

Chapter 19

The Evolution of Auditory Cortex: The Core Areas

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Abbreviations

A	anterior auditory area
AAF	anterior auditory field
AchE	acetylcholinesterase
AI	primary auditory cortex
AII	second auditory cortex; nonprimary auditory cortex
CM	caudal medial field
CO	cytochrome oxidase
DC	caudodorsal field
DZ	dorsal zone
fMRI	functional magnetic resonance imaging
MG	medial geniculate body
MGm	medial division of the medial geniculate body
MGd	dorsal division of the medial geniculate body
MGv	ventral division of the medial geniculate body
P	posterior auditory area
PAF	posterior auditory field
PL	posterior lateral field
PPF	pseudosylvian field
PSF	posterior suprasylvian field
R	rostral area
RT	rostromedial temporal area
SI	primary somatic sensory cortex
SSF	suprasylvian fringe
UF	ultrasylvian field
VP	ventral posterior area

1 Introduction

An alternative title might be “What, if Anything, is AI?” AI, of course, is primary auditory cortex, an area of cortex that likely all mammals have. Thus, this seems a naive or a

puzzling question. Yet, an important issue is hidden in this question. And this type of question was formulated long ago: “What, if anything, is a rabbit?” (Wood 1957). Classification was the issue, and it concluded that rabbits had been mistakenly classified as rodents. That view has prevailed, and rabbits are now considered Lagomorphs. Some time ago, I asked “What, if anything, is S1?” (Kaas 1983). I felt that the term S1 was being used inconsistently to refer to four areas (areas 3a, 3b, 1 and 2) in human and other anthropoid primates, while only one of these areas was considered to be S1 (area 3b) in most mammals. Again, this pertains to the issue of proper identification. All mammals appear to have a region of auditory cortex, but the descriptions of how it is organized vary across species, and even between studies on the same species. Rather than deal with the daunting task of considering the many auditory areas proposed, this review focuses on the so-called core areas, those better-defined areas that have many or most of the characteristics of primary auditory areas, such as AI. In many of the well-studied mammals, where AI has been identified, one or two other areas have been described that have many of the defining features of AI, such as inputs from the ventral division of the medial geniculate complex (MGv), pronounced architectonic features of sensory cortex, and a tonotopic organization. Ambiguous designations of AI could create confusion and misidentification, and the conclusion here is that this has happened. We wish to identify in different species for the same area originally identified as AI in cats, that is, the area in other species that is homologous to cat AI. While homologues originally were defined as features or body structures that were the same in two or more species, a modern definition more specifically requires that the similarity is the result of the retention of the feature or structure from a common ancestor, and that the resemblance is not simply the result of convergent evolution. In addition, homologous structures need not be identical or similar in all ways since they evolve different specializations in branching lines of descent. Thus, AI need not be identical across species, and other non-homologous areas might resemble AI closely because of convergent or parallel evolution. AI is therefore best identified by features

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that are unlikely to be present in other fields. One criterion would feature position relative to other areas. For AI, we add the feature of the orientation of the tonotopic gradient. While other areas may have the same tonotopic gradient as AI, they would not have both the same position relative to other areas and the same tonotopic gradient. Using this line of reasoning, the goal is to identify homologous core areas across taxa. Given the present stage of understanding, the homologues of secondary auditory areas present an even more challenging task best left for another occasion.

2 Cortical Areas Are the Larger Subdivisions of the Cortical Sheet

Cortical areas have been called the organs of the brain (Brodmann 1909). This implies that each cortical area has a unique set of functions. To perform these functions, this often meant some level of specialization of cortical cellular structure within the area. Therefore, early anatomists used histological differences in the appearance of cortical regions to identify subdivisions with presumed functional significance, the cortical areas. As cortical areas mediate function by transforming inputs and redistributing information to their outputs, each area should also be distinguished by a unique pattern of extrinsic connections. Often this includes a systematic arrangement of inputs and outputs so that an orderly map of these arrangements can be revealed within an area. For sensory areas such as the several auditory areas, this suggests an orderly representation of the peripheral receptor array leading to patterns of tonotopic or cochleotopic organization. Neurons in auditory and other sensory areas may also have other response properties that distinguish the areas. Areas are most reliably identified by a congruence of histological, connectional, and physiological distinctions (Kaas 1982). The hypothesis that an area has been identified validly by distinctive traits can be tested by inactivation, ablation, and microstimulation experiments that show that the proposed area is uniquely involved in certain brain functions.

3 The Origin of Auditory Cortex

Components of the mammalian brain stem auditory system can be found in amphibians, reptiles, and birds (Bruce 2007; Sterbing-D'Angelo 2007). However, comparative studies do not reveal how auditory cortex emerged in mammals. While the immediate ancestors of mammals are traditionally called mammal-like reptiles (Colbert and Morales 1991), present day mammals and reptiles are not closely related. Thus, early reptiles are now referred to as stem amniotes (descendants of amphibians which adapted to terrestrial life by developing an amniote egg or amniotic membranes in

live-bearers). These stem amniotes formed two major clades some 320 million years ago: the Sauropsida leading to modern reptiles and birds, and the Synapsida, with only mammals surviving. Thus, nothing is known about the forebrain organization of the extinct mammal-like reptiles that preceded mammals. It is a reasonable surmise that the amniote ancestors of mammals had a dorsal cortex much like that of extant reptiles, which is widely regarded as homologous to mammalian neocortex (sometimes called isocortex) (Northcutt and Kaas 1995; Striedter 1997; Kaas 2007; Medina 2007). The dorsal reptilian cortex is a thin, with only one main layer of cells, while neocortex is thick and has six traditionally defined layers. The inputs to dorsal cortex are widespread within it (Ulinski 2007), and there are few functional subdivisions that could define regional areas. More importantly, there is no evidence that any of dorsal cortex is auditory, as most or all of the projections from the auditory thalamus terminate in the striatum or the dorsal ventricular ridge, rather than dorsal cortex (Bruce 2007; Medina 2007). How a structure like dorsal cortex might transform into a much larger, thicker, and laminated neocortex with distinct sensory areas is unknown. Thus, this review is restricted to mammalian auditory cortex. Before considering auditory cortex organization in a phylogenetic distribution of species (Fig. 19.1), we begin by reviewing proposals for how auditory cortex is organized in domestic cats, and then other studied carnivores. The justification for this is that cat auditory cortex has been the focus of many early studies in which key concepts of auditory cortical organization were developed.

4 Auditory Cortex Organization in Cats and Other Carnivores

Current understanding of auditory cortex organization in cats began when electrical stimulation of different sectors of the cochlea was used to activate auditory cortex and identify two systematic representations of the cochlea, areas AI (primary auditory cortex) and AII (nonprimary auditory cortex) (Woolsey and Walzl 1942). This early AI was somewhat larger than AI as presently construed (Fig. 19.2), and included parts of the present day AAF (anterior auditory field). This early AI was larger because the methods then used, brain-surface electrode recordings with electrical stimulation of the cochlea, were not very sensitive to reversals of tonotopic organization and other boundary markers. Early AI represented the cochlea from base to apex in a caudal to rostral direction, corresponding to a low-to-high tone frequency representation repeatedly confirmed in more modern studies of AI (e.g., Merzenich et al. 1973, 1975). Thus, for any caudorostral series of recording sites across AI, the characteristic or best frequency (the frequency of

The Evolution of Present-day (extant) Mammals

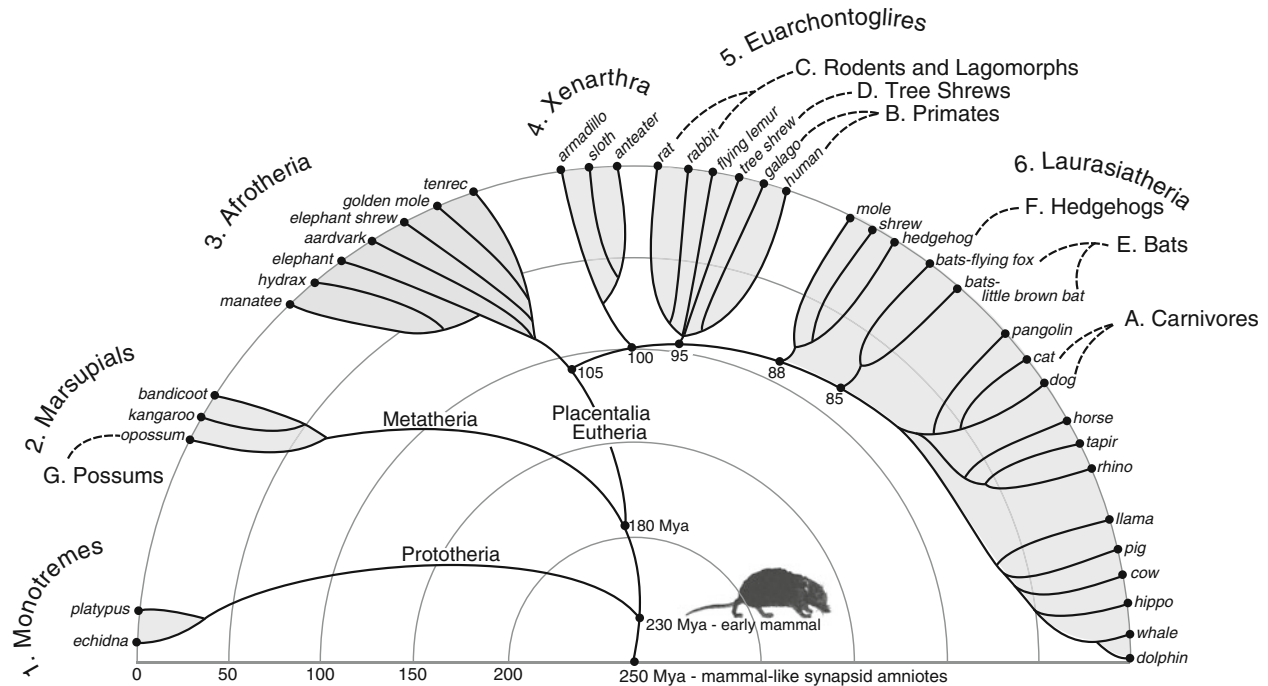


Fig. 19.1 The phyletic distribution of present-day (extant) mammals. Studies of molecular similarities divide extant mammals into six major clades or superorders (Murphy et al. 2004). Numbers denote the estimated times of divergence of each clade and several of its major branches from its ancestral common origin from another clade.

