC and MCC have differential interactions with visual cortex.

The ACC/MCC border is supported by thalamic afferents in a study by Horikawa et al. (1988). Area 24 receives primarily anteromedial (AM) input, while area 24′ receives

mainly AM and anterodorsal (AD) afferents. Further, Shibata (1993) showed that area 24 receives more input from the interanteromedial nucleus, while area 24′ has a higher density input from AM proper, although AM input is also extensive throughout cingulate cortex. Finally, the midline and intralaminar thalamic nuclei (MITN) differentiate between ACC and MCC. The reuniens nucleus projects most intensely to areas 25 and 24 and less so to area 24′ (also, Herkenham 1976), while the parafascicular nucleus projects to the deep layers of ACC (Marini et al. 1996). Vertes and Hoover (2008) showed that projections from the parataenial nucleus are greatest to ACC, and although they did not identify MCC separately, this projection is quite weak to MCC and terminates mainly in the deep layers versus ACC where they end mainly in superficial layers.

Anterior thalamic projections to RSC are well known and reports by van Groen et al. (1993) and van Groen and Wyss (1995) provide important information regarding the thalamo-retrosplenial projection system. Each nucleus has a different area and laminar projection pattern with the AD and anteroventral (AV) nuclei projecting mainly to area 29c and laterodorsal (LD) projecting to both areas 29c and 30. The AD nucleus projects diffusely throughout layer I and it is more dense in layer IV. In contrast, AV projects mainly to layer Ia in cone-shaped clusters. Other classes of axons terminate diffusely throughout the remainder of layer I and in a tight band in layer IV. Finally, LD projects mainly to layer I in areas 29c and 30, lightly to layer IV in area 29c and densely to layer IV in area 30. This latter observation supports the view that there is an incipient (area a30) and dysgranular (area p30) layer IV in area 30. Thus, the three-region rodent model demonstrated with cytoarchitecture is supported by intracingulate, visual and thalamocortical connections.

There is a critical difference between primates and rodents that must be emphasized; the corticospinal system in rats originates in ACC, while that in primates originates in MCC. The distribution and connections of the cingulate premotor areas in cingulate sulcal cortex in the monkey and human MCC are well established (Morecraft and Tanji 2009; Vogt 2009) as are autonomic projections originating from subgenual ACC (Vogt and Derbyshire 2009). In contrast, the rat corticospinal system arises mainly from ACC areas 32 and 24b (Gabbott et al. 2005) and terminates prominently to the central autonomic area of the thoracic spinal cord where axons form excitatory synapses (Bacon and Smith 1993). Thus, it appears that these two motor regulatory systems overlap to some extent in rodents in contrast to primates where they are clearly segregated.

With the maps in Fig. 6, the topographies of rodent and human (Vogt 2009) cingulate cortices can be compared by region and area. The arrows emphasize positions of ACC, MCC and RSC in human and rat brains. There are a number of striking differences between these species as well as the mouse. First, since rodents do not have a cingulate sulcus, they are devoid of sulcal areas d32, 24c, 32′, a24c′, p24c′, 24d and 23c. Second, while the human has anterior and posterior divisions of MCC, rodents have a relatively uniform MCC. Third, although the ectocallosal area 33 spans the full extent of human ACC and MCC, it has only a minor presence in rat and none in the mouse. Fourth, there are no posterior cingulate areas 23 and 31 in rodents where posterior cortex is composed entirely of RSC. These maps provide the basis for assessing the value of functional rodent studies as they relate to human brain function and the extent to which any rodent model of a human disease reflects the topographic organization of cingulate cortex.

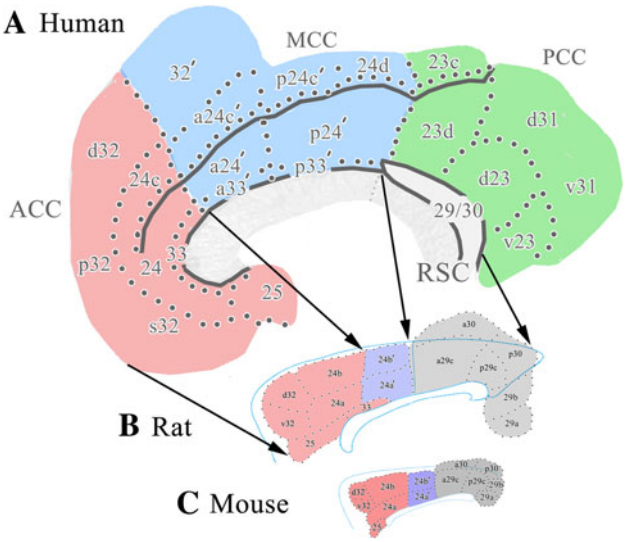

Fig. 6 Rodent maps compared to one in the human with similar *color* coding and *arrows* between the human and rat to emphasize relationships between ACC, MCC and RSC. Rodents do not have posterior cingulate areas 23 and 31. The MCC has a prominent differentiation into anterior (a) and posterior (p) divisions in human. The substantial expansion of MCC and addition of PCC in the human results in a major displacement of ACC rostrally and ventrally around the genu of the corpus callosum

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