Prototherian mammals (monotremes) thus diverged from the ancestors that gave rise to other extant mammals ~230 million years ago. The mammal-like reptiles that gave rise to mammals are designated cladistically as synapsid amniotes. Some of the mammals considered in this review are noted (A–G)

the tone that would activate the recorded neuron or neuron cluster at the lowest sound intensity) for activating cells progressed from low-to-high tones. In the dorsoventral axis across AI, best frequencies did not change, and this was considered the direction of isorepresentation of tone frequency. The early AI was associated with a region of architectonically distinct cortex (Rose and Woolsey 1949a) and a pattern of thalamic connections with the medial geniculate complex (Rose and Woolsey 1949b). Subsequent studies further defined the features of AI. While the general location of cat AI has been readily established physiologically, determining the precise boundaries can be difficult as adjacent areas have a tonotopic sequence bordering AI (Fig. 19.2). In addition, the neuronal properties of AI cells vary within it (Read et al. 2002), and between AI and other areas. Thus, some investigators even distinguish dorsal, central, and ventral sectors of AI, and central AI neurons have the lowest response thresholds and more regular response properties (Mendelson et al. 1997). AI subregions also vary in the spatial representation of spectral integration (Imaizumi and Schreiner 2007). Because borders of AI and other areas can be difficult to precisely locate with physiological measures, architectonic studies can be useful in delimiting

AI and other fields, although AI and adjoining primary-like fields (e.g., AAF in cats) can have a similar architecture. Cytoarchitectonically, cat AI has a thick layer 4 that is densely packed with smaller neurons (Rose 1949; Winer 1984) and the middle layers are more densely myelinated and express more cytochrome oxidase (CO), parvalbumin, and acetylcholinesterase (AChE) than do non-primary cortical areas (Wallace et al. 1991). AI also has a denser staining pattern with the monoclonal antibody (CAT-301) which recognizes a cell-surface proteoglycan. AI receives a dense, topographically organized input from the ventral (principal) division (MGv) of the medial geniculate complex, which is also tonotopically organized (Winer et al. 1977; Morel and Imig 1987; Brandner and Redies 1990; Lee et al. 2004; Lee and Winer 2008a). Ipsilateral cortical connections with adjoining and other auditory areas are widespread, including AAF, AII, and P (the posterior auditory area) (Lee et al. 2004; Lee and Winer 2005, 2008b; Winer and Lee 2007). A second auditory area, AII, was also proposed and was thought to have a tonotopic organization reversed from that in AI, with high tone frequencies represented caudally and low frequencies represented rostrally (Woolsey and Walzl 1942). This erroneous assumption was likely influenced by results from

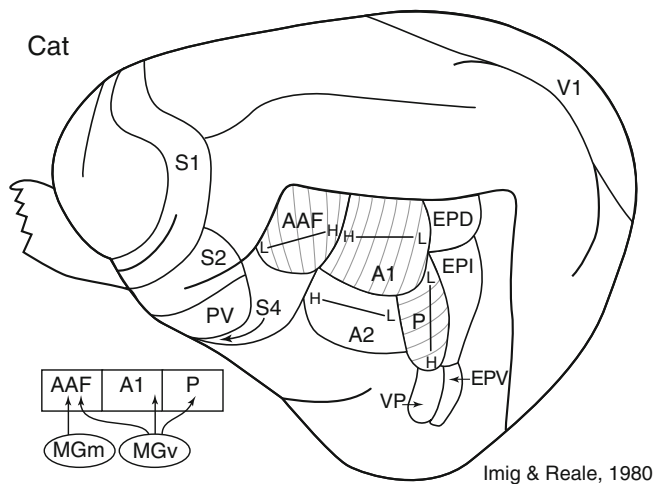


Fig. 19.2 Auditory cortex subdivisions for domestic cats on a dorso-lateral view of the left cerebral hemisphere. Auditory areas include the primary area (AI), the second area (AII or A2), the anterior auditory field (AAF), the posterior auditory field (P), the ventroposterior field (VP), and dorsal (EPD), intermediate (EPI) and ventral (EPV) divisions of auditory cortex of the ectosylvian gyrus. For reference, primary visual (V1) and somatic sensory (S1) are outlined, as well as the second (S2), fourth (S4), and parietal ventral (PV) somatic sensory fields. Boxes (lower left) indicate that AAF, AI, and P all receive inputs from the ventral nucleus of the medial geniculate complex (MGv). AAF may receive more input than AI from the medial nucleus (MGm) (Imig and Reale 1980)

cortex now considered to be outside of AII. The current, smaller extensive AII has a tonotopic organization parallel to that of AI, ranging from low to high frequencies in a caudorostral sequence (Fig. 19.2) (Schreiner and Cynader 1984). AII has a less precise tonotopic organization than AI, neurons with broader frequency tuning and a higher response threshold, and a marked reduction in the architectonic features pronounced in AI and other primary cortical areas. Projections from the ventral nucleus of the medial geniculate complex to AII are sparse (Morel and Imig 1987; Lee and Winer 2008a). Overall, cat AII would be considered as part of the auditory belt (nontotopic areas) in primates, while AI would be part of the primary or primary-like (tonotopic) core (Kaas and Hackett 2000). Cortex on the dorsal AI border, the poorly defined suprasylvian fringe (SSF) or dorsal auditory zone (DZ) area, in the suprasylvian fissure, also has belt-like physiological and anatomical features (Wallace et al. 1991; He and Hashikawa 1998), and would be considered belt cortex in primates. The part of the SSF immediately adjoining AI has been redefined as the dorsal zone (DZ) (Reale and Imig 1980; Stecker et al. 2005).

In contrast to AI bordering areas AII and SSF, the cortex rostral to AI is primary-like. The anterior auditory field (AAF) (Fig. 19.2) includes cortex that was originally considered part of AI but is distinguished by a tonotopic organization that is a reversed or a mirror image of that in AI

(Knight 1977; Imaizumi et al. 2004). Thus, AAF represents tone frequencies from high to low in a caudorostral sequence, and isorepresentation lines course dorsoventrally as in AI. AAF has architectonic features like those of AI, and receives dense projections from MGv, although lighter than those to AI (Imig and Morel 1985; Huang and Winer 2000; Lee et al. 2004; Lee and Winer 2005, 2008a). Both AI and AAF also receive other significant inputs from the dorsal and medial (magnocellular) divisions of the medial geniculate complex. The interconnections between AI and AAF place them at the same hierarchical level of cortical processing (Rouiller et al. 1991). Finally, the response properties of AAF neurons resemble those in AI (Knight 1977; Eggermont 1998; Imaizumi et al. 2004) but are more broadly tuned for frequency, and have shorter response latencies. AI and AAF both are primary areas, processing subcortical auditory inputs in parallel, as originally postulated (Knight 1977). However, the two fields are functionally distinct since the deactivation of AI, but not AAF, results in sound localization deficits in the contralateral auditory field (Malhotra and Lomber 2007). Cortex on the caudoventral border of AI, the posterior area (P) (Fig. 19.2), is also tonotopically organized (Reale and Imig 1980). The tonotopic organization of field P reverses from that in AI, with low tones represented next to the dorsal part of AI and high tones in ventral P. The orientation of P is thus rotated so that isofrequency lines are roughly caudorostral in orientation. The response properties of P neurons are primary-like, but less so than in AI (Phillips and Orman 1984). Their response latencies are longer than those in AI and AAF, and neurons may be more involved in coding stimulus intensity. Thalamic inputs include those from MGv, and from other divisions of the medial geniculate complex (Morel and Imig 1987; Huang and Winer 2000; Lee and Winer 2008a). The architectonic features of P have not been described. P has some of the characteristics of a primary cortical field, and may be part of a primary-like core, but this is less certain than for AI and AAF.

Several other auditory cortical areas have been proposed for cats (Lee et al. 2004), including the ventral posterior area (VP) (Fig. 19.2). VP represents tones from high to low in a dorsoventral sequence (Imig and Reale 1980), and the area receives significant inputs from MGv (Huang and Winer 2000; Lee and Winer 2008a). Thus, VP has some of the features of primary cortex, although it is widely considered to be a secondary area. Auditory cortex subdivisions of the posterior ectosylvian gyrus (EPD, EPI, and FVP) all appear to be secondary or higher-order auditory fields.

In summary, cat auditory cortex consists of a core of two, or possibly three, primary or primary-like fields surrounded by a fringe or belt of secondary or higher-order fields. The question addressed next is how the organization proposed for cats compares to that proposed for auditory cortex in other mammals, beginning with other carnivores.

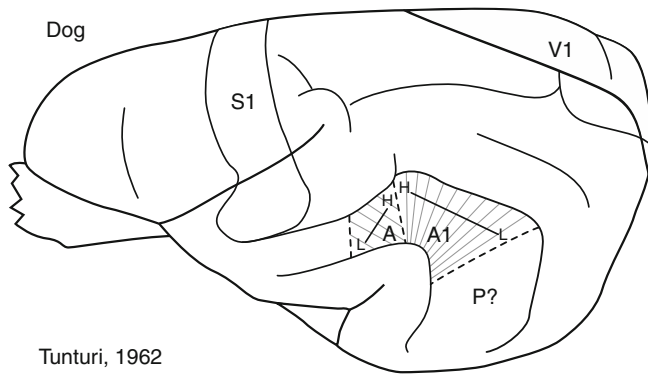


Fig. 19.3 Auditory cortex in dogs. Two areas were defined; one corresponding to AI and the other to AAF of cats (Tunturi 1962). The region (P?) may partly correspond to the posterior area (P) of cats, and was also responsive to sounds. Conventions as in Fig. 19.2 (Tunturi 1962)

In addition to cats, auditory cortex organization has been studied in dogs and ferrets, although not to the same extent. Evoked responses to different tone frequencies in dog auditory cortex, recorded with surface electrodes, provided early evidence for areas corresponding to AI and AAF in dogs (Tunturi 1962). As in cats, frequencies were represented from low to high in a caudorostral sequence in AI and in a rostrocaudal sequence in AAF (Fig. 19.3), and there was evidence for an auditory region caudal to AI, which could correspond to the cat posterior area P. Lesions of the medial geniculate complex produced fiber degeneration in AI and AAF (Tunturi 1970). Subsequent studies using injections of retrograde tracers found that AI and the AAF regions receive major inputs from MGv, and that P and AAF have connections with AI (Kosmal 2000; Malinowska and Kosmal 2003). Thus, there is good evidence for AI and AAF in dogs, and other areas, including P, may exist.

The organization of carnivore auditory cortex has also been studied in ferrets (Fig. 19.4) and two primary-like fields, AI and AAF, have been identified (Kelly et al. 1986; Phillips et al. 1988; Shamma et al. 1993; Kowalski et al. 1995; Wallace et al. 1997; Nelken et al. 2004; Bizley et al. 2005). As in cats and dogs, these areas are tonotopically organized, but they are not simple mirror reversals of each other. Unlike cats and dogs, AI in ferrets represents low-to-high frequencies in a ventrodorsal direction with a rostralward slope, while AAF represents low-to-high frequencies in a ventrodorsal direction with a caudalward slope, as if AI and AAF were folded at their dorsal junction and shared a longer common border, with similar tonotopic progressions. Neurons in both fields were primary-like and responded well to pure tones, with narrow tuning curves at characteristic frequency (Bizley et al. 2005). AAF neurons had slightly shorter response latencies, and similar or slightly broader frequency turning curves (Kowalski et al. 1995; Bizley et al. 2005) as in cats. Although the thalamic connections of these areas have

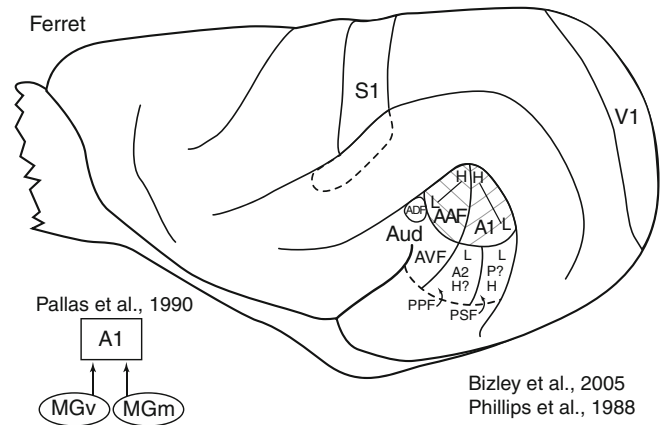


Fig. 19.4 Auditory cortex in ferrets. Both AAF and AI have been identified, and homologues of P and A2 (AII) have been suggested, a posterior pseudosylvian field (PPF) and a posterior suprasylvian field (PSF); the anterior dorsal (ADF) and the anterior ventral (AVF) fields are also noted. Conventions as in Fig. 19.2 (Pallas et al. 1990; Bizley et al. 2005; Phillips et al. 1988)

not been studied in detail, AI receives inputs from MGv and from other divisions (Pallas et al. 1990; Pallas and Sur 1993). AI and AAF are both densely myelinated in ferrets (Wallace et al. 1997), as are primary areas in other mammals. Layer 4 of AAF and AI also has a koniocellular appearance in Nissl preparations and a dense expression of cytochrome oxidase (Bajo et al. 2007). In addition, AI, AAF, and a posterior area are more metabolically active than other areas, as shown by deoxyglucose utilization (Wallace et al. 1997). Finally, only AAF and AI project to the tonotopically organized central nucleus of the inferior colliculus (Bajo et al. 2007). Thus, AAF and AI have been identified in ferrets, and resemble primary sensory cortex. They form two separate tonotopic gradients that join dorsally and drift apart ventrally.

Other auditory fields besides AAF and AI have been proposed in ferrets (Bizley et al. 2005), with two fields immediately ventral to AI, a posterior pseudosylvian field (PPF), and a posterior suprasylvian field (PSF). PPF was thought to be homologous to cat AII, while PSF to the cat field P. PSF is weakly tonotopic, with neurons having longer response latencies than AI or AAF (Bizley et al. 2005). PSF is also referred to as the ventral posterior area, VP (Wallace et al. 1997), a term that can be confused with the differently located cat ventroposterior field (Fig. 19.2). Ferret PSF expresses less myelin than AI and AAF, but more than other auditory areas. PSF also has a glucose uptake level (deoxyglucose) comparable to that of AAF and AI (Wallace et al. 1997). Both AAF and PSF are reciprocally connected to AI (Wallace and Bajwa 1991). Thus, PSF has primary-like features, but they are not as marked as in AI or AAF. PSF (or VP) is the likely homologue of the cat area P. Other auditory areas lacking the characteristics of primary sensory

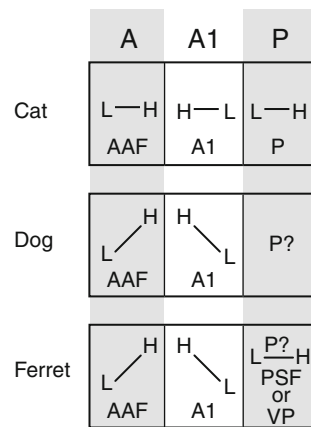


Fig. 19.5 Tonotopic gradients for A (AAF), AI, and P in carnivores. L-H, gradients of tonotopic organization from low-to-high frequencies. Area P in ferrets has been called the posterior suprasylvian field (PSF) or the ventroposterior field (VP). P? reflects a proposed change in nomenclature or uncertainty about the presence of P

cortex have also been proposed for ferrets, including the anterior dorsal (ADF), and the anterior ventral (AVF) fields, both ventral to AAF (Bizley et al. 2005).

Cats, dogs, ferrets, and presumably other carnivores have two primary-like auditory areas, AAF and AI, and a third field with lesser primary-like characteristics, P (Fig. 19.5). These fields form a rostrocaudal sequence of tonotopic representation that reverses at high or low tone boundaries, but this pattern is distorted in ferrets where AI and AAF fold on each other. In these carnivores, P extends ventrally from the caudal margin of AI. Auditory areas surrounding these fields are secondary in nature, and constitute an auditory belt, while AAF, AI, and possibly P form the auditory core. As there are at least two primary fields in cats and other carnivores, criteria for identifying them as homologous across taxa are needed. Clearly not just any tonotopically organized area can be assumed to be AI.

5 Primate Auditory Cortex

It might seem illogical to first compare carnivores (superorder Laurasiatheria) to primates (superorder Euarchontoglires) (Fig. 19.1), but the monkey organization of auditory cortex was a focus of early research that soon followed studies on dogs and cats, so that the concepts of cat cortical organization were applied to monkeys. Early studies in monkeys identified AI, and an adjoining region of cortex was termed AII (Woolsey et al. 1971). Subsequent investigators abandoned the concept of AII and retained a modified AI. As in carnivores, another primary-like area was identified, the rostral area (R), and a further, rostromedial

area (RT) has some features of primary cortex. A belt of secondary fields surrounds these three primary-like core fields. How do the fields in primates compare to those in carnivores? Can any fields be regarded as homologous?

There is a large literature on primate auditory cortex (Merzenich and Brugge 1973; Imig et al. 1977; Morel and Kaas 1992; Morel et al. 1993; Rauschecker et al. 1995; Hackett et al. 1998a; Kaas and Hackett 2000, 2005). Much of the research was on macaque monkeys, whose primary areas are buried in the cortex of the ventral bank of the lateral sulcus (Fig. 19.6). Auditory cortex consists of a core of three primary-like areas which are tonotopically organized, respond well to pure tones, receive input from the MGv and other divisions of the medial geniculate complex, and resemble primary auditory cortex architectonically (Merzenich and Brugge 1973; Morel et al. 1993; Kosaki et al. 1997; Hackett et al. 1998a,b, 2001). The core areas project to the belt areas, and the belt to the parabelt (Galaburda and Pandya 1983; Morel et al. 1993; Hackett et al. 1998b; Jones 2006). Of the belt areas, the caudomedial area (CM) is unusual in having architectonic features intermediate to those of the core and those of the belt (Hackett et al. 2001; de la Mothe et al. 2006a). However, CM may depend on AI input for its tonotopic organization (Rauschecker et al. 1997), and many CM neurons are responsive to somatic sensory as well as auditory stimuli (Schroeder et al. 2001; Fu et al. 2003). It has been postulated that cortex in the medial belt adjoining AI was AII (Woolsey 1971), but that cortex is now included in the medial belt areas. The organization of the primate auditory core can be considered further by comparing the conclusions of various investigators in different monkeys and prosimian galagos. The proposed organization of the core auditory cortex in four species of monkeys (Fig. 19.7) shows Old World macaque monkeys have three core areas, with AI and R forming mirror reversals of each other in tonotopic organization (Fig. 19.7a). RT may form a third reversal, but this has not been fully established in macaques. New World owl monkeys (Fig. 19.7b) have a similar arrangement of three core areas, and a lateral part of RT represents low tones (Imig et al. 1977; Morel and Kaas 1992; Kaas and Morel 1993; Recanzone et al. 1999). Auditory cortex in New World marmoset monkeys (Fig. 19.7c) shows extensive evidence for a representation of high-to-low tones in a caudorostral direction that conforms to AI (Aitkin et al. 1986; Luethke et al. 1989; Kajikawa et al. 2005; Philibert et al. 2005), with evidence for a rostral area (R), and a rostromedial area (RT) (Bendor and Wang 2005). R represents low-to-high tones progressing from the AI border; RT represents high-to-low tones from the RT border. Area CM has been found on the caudomedial AI border (Kajikawa et al. 2005). Although the tonotopic organization of CM in marmosets mirrors that of AI, CM does not have core architectonic features, and its neurons are often bisensory and receive inputs from dorsal

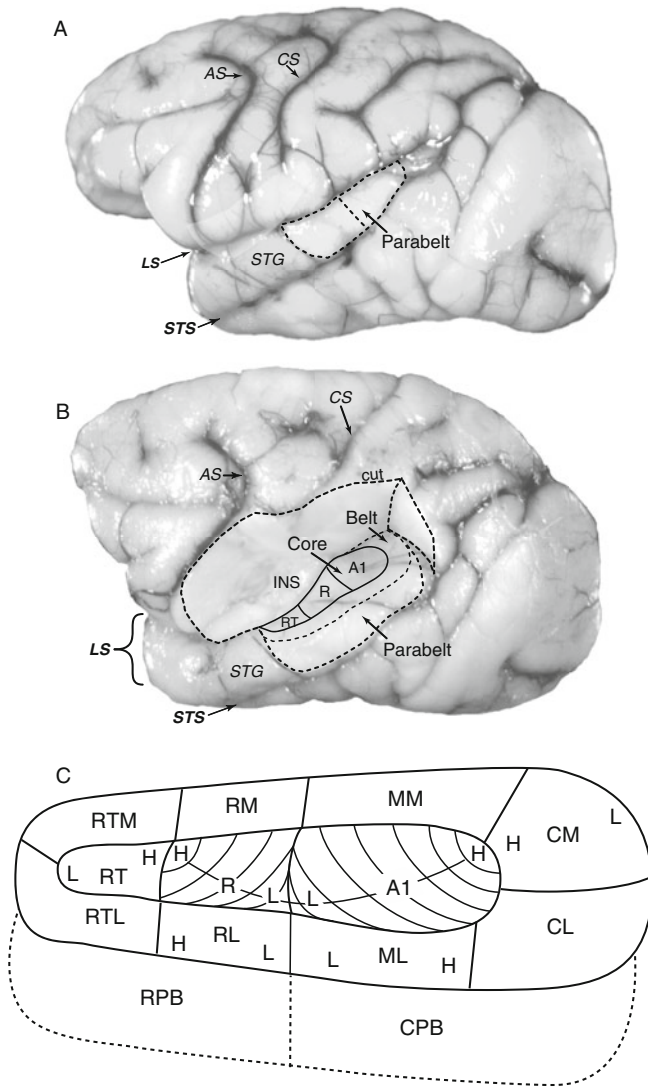


Fig. 19.6 The locations of primary and secondary auditory areas in the cortex of macaque monkeys. **a** The primary areas are within the ventral bank of the lateral sulcus, and are not apparent in this lateral view of the intact brain. Only the parabelt, a third level of auditory processing, is apparent. The lateral sulcus (LS), superior temporal sulcus (STS), and the central sulcus (CS) are indicated for reference. **b** Cortex of the upper bank of the lateral sulcus has been removed (*dashed line*) to reveal the auditory core and belt on the lower bank of the lateral sulcus. The insula (INS) is an island of cortex between the two banks. **c** A schematic of auditory cortex organization. A core of primary-like areas includes AI, a rostral area (R), and a rostrotemporal area (RT). Each of these areas is tonotopically organized from low (L) to high (H) frequencies. *Lines* of isorepresentation are shown for AI and R. The core is surrounded by a belt of secondary areas denoted by location: CL, caudolateral area; CM caudomedial area; ML, middle lateral area; RM, rostromedial area; AL, anterolateral area; RTL, lateral rostrotemporal area; RTM, medial rostrotemporal area. The lateral parabelt, a third level of processing, has been divided into rostral (RPB) and caudal (CPB) zones. Many of the belt areas are at least crudely tonotopically organized (Kaas and Hackett 2000)

and medial divisions of the medial geniculate complex rather than the ventral division.

New World squirrel monkeys have been the subjects of microelectrode mapping studies (Fig. 19.7d), and the area explored in detail was termed AI (Cheung et al. 2001; Cheung 2005; Godey et al. 2005), though the region identified had a pattern of tonotopic organization (low-to-high tones in a caudorostral direction) like that of R rather than AI. There were primary-like areas both rostral and caudal to the proposed AI (Cheung et al. 2001). It seems possible that R was identified as AI, and that squirrel monkeys have AI, R, and RT, as do other monkeys.

An auditory core has been described in prosimian galagos (Brugge 1982), with AI having the tonotopic organization expected for primates, and an area R with a reversed tonotopic organization, as expected (Fig. 19.8). A posterior lateral field (PL) had a mirror reversal tonotopic organization to that in AI and may correspond to the CM field of macaque monkeys, which is intermediate to core and belt in response and architectonic characteristics. The evidence for CM in galagos and in both New World and Old World monkeys suggests that it exists in all or most primates.

Less is known about auditory cortex organization in apes and humans. Architecturally, the chimpanzees' and humans' core has the same elongated shape as that in macaque monkeys (Hackett et al. 2001). This suggests that the same three divisions of the core exist in these primates. Functional imaging (fMRI) studies in humans that reveal cortical regions activated by different frequencies, provide evidence for two tonotopic maps in the architectonic core that form mirror-image representations reversing at a low frequency border. Talavage et al. (2004) proposed that the medial auditory koniocortex defined by others (Galaburda and Sanides 1980) corresponds to macaque area R, while lateral koniocortex corresponds to AI. Both regions had been considered subfields of AI. However, various investigators have delimited human primary auditory cortex (koniocortex) in different ways, usually as a region smaller than original descriptions (Brodmann 1909) of area 41 (Hackett 2002; Talavage et al. 2004; Sweet et al. 2005).

In summary, studies in primates recognize a core of two or three primary areas (Fig. 19.9) that include an AI and a very similar rostral area R. The similarities in neuron response properties in AI and R are so great that it is likely that area R has been mistaken for AI in squirrel monkeys. In other studies, some of R may have been included in AI.

A critical question implicit in the discovery of three core-like primate areas (RT, R, and AI) is how these compare to the core-like areas in carnivores (AAF, AI, and P). Note that monkey AI has a caudorostral tonotopic organization from high to low, while in carnivores the high-to-low tonotopic gradient is rostrocaudal. If tonotopic gradients are stable in evolution, cat AI is more like area R than AI of monkeys.

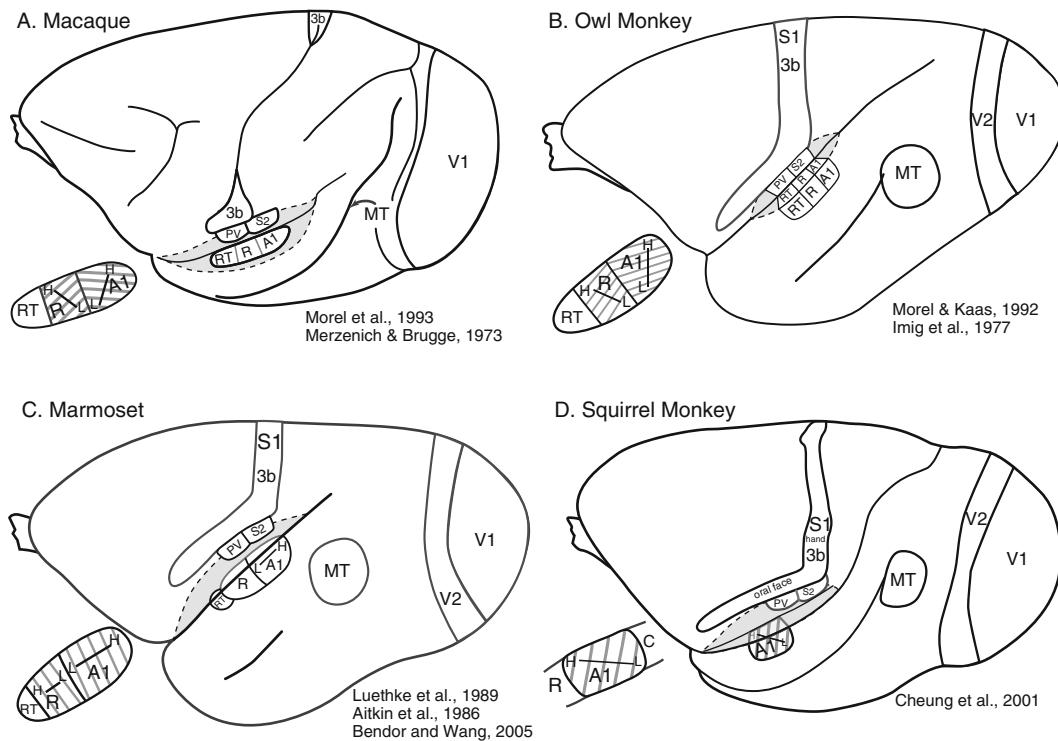


Fig. 19.7 Core auditory areas in monkeys. Areas on the hidden lower bank of the lateral sulcus are shown on dorsolateral views with the sulcus partly opened to reveal them. Figures are based largely on the results of studies cited in the text. **a** Macaque brain showing areas RT, R, and AI. Tonotopic patterns of representation and lines of isorepresentation for AI and R are on the *lower left*. The organization of RT has not been fully determined. Exposed parts of area 3b (S1), which is largely in the central sulcus, somatic sensory areas S2 and PV, visual area MT in the

superior temporal sulcus, and V1 are shown for reference. **b** Core areas in owl monkeys. Conventions as in **(a)**. **c** Core areas in marmosets. **d** Core areas in squirrel monkeys. The area identified as AI may actually be R, with the rostral region (R) corresponding to RT and the caudal region (c) to AI (see text). Based on: Morel et al. 1993; Merzenich and Brugge 1973; Morel and Kaas 1992; Imig et al. 1977; Luethke et al. 1989; Aitkin et al. 1986; Bendor and Wang 2005; Cheung et al. 2001

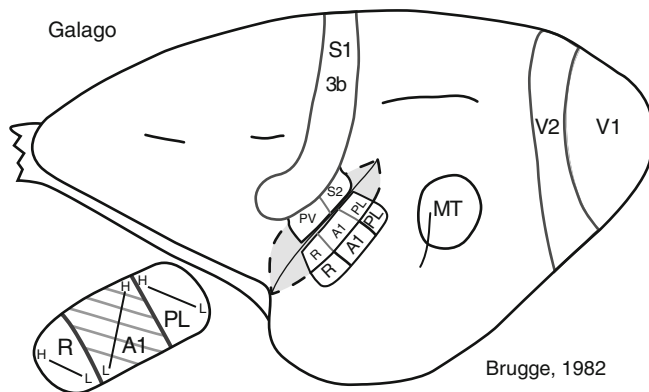


Fig. 19.8 Core auditory areas in galagos, a prosimian primate. PL, posterior lateral area. Other conventions as above (Fig. 19.7). By position and tonotopy, PL is likely to correspond to area CM of other primates (Brugge 1982)

If area R of squirrel monkeys can be misidentified as AI of monkeys, perhaps area R of monkeys is homologous with AI of cats (Kaas 2005). However, an argument against this is

that the expansion of the monkey temporal lobe has rotated auditory core nearly 180° reversing the monkey tonotopic relationship of AI to that of cats (Jones 2006).

One way to further evaluate the premise of the monkey AI rotation is to visualize AI and other auditory areas in these species relative to somatic sensory and visual cortex on flattened, surface views of cortex (Fig. 19.10) where owl monkey (Fig. 19.10a) and cat (Fig. 19.10b) neocortex have been flattened manually and histologically processed to identify primary cortical areas. The core is rotated by an expansion of monkey temporal cortex so that the long axis of the core becomes more vertical (mediolateral) than in cats. RT is rotated further forward by the lateral fissure. With the expanded temporal cortex and the presumed rotation of the auditory core, monkey AI attains a high-to-low tonotopy comparable to cat AI, and AI would be the most rostral core field, while RT would be the most caudal. The argument from relative positions suggests that if AI of monkeys is homologous to cat AI, then monkey area R is homologous with cat area P, and possibly monkey area RT of monkeys is homologous with cat VP. This leaves the puzzle of cat area

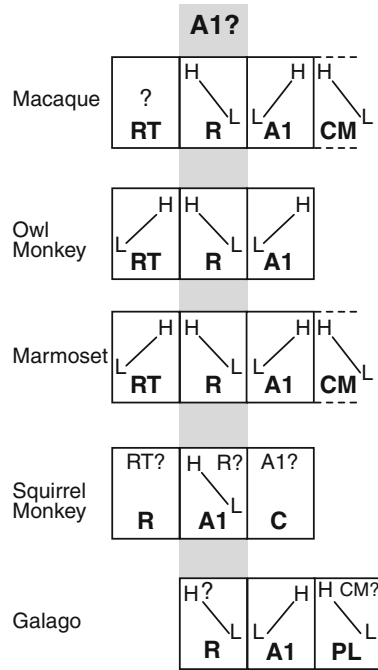


Fig. 19.9 A summary of the proposed organization of core auditory areas in primates. The relative position and the tonotopic organization of squirrel monkey area ‘AI’ better fits that of R

AAF, which certainly is a primary field. Is area AAF a homologue of monkey area CM, meaning that AAF and CM have rotated relative to AI and somatic sensory cortex in different directions (counterclockwise while anchored to cat AI and clockwise in monkey). While such rotations seem possible, other major changes would have also occurred, as CM does not have the primary features of AAF. Most notably, CM appears to depend on AI input for its tonotopic organization, while AAF does not, and CM does not receive input from MGv, as primary auditory areas do. Other parallels between CM and AAF would need to be considered. Evidence for homologues depends not only on the similarities between species, but also on the cladistic distribution of the characters (auditory areas) under consideration. Thus, the organization of auditory cortex in the well-studied rodents is considered next, then that of auditory cortex in other mammals.

6 Auditory Cortex in Rodents and Lagomorphs

Lagomorphs (rabbits, hares, and pikas) and rodents are sister orders in the clade Glires (Fig. 19.1), which diverged from other placental mammals (Asher et al. 2005) ~67 million years ago, and lagomorphs diverged from rodents over the

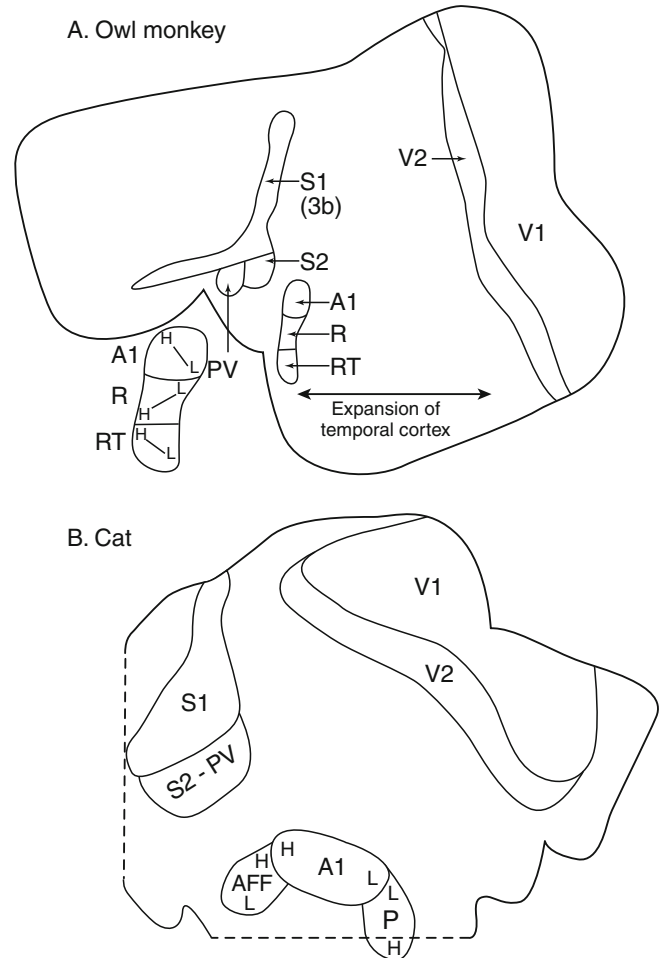


Fig. 19.10 Auditory core areas of owl monkeys (a) and cats (b) on surface views of the flattened neocortex. **a** In owl monkeys, areas AI, R, and RT are shown in temporal cortex, and again on the lower left so that tonotopic patterns of representation from low (L) to high (H) frequencies can be shown. **b** For cats, auditory areas a (AAF), AI, and P are shown in a similar manner. The dashed line in b is where some cortex was removed. The flattened owl monkey cortex was based on prior work (Tootell et al. 1985) as is the flattened cat cortex (Olavarria and Van Sluyters 1985). Somatic sensory areas and visual areas are indicated for reference

next few million years. The rodent radiation includes several distinct groups. There is information on the organization of auditory cortex in South American Caviomorphs (guinea pigs, chinchillas, and degus), Muroides (rats, mice, hamsters, and gerbils), and Sciurormorphs (grey squirrels). Auditory cortex organization has also been studied in domestic rabbits.

The Mongolian gerbil is sensitivity to low frequencies, has an accessible cochlea and central auditory structures, and is robust as a laboratory animal. In microelectrode mapping, 2-deoxyglucose and other experiments, the tonotopic organization of several auditory cortex divisions have been determined (Thomas et al. 1993; Scheich and Zuschratter 1995; Goldschmidt et al. 2004). A primary auditory area (AI), with a tonotopic gradient from low-to-high frequencies

in a caudorostral direction and an anterior auditory field (AAF), with a reversed tonotopic organization was defined (Fig. 19.11a), much like the AI and AAF gradients in cat (Fig. 19.2). Two fields were defined caudal to AI, a dorsal posterior field (DP) with a tonotopic organization of concentric rings from a low tone perimeter to a high tone center, and a ventral posterior field (VP) with a low-to-high frequency sequence rostrocaudally from the low frequency AI border. AAF and AI have the densely packed layer 4 of cells that characterized primary auditory cortex, more myelin than surrounding fields, dense immunoreactivity for parvalbumin, and a distinctive laminar banding pattern when reacted for the neurofilament protein labeled by SMI-32 antibody (Budinger et al. 2000a). VP has some of these features, but so less than in AI and AAF. Both AI and AAF receive dense inputs from MGv, while AAF also receives substantial inputs from the medial nucleus (MGm) (Budinger et al. 2000b). Areas DP and VP received input from MGv, MGm, and the dorsal nucleus (MGd). An auditory belt ventral to these did not appear to be tonotopically organized, nor was a dorsal fringe area. The ventromedial field (VM) is in the relative position of cat AII. Gerbils have an auditory core of AAF and AI, and perhaps a DP-VP region. Gerbil AAF, AI, and VP have the relative positions and tonotopic organizations of cat AAF, AI, and P.

Rats have been a common target of auditory cortex studies (Polley et al. 2007), and have a large AI flanked by anterior (A) and posterior (P) fields (Fig. 19.11b). A detailed microelectrode map of AI found that this large AI represents low-to-high frequencies caudorostrally (Sally and Kelly 1988). AI and adjoining posterior (P) and anterior (A) fields have been mapped in microelectrode recordings (Doron et al. 2002; Rutkowski et al., 2003; Kalatsky et al., 2005; Polley et al., 2007) and optical imaging (Kilgard and Merzenich 1999; Kalatsky et al. 2005) experiments. Fields A and P have mirror reversals of the AI representation and the three fields are within the architectonically defined auditory cortex core (Doron et al. 2002) and receive input from MGv (Ryugo and Killackey 1974; Horikawa et al. 1988; Roger and Arnault 1989; Clerici and Coleman 1990; Romanski and LeDoux 1993). AI and A cells have short latency responses, while P neurons have longer latencies and less evidence of a tonotopic gradient (Pandya et al. 2008; Polley et al. 2007). Non-primary areas in rat about the borders of A, AI, and P, but are not well established. They include a ventral secondary belt (Fig. 19.11b), part of which is delineated as an anterior ventral area (Horikawa et al. 1988) or a ventral area (Donishi et al. 2006) ventral to the anterior field, and a posterior dorsal area (PD) dorsal to caudal AI (Horikawa et al. 1988). A supra-rhinal auditory field (Polley et al. 2007) was renamed from earlier work (Kalatsky et al. 2005). The ventral auditory field and the supra-rhinal auditory field appear to be tonotopically organized.

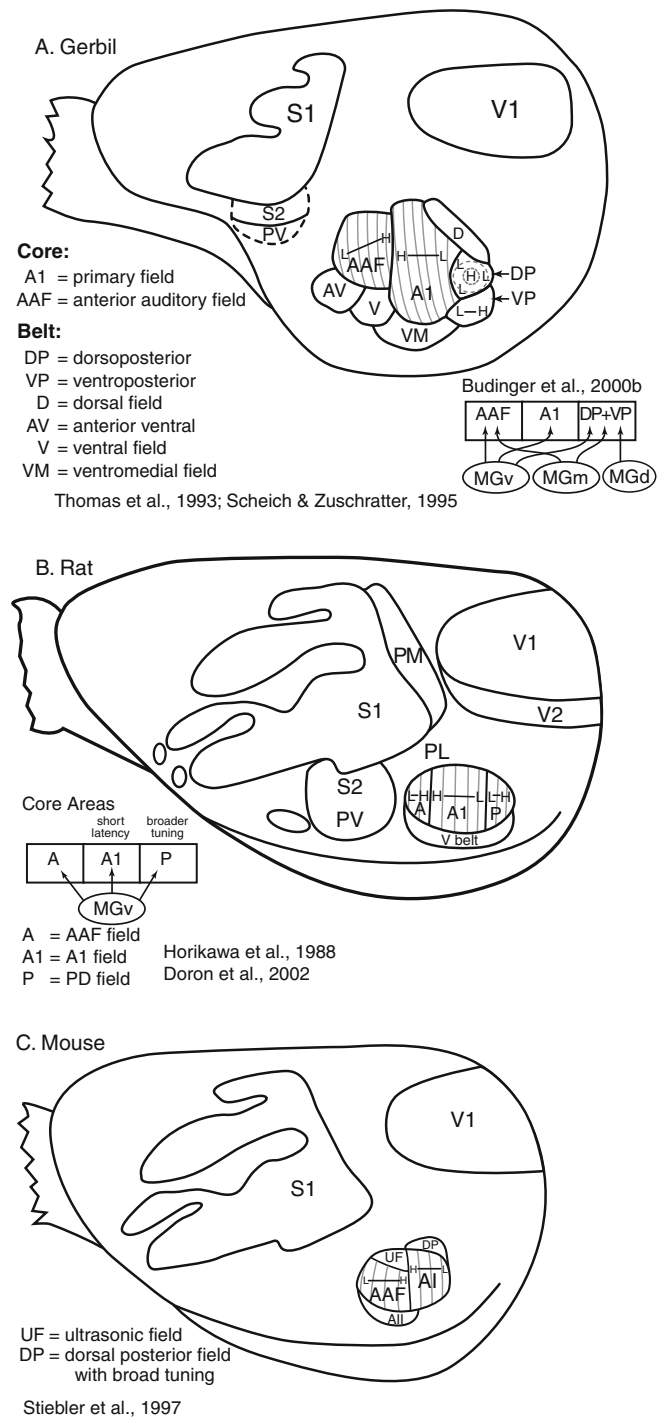


Fig. 19.11 Auditory cortex organization in Muroide rodents (gerbils, rats, and mice). **a** Some auditory areas proposed for gerbils. Gradients of tonotopic organization are indicated for high (H) to low (L) frequencies. Area DP may have a complex tonotopic organization with low tones represented along the periphery and higher frequencies in the center. Areas are identified on the *lower left* and connections with subdivisions of the medial geniculate complex are noted on the *lower right*. Conventions as in previous figures. **b** Auditory areas proposed for rats. **c** Auditory areas proposed for mice. Based on: Budinger et al. 2000b; Thomas et al. 1993; Scheich and Zusratner 1995; Horikawa et al. 1988; Doron et al. 2002; Stiebler et al. 1997

Rats thus have at least two primary fields, AI and A (or AAF); A third field, P (or PAF) has some features of a core area, but somewhat more broadly tuned cells, longer response latencies, and less pronounced tonotopy.

Mice have been less studied than rats, and two primary areas have been described, AI and AAF (Stiebler et al. 1997), which are tonotopically organized mirror-image representations reversing at the high frequency common border (Fig. 19.11c). Part of this border represents frequencies >45 kHz (Stiebler et al. 1997) and has been called the ultrasonic field (UF). Such a specialization may include parts of both AI and AAF, and may also occur in rats (Polley et al. 2007). In mice, UF receives MGv input, as does AI and AAF (Hofstetter and Ehret 1992). AI and AAF may be in the koniocortical architectonic area 41 (Caviness 1975). Mice also have a cortical zone ventral to AAF with broadly tuned neurons that rapidly habituate and which is designated as AII (Stiebler et al. 1997). A dorsoposterior field (DP) on the dorso-caudal border of AI had no tonotopy, and broadly tuned cells.

Of the Caviomorph South American rodents, auditory cortex has been studied in guinea pigs, chinchillas, and Degus. Guinea pigs have large bulla, accessible cochlea, and breed easily (Wallace et al. 2000). Their core has at least two fields that have been named differently than in gerbils, rats, and mice. Some defined a rostral AI and a caudodorsal field (Wallace et al. 2000), DC (Fig. 19.12a), and others also identified the rostral field as AI and a caudal AII (Fig. 19.12b) (Horikawa et al. 2001). In both schemes, the rostral AI field has the position and tonotopic organization of gerbil AAF and the caudal DC or AII field has the position and tonotopic organization of AI. The two core guinea pig fields were originally called anterior and posterior or dorso-caudal fields (Kayser and Legoux 1963; Hellweg et al. 1977). While it was insightfully speculated that the anterior field corresponded to cat AAF and the posterior field to AI, this identification did not persist (Redies et al. 1989). The tonotopic patterns in these fields have been shown in micro-electrode mapping (Hellweg et al. 1977; Redies et al. 1989; Wallace et al. 1997) and optical imaging (Taniguchi et al. 1997; Hosokawa et al. 2004; Nishimura et al. 2007) experiments. Both fields receive significant MGv input (Redies et al. 1989), and both lie within densely myelinated cortex that expresses high levels of cytochrome oxidase (Wallace et al. 2000). Other surrounding belt or secondary fields show some tonotopy (Nishimura et al. 2007). Part of a field has been denoted as rostral (R), and the ventrorostral belt (Wallace et al. 2000) has been subdivided (Nishimura et al. 2007). In brief, guinea pigs have a core of two or three areas resembling those in gerbils, rats and mice, but named differently. More specifically, AI in guinea pigs appears to be AAF, and DC or AII may correspond to AI. Part of the posterior belt may be DCB (dorsocaudal belt in Fig. 19.12a) or

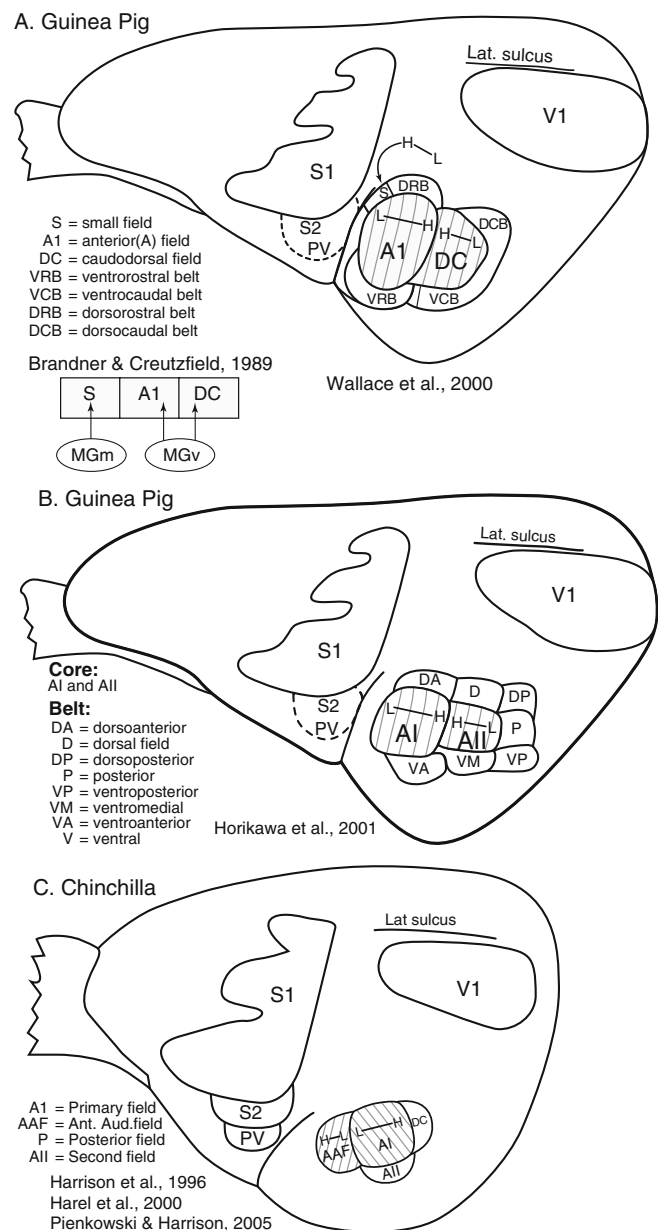


Fig. 19.12 Auditory areas in Caviomorph rodents (guinea pigs and chinchillas). Note that the field in the position of the AAF of Muridae rodents (Fig. 19.11) has been called AI in guinea pigs. In addition, the AAF and AI fields proposed for chinchillas have tonotopic organizations that are reversed from those for AAF and AI of Muridae rodents. Comparisons with other rodents suggest that AI of guinea pigs and chinchillas is AAF and P or DC is AI. **a** Guinea pigs (Wallace et al. 2000). **b** Guinea pigs (Horikawa et al. 2001). **c** Auditory cortex in chinchillas. Conventions as in previous figures. Based on: Brandner and Creutzfeldt 1989; Wallace et al. 2000; Horikawa et al. 2001; Harrison et al. 1996; Harel et al. 2000; Pienkowski and Harrison 2005

posterior area P (Fig. 19.12b). Auditory cortex organization has been investigated in two other caviomorph rodents, the chinchilla and the degus. Chinchillas have been used extensively in studies of the peripheral auditory system. Two cortical auditory fields include an AI (Fig. 19.12c) (Harrison

et al. 1996), although its tonotopic gradient was reversed from that of AI of rats, mice, and gerbils (Fig. 19.11), with high-to-low frequencies in a caudorostral sequence (Harel et al. 2000; Pienkowski and Harrison 2005a, b). A field rostral to AI was not fully explored, but it had a reversed tonotopic organization, from low to high in a caudorostral sequence and was named AAF (Harrison et al. 1996). Both were considered as part of the auditory core since cells had short response latencies and responded well to tones. They also found a posterior field of uncertain tonotopic organization (Harrison et al. 1996). The posterior field was later defined as the dorsocaudal belt (DC) where neurons were broadly tuned to frequencies without tonotopic organization (Pienkowski and Harrison 2005a,b). Area AII was defined along the ventral AI border, with broadly tuned neurons that formed a tonotopic pattern in parallel to AI (Pienkowski and Harrison 2005b), although AII organization was also described as orthogonal to that of AI (Harel et al. 2000). In these studies, AII was considered to be part of the auditory core.

These results from chinchillas pose a puzzle, as areas termed AI and AAF have opposite tonotopic gradients than areas defined as AI and AAF in other rodents. Possibly the area termed AI is AAF, and the area termed AAF is specific to chinchillas or chinchilla AAF could be AI of other rodents, and AI is a modified posterior field. In this alternative, with AAF serving as AI, AAF has been lost or it has not been detected. AII is not different than AI and both might be parts of the same field.

Another caviomorph rodent in which auditory cortex organization has been studied is the degu from Chile and Argentina (not illustrated). In 2-deoxyglucose labeling experiments, evidence was found for five auditory fields (Braun and Scheich 1997). The largest area was AI and limited evidence suggested that it represented high-to-low frequencies in a caudorostral gradient, as does chinchilla AI (Fig. 19.12c).

The final rodent to be considered is the gray squirrel, where visual and somatic sensory areas have been studied more extensively than auditory cortex. A primary area, AI, had high frequencies were represented caudally and low frequencies rostrally (Fig. 19.13d) (Luethke et al. 1988). This AI corresponded well with most of the primary architectonic anterior temporal cortex field (TA) (Kaas et al. 1972) and had densely packed cells in layer 4 and heavy myelination. A more rostral field (R) was not fully explored, but may have a reversed tonotopic organization from that in AI. Subsequent auditory cortex recordings (Luethke et al. 1988) confirmed a reversed tonotopic pattern in R. Area R is within the architectonic field TA, but TA is not uniform in appearance, and the distinctive primary-like features of TA are reduced in R (Merzenich et al. 1976). Cortex caudal to AI, the temporal intermediate field (TI), lacks the characteristics of primary sensory cortex (Kaas et al. 1972), and was unresponsive to auditory stimuli (Merzenich et al. 1976). Cortex rostral and ventral to AI was variably responsive to sound, with area R most consistently responsive. Some neurons in the somatic sensory parietal ventral field (PV) (Krubitzer et al. 1986) responsive to acoustical stimuli (Luethke et al. 1988). The cortical connections of AI included areas R, cortex ventral to AI, and PV (Luethke et al. 1988). Both AI and R receive MGv input.

The results from various rodents present a confusing picture. Considering only the tonotopically organized and most readily characterized fields reveals great variation in the profile of cortical organization across rodent species and between groups of investigators (Fig. 19.14). For the gerbil, there is a rostrocaudal sequence of tonotopically organized areas (AAF, AI, and VP or VP and DP) with tonotopic gradients and reversals that match cat areas AAF, AI, and P. Thus, based on relative position and tonotopic organizations, gerbil AAF and AI at least, may be homologues of cat AAF and AI, and of AAF and AI in other carnivores. Similar patterns exist in rats, where AAF, AI, and P have been identified, and mice,

Fig. 19.13 Auditory areas proposed for squirrels. The rostral area, R, has the tonotopic organization of AI in most other rodents, while squirrel AI matches the posterior area (P) (Fig. 19.11). Conventions as in previous figures (Merzenich et al. 1976; Luethke et al. 1988)

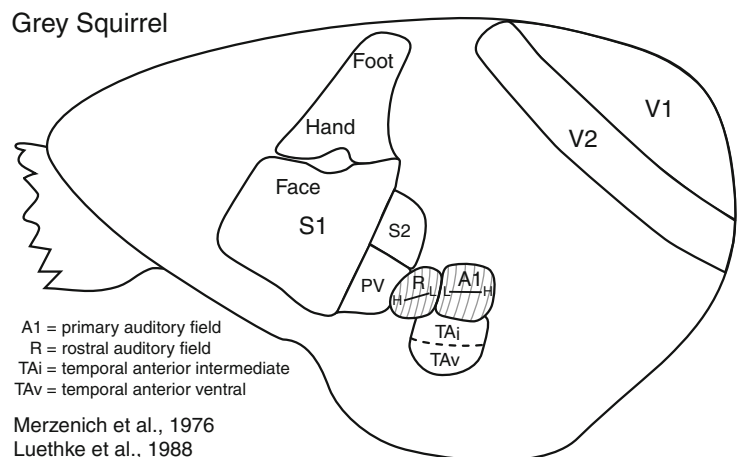
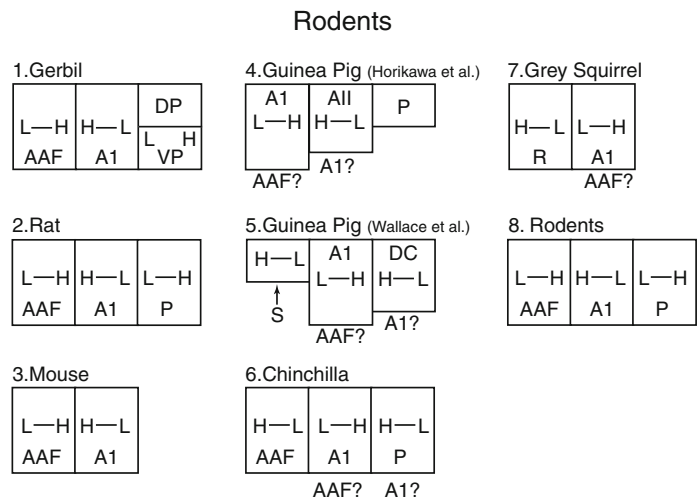


Fig. 19.14 Schematic of auditory core organization in rodents. Areas are designated after the current proposals (Figs. 19.11 and 19.12). To promote consistency in names between studies in rodents, some proposed areas have been renamed below the boxes. A proposal for the organization of the auditory core in most or all rodents is shown in schematic 8



where AAF and AI have been described. Guinea pigs fit into this scheme less easily, but one approach identified AI and AII (Fig. 19.12B), except that AI would correspond to AAF and the area designated as AII (Horikawa et al. 2001) would be AI. There is evidence for an area P caudal to this renamed AI. This renaming results in a close correspondence of two or three areas in guinea pigs, gerbils, rats, and mice. Another interpretation of auditory cortex organization in guinea pigs (Wallace et al. 2000) would also fit this rodent scheme with a renaming of areas (Fig. 19.12A). Thus, AI would become AAF, and DC would become AI. Unfortunately, the proposed plan of the chinchilla and squirrel auditory core does not fit this scheme so easily. The most clearly characterized field in both, AI, has a tonotopic gradient that is reversed from that of other rodents. Perhaps AI is actually AAF in both rodents, as the tonotopic gradient corresponds to AAF, but this interpretation leaves no AI in squirrels, and only an ill-defined chinchilla area P for AI. Perhaps squirrels and chinchillas have lost or greatly modified AI, so that only AAF remains as a dominant primary area, which seems unlikely. In addition, this would place primary-like auditory fields rostral to the renamed AAF (area R in squirrels and AAF in chinchillas), and no such fields have been identified in other rodents. Alternatives are that AAF and AI have reversed their tonotopic organization in squirrels and chinchillas, which also seems unlikely, as there are no known examples where a primary sensory area has reversed its internal organization. A reasonable proposal is that auditory cortex in most rodents has two or three core or core-like areas, an AAF with a low-to-high tonotopic organization from rostral to caudal, an AI with a reversed tonotopic organization, and possibly an area P with a reversed tonotopic organization. However, most evidence would exclude area P from the primary core. For the secondary auditory areas, present descriptions are too variable and incomplete to homologize these fields across rodents.

The proposed scheme for rodents would be further supported if a similar pattern of cortical organization could be demonstrated in lagomorphs (rabbits, hares, and picas), which are the closest living relatives of rodents (Fig. 19.1), so that parallels in cortical organization would be much more expected than with distantly related carnivores. The tonotopy of rabbit auditory cortexes has been incompletely studied, and only in dorsoventral microelectrode penetrations coursing parallel to the cortical layers, rather than perpendicular (McMullen and Glaser 1982; Velenovsky et al. 2003). Information on the tonotopic gradient exists in the dorsoventral plane only. An auditory area was described in which high frequencies were represented dorsally and low tones ventrally, with a slight inclination of the isorepresentation lines dorsocaudally to ventrorostrally (Fig. 19.15) (McMullen and Glaser 1982; Velenovsky et al. 2003). That

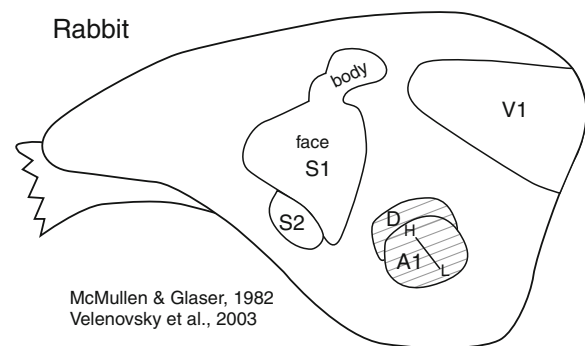


Fig. 19.15 Auditory cortex in domestic rabbits. A primary area with a predominantly dorsoventral tonotopic gradient from high-to-low frequencies with a caudalward slant has been described as AI. As the high frequency representation is displaced rostrally, this organization, allowing for some rotation, is consistent with the area often considered as AI in rodents. A dorsal area (D) may correspond to AAF. Conventions as in previous figures. Based on: McMullen and Glaser 1982; Velenovsky et al. 2003

this area is AI is supported by the evidence for this slight slant, which places the high frequency representation somewhat rostral, as in the rodent schematic (Fig. 19.14). There was less evidence for a dorsal area (D) on the dorsal margin of AI with a reversed tonotopic organization. If this dorsal area is actually rostradorsal to the proposed AI, then area D could correspond to AAF. AI in rabbits has connections with MGv, and has characteristic core architectonic features, such as dense laminar immunostaining for parvalbumin (McMullen et al. 1994; de Venecia et al. 1998). Thus, rabbits could have areas AAF and AI that are organized much as in gerbils and rats, and secondary areas.

7 Auditory Cortex Organization in Tree Shrews (Scandentia)

The superorder Euarchontoglires includes Glires (rodents and lagomorphs), and Euarchontans, consisting of primates, flying lemurs, and tree shrews. Flying lemurs (Dermoptera) are rare, leaving tree shrews (Scandentia) as the closest living relative of primates available for study. Unfortunately, little is known about the organization of tree shrew auditory cortex. One study (J.H. Kaas, W.C. Hall and M.M. Merzenich, unpublished observations) used microelectrodes to map its tonotopic organization and found evidence for only one tonotopically organized area, a large area designated as AI, with an organization from high-to-low frequency in the rostrocaudal direction, with isorepresentation lines in a dorsoventral axis, inclined slightly rostrally (Fig. 19.16). This organization is consistent with that of the proposed rodent (and possibly rabbit) AI, as well as cats. Tree shrew AI has a primary architectonic appearance, and it receives MGv input (Casseday et al. 1976). The location of tree

shrew AI would seem to leave little room for a more anterior area (AAF), and the existence of other fields remains uncertain.

8 Auditory Cortex in Bats

Bats and carnivores have the same (superorder Laurasiatheria). Bats belong to the order Chiroptera, which contains megachiroptera (megabats), the fruit eating bats without echolocation, and microchiroptera (microbats), which echolocate and feed predominantly on insects. Most interest in bats has been on echolocating bats, whose auditory system is highly specialized. The somatic sensory system is also unusual as well, with adaptations related to use of the forelimb as a wing (Calford et al. 1985; Wise et al. 1986) and somatic sensory modulation of flight (Zook 2007).

Recordings from mustached bat auditory cortex provide evidence of specialized cortical auditory areas, most with no apparent homologues in other mammals (Suga 1990, 1994; Fitzpatrick et al. 1998). Only one of these areas is considered here. A primary area, AI has a low-to-high frequency caudorostral gradient (Fig. 19.17A) from 10 to 100 kHz. An expansion in central AI represents biosonar pulse frequencies of 60–62 kHz. It is uncertain if there is an AAF-like area rostral to AI, although other, possibly secondary fields have been described. AI (divided into three sectors) receives input from MGv, as expected (Pearson et al. 2007). An unusual feature of the auditory system of the mustached bat, and perhaps other echolocating bats, is a direct MG projection to frontal cortex, where neurons respond to auditory stimuli (Casseday et al. 1989; Kanwal et al. 2000).

Auditory cortex organization has also been studied in the big brown bat (Fig. 19.17b) that has a large tonotopically organized area, with a caudorostral gradient of low-to-high frequencies, characterized as AI (Dear et al. 1993). A

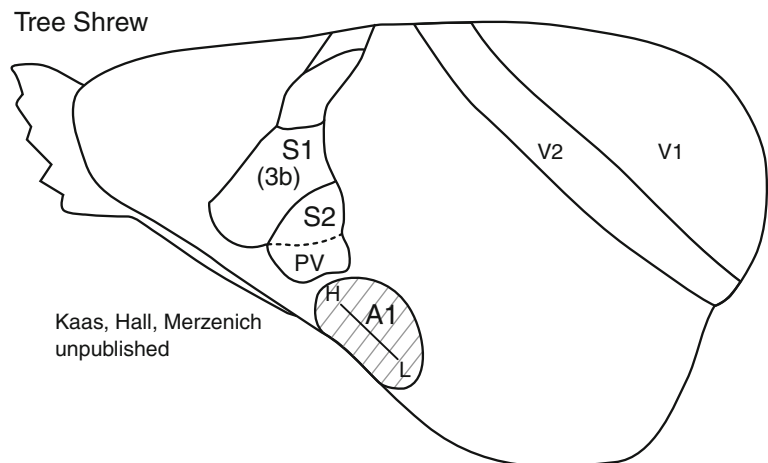
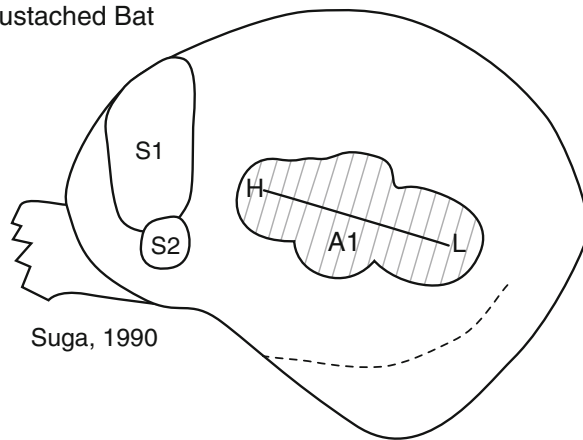


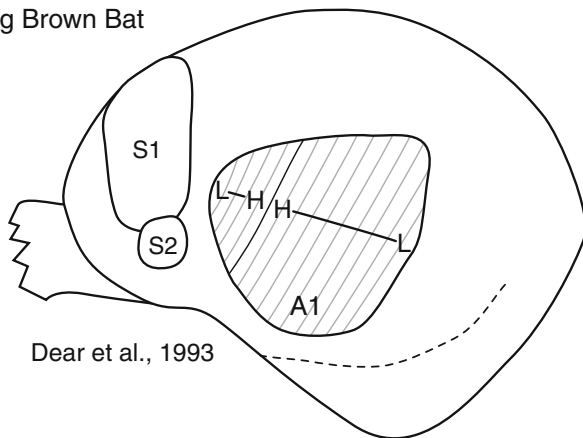
Fig. 19.16 Auditory cortex organization in tree shrews. Only one auditory area has been identified, and was denoted as AI. Conventions as in previous figures

A. Mustached Bat

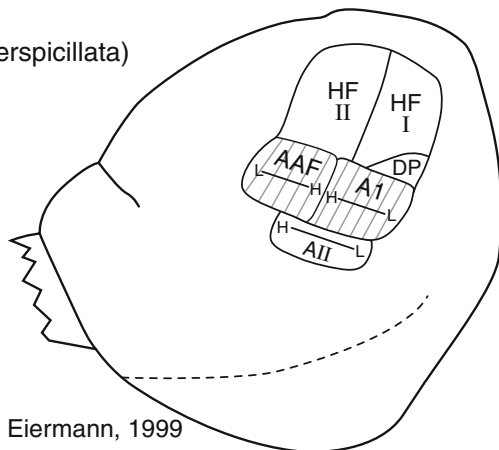


Suga, 1990

B. Big Brown Bat



Dear et al., 1993

C. FM Bat
(*Carollia perspicillata*)

Esser & Eiermann, 1999

Fig. 19.17 Auditory cortex organization in echolocating bats. **a** The location of the primary area, AI in the mustached bat. Other highly specialized areas have been identified, but none obviously correspond to areas in other mammals. **b** Two tonotopic areas are described in the big brown bat, one with the tonotopic organization of AI and the other matching the relative position and tonotopic organization of AAF. **c** Three tonotopic fields have been proposed for the short-tailed FM fruit bat, two corresponding to AI and AAF, respectively, and a more ventral region proposed as AII. A dorsoposterior area (DP) and two high frequency areas have also been proposed. Conventions as in previous figures

smaller, anterior region had a reversed tonotopic organization, and a relative position and tonotopic organization like that of AAF. The border region between these fields was activated by 60–90 kHz frequencies and was variable among bats.

Other aerial insectivore bats studied include the rufous horseshoe bat (not illustrated), whose AI has a caudorostral low-to-high frequency tonotopic gradient, and tonotopic anterior and posterior fields which have been homologized with cat and rodent AAF and ventroposterior and posterior fields (Radtke-Schuller and Schuller 1995). Both AI and the posterior field receive MGv input, suggesting that they are parts of a primary-like auditory core, together with AAF (Radtke-Schuller 2004). AI has primary-like architectonic features, while AAF has architectonic features intermediate to AI and dorsal secondary auditory fields (Radtke-Schuller 2001). Finally, in a frequency modulating (FM) bat (*Myotis lucifugus*), auditory cortex (not illustrated) has a tonotopically organized AI (with low frequencies caudal), and an anterior field with lower frequencies again represented, possibly corresponding to AAF (Wong and Shannon 1988).

Besides the above insectivorous bats, auditory cortex has been investigated in the short-tailed FM microchiropteran fruit bat (*Carollia perspicillata*), an FM bat with biosonar echolocating capacity that is less specialized than the bats discussed above, as it eats fruits and nectar, and seeks insects opportunistically. Microelectrode mapping defined three tonotopic fields: AI, AAF, and AII (Fig. 19.17c) (Esser and Eiermann 1999). AI and AAF had caudorostral progressions from low-to-high frequencies in AI and high-to-low in AAF, and both fields were considered core. A secondary area, AII, with tonotopic organization lies along the ventral AI and AAF border and these cells were habituated rapidly and were more broadly tuned. A dorsoposterior field above AI had no tonotopic organization and high response thresholds. Much of auditory cortex consisted of high-frequency representations dorsal (HF-I and HF-II) to AI and AAF.

There have been no studies of auditory cortex organization in the non-echolocating fruit bats, the megabats of tropical areas. Their auditory areas may be less specialized than in echolocating bats.

Echolocating bats have a highly specialized auditory system. Nevertheless, a primary area, AI, with a caudorostral frequency representation has been consistently recognized. An AAF with features that suggest that it could be part of the auditory core has also been identified. AI and AAF have tonotopic organizations and other features that suggest that they are homologues of cat AI and AAF. An AII-like area is found in an FM fruit-eating bat, while all bats have highly specialized, dorsally located, secondary auditory

fields. In addition, the organization of AI is distorted by having a large auditory foveal region for the echolocation frequencies.

9 Auditory Cortex in Other Mammals

Little is known about auditory cortex organization in other mammals. An auditory region has often been identified architectonically, and is assumed to be AI, but without experimental studies that conclusion is uncertain.

Hedgehogs are insectivores in the Laurasiatherian super-order (Fig. 19.1). They have small brains with little neocortex, and have long been of interest in comparative studies of brain evolution. Auditory cortex investigation of the long-eared hedgehog has found at least two auditory areas (Fig. 19.18), AI and P (posterior) (Batzri-Izraeli et al. 1990). Both were organized tonotopically, with a caudorostral representation of low-to-high frequencies in P, and a reversed pattern in AI. Both areas are in a more densely myelinated region of cortex. Hedgehog cortex is not well differentiated, lacks a koniocellular architectonic appearance and was difficult to distinguish from adjoining cortex. Tracer injections into AI labeled MGv neurons. The connections of P were not determined. The response properties in both fields were similar, although P neuron latencies were slightly shorter than in AI (Batzri-Izraeli and Wollberg 1992). As

hedgehog AI compares very well with carnivore and rodent AAF, and P with AI, these authors weighed the possibility that the two fields had been misidentified, and felt that more evidence was needed before renaming them. The present comparative evidence strongly favors the alternative view of two core fields, an anterior AAF and a posterior AI.

Possums belong to the impressive marsupial radiation of mammals (Fig. 19.1), and it would be important to determine auditory cortex organization in species distantly related to eutherian mammals. Few studies of auditory cortex organization are available in the brush-tailed opossum. An auditory region with dense myelination has been identified in several marsupials (Beck et al. 1996; Huffman et al. 1999), but the tonotopic organization has been determined only in the brush-tailed possum (Fig. 19.19). Dorsorostral electrode penetrations through auditory cortex recorded neurons at successively lower frequencies. One field, thought to be AI, had high-to-low frequencies in a dorsoventral axis (Gates and Aitkin 1982). As in rabbits (Fig. 19.15), either AI or AAF with high tones represented more dorsally would yield a dorsoventral progression of neurons responsive to progressively lower frequencies. Without precise alignment of recording sites in the parallel, vertical electrode penetrations, any rostrocaudal component of a frequency gradient is difficult to detect. Thus, both rabbits and possums could have areas with tonotopic gradients that could correspond to AI or AAF in other mammals. The dorsoventral frequency progressions in rabbit and possum likely reflect the similar dorsoventral mapping procedures in these investigations. Other approaches are needed to determine if other core areas exist. This would be essential in identifying areas homologous to those in other mammals. It is disappointing that so little is known about Monotreme auditory cortex, or Afrotheria or Xenarthra species (Fig. 19.1). Any organizations of their auditory regions remain to be determined.

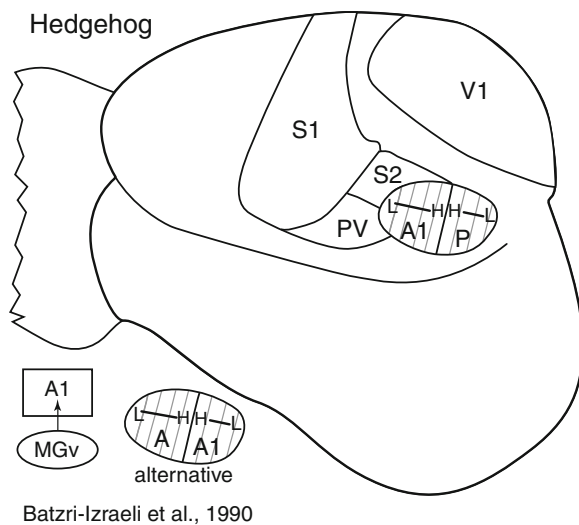


Fig. 19.18 Auditory cortex organization in hedgehogs. Two tonotopically organized fields were described (AI and P (posterior)). AI thalamic connections of were largely from MGv. The comparative evidence favors the alternative interpretation that the anterior field is homologous with AAF of rodents, carnivores, and bats, and the posterior field is AI. The somatic sensory areas (S2, PV and S1) are based on prior work (Catania et al. 2000). Conventions as in previous figures

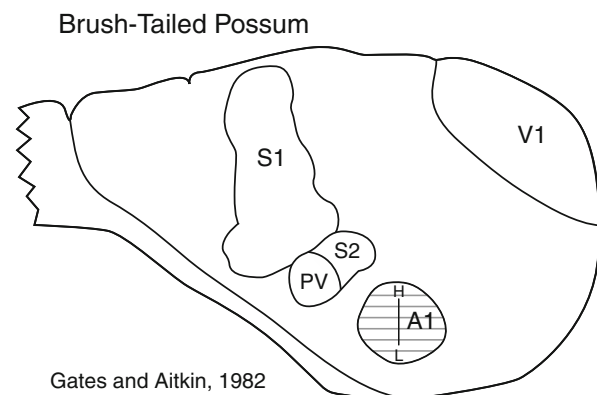


Fig. 19.19 Auditory cortex organization in the brush-tailed possum. Conventions as in previous figures

10 Summary and Conclusions

10.1 Defining the Auditory Cortex

Early studies in cats designated a primary area (AI) and a secondary field (AII). Subsequently, another primary-like field, the anterior auditory field (AAF) was found rostral to AI, and a less primary-like posterior field (P or PAF) caudal to AI. AI and AAF primary-like attributes include tonotopic organization with sharply tuned neurons, direct inputs from the ventral nucleus of the medial geniculate complex and architectonic features of primary sensory cortex. Cats have two, and possibly three, primary areas (AI, AAF, and perhaps P). Adjoining auditory fields in cats are secondary in structure, function, and connections. Comparable but more limited studies in dogs and ferrets suggest that areas AI, AAF, and P likely exist in all carnivores.

10.2 Core Fields of Auditory Cortex

A core of three primary or primary-like areas has also been identified in primates. From caudal to rostral along the lower bank of the lateral sulcus, these areas have been termed AI, the rostral area (R), and the rostrot temporal area (RT). Because both AI and R have pronounced primary-like features, either could be homologous with area AI of cats. As AI in cats has a caudorostral representation of tone frequencies from low to high, and the proposed AI of monkeys has a rostrocaudal progression, these opposite tonotopic gradients do not appear to support the assumption that the two areas termed AI are homologous. However, the possibility that AI of monkeys has been rotated nearly 180° by the expansion of the temporal lobe in primates has been proposed as an explanation for the opposite orientations of the tonotopic gradients. A further consideration of this possibility indicates that a rotation of as much as 90° may have occurred in New World monkeys, and perhaps more in some anthropoids, but the rotation hypothesis is still questionable. In addition, the rotation hypothesis would leave no primary-like area such as AAF on the caudal border of primate AI where CM is located. Thus, the rotation hypothesis seems inconsistent with other observations. Alternatively, R could be the homolog of carnivore AI (and seems to have been mistaken for AI in one detailed study). However, if primate area R is actually AI, the area more caudal to R, now defined as AI, seems too primary-like to correspond to carnivore area P (or PAF). Primate area RT closely resembles carnivore area AAF, in position and tonotopy relative to R redefined as AI, but RT is less primary-like, and smaller than expected for AAF. Thus, the homologies between core areas in primates and carnivores remain uncertain.

10.3 Common and Unique Features in Defining Auditory Cortex

Results from most, but not all rodents, conform to the carnivore pattern of an AI and an anterior auditory field. The two rodent fields have not been consistently named, but their tonotopic gradients, inputs from MGv, and histological features all support homologies between fields AI and AAF in carnivores and most rodents. There is also support for considering the posterior fields in rodents and carnivores as homologues. The apparent differences between results from most rodents, and those from squirrels and chinchillas are difficult to explain, but fundamental differences in the presence or absence of AI and AAF across rodent taxa would be surprising.

10.4 Bats and Other Species

Bats are the only other taxon whose auditory cortex has been well studied in special species and there is good evidence for adjoining core areas homologous to carnivore AAF and AI. The parallels in these two areas in bats, rodents, and carnivores – all different branches of the placental mammal radiation – suggest that early placental mammals had both AAF and AI, and these core areas were widely, perhaps universally, retained by subsequent placentals. The posterior area (P) could be part of this primitive constellation.

10.5 The Future of Comparative Studies of Auditory Cortex

While one tonotopically organized, primary-like area has been demonstrated in a marsupial, there is insufficient information to reach firm conclusions about auditory cortex organization in this mammalian radiation. Nothing is known about the organization of auditory cortex in monotreme mammals. Even our understanding of auditory cortex in placental (eutherian) mammals is highly fragmented, resting largely on two orders (carnivora and chiroptera) of the Laurasiatherian superorder, and on rodentia and primates of the Euarchontoglires superorder, with no species from the Afrotheria and Xenarthra superorders. Bridging this gap in comparative research on auditory cortex should be a major feature of any future agenda.

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