

Anatomical Organization of the Auditory Cortex

DOI: 10.3766/jaaa.19.10.5

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Abstract

The identification of areas that contribute to auditory processing in the human cerebral cortex has been the subject of sporadic investigation for more than one century. Several anatomical schemas have been advanced, but a standard model has not been adopted by researchers in the field. Most often, the results of functional imaging or electrophysiological studies involving auditory cortex are related to the cytoarchitectonic map of Brodmann (1909). Though useful as a guide and point of reference, this map has never been validated and appears to be incomplete. In recent years, renewed interest in the organization of auditory cortex has fostered numerous comparative studies in humans, nonhuman primates, and other mammalian species. From these efforts, common features of structural and functional organization have begun to emerge from which a working model of human auditory cortex can be derived. The results of those studies and the rudiments of the model are reviewed in this manuscript.

Key Words: Anatomy, cerebral cortex, hearing, pathway, primate

Abbreviations: LS = lateral sulcus (Sylvian fissure); MGd = medial geniculate, dorsal division; MGv = medial geniculate, ventral division; STG = superior temporal gyrus; TTG = transverse temporal gyrus

Sumario

La identificación de áreas que contribuyen al procesamiento auditivo en el corteza cerebral humana ha sido un tema de investigación esporádica por más de un siglo. Varios esquemas anatómicos han sido presentados, pero los investigadores en el campo no han adoptado un modelo estándar. Más a menudo, los resultados de imágenes funcionales y de estudios electrofisiológicos involucrando la corteza cerebral se ha relacionado con el mapa cito-arquitectónico de Brodmann (1909). Aunque útil como guía y por sus puntos de referencia, este mapa nunca ha sido validado y parece estar incompleto. En años recientes, un interés renovado por la organización de la corteza auditiva ha promovido numerosos estudios comparativos en humanos, en primates no humanos y otras especies de mamíferos. De estos esfuerzos, rasgos comunes de organización estructural y funcional han empezado a emerger, a partir de los cuales puede derivarse un modelo de trabajo de la corteza auditiva humana. Los resultados de estos estudios y los rudimentos del modelo se revisan en este artículo.

Palabras Clave: Anatomía, corteza cerebral, audición, vía, primate

Abreviaturas: LS = surco lateral (fisura de Silvio); MGd = geniculado medial, división dorsal; MGv = geniculado ventral, división ventral; STG = giro temporal superior; TTG = giro temporal transverso

The long-term goal of our research program is to develop a comprehensive description of human auditory cortex organization. What are its structural components, and what are their functions? How do these elements work together to produce the perceptual experience of hearing? Research in humans and other mammals indicates that the auditory cortex is comprised of an interconnected group of distinct areas, but the number of areas involved and their connections are unknown for humans. A testable *working model* of human auditory cortex has not been

developed, even though such models have been developed for other species. Early descriptions of the auditory cortex include several anatomical and lesion studies conducted in the late 1800s and early 1900s (Broca, 1865; Wernicke, 1874; Ferrier, 1875; Brodmann, 1905, 1909; von Economo and Koskinas, 1925; Beck, 1928, 1929; von Economo and Horn, 1930; Poljak, 1932; Clark, 1936; Walker, 1937; von Bonin, 1938). These classic studies localized auditory cortex to the superior temporal gyrus of humans and nonhuman primates and remain influential even today. For

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This research was supported by NIH/NIDCD grant R01 DC04318.

example, the nomenclature derived from Brodmann's map of the cerebral cortex is widely used to denote areas of the brain in functional imaging, electrophysiology, and related clinical applications. In the mid-1900s, electrophysiological studies revealed that the representation of the basilar membrane was preserved in the primary auditory cortex (Ades and Felder, 1942; Licklider and Kryter, 1942; Bailey et al, 1943; Pribram et al, 1954; Hind et al, 1958; Katsuki et al, 1962; Gross et al, 1967; Celesia and Puletti, 1969). These studies were followed by others in which the anatomical and physiological features of this region were explored in more detail, showing tonotopic organization of areas, subcortical inputs, and connections between fields (Nauta, 1957; van Buren and Yakovlev, 1959; Pandya et al, 1969; Merzenich et al, 1973; Mesulam and Pandya, 1973; Pandya and Sanides, 1973; Imig et al, 1977). Studies of the auditory cortex of nonhuman primates and humans since that time represent stepwise refinements of previous findings, culminating in a working model that is the subject of ongoing testing and modification (Kaas and Hackett, 1998, 2000; Hackett, 2003; Hackett, 2007a, 2007b).

IDENTIFICATION OF AUDITORY AREAS IN THE BRAIN

In the cerebral cortex of the brain, the term *auditory cortex* refers to areas that are the principal targets of either the ventral (MGv) or dorsal (MGd) divisions of the medial geniculate complex (MGC) in the thalamus. By that definition, auditory cortex occupies a large portion of the ventral (lower) bank of the lateral sulcus (LS) and superior temporal gyrus (STG) in humans and nonhuman primates (Fig. 1). In humans, these areas encompass the transverse temporal gyri (TTG) of Heschl (HG) and the planum temporale, roughly corresponding to areas 41, 42, 52, and 22 of Brodmann (1909). Outside the boundaries of auditory cortex are numerous areas of the brain that receive inputs from auditory cortex, but few or no inputs from the MGv or MGd. These *auditory-related* areas are located elsewhere in the temporal, parietal, and frontal lobes, and tend to be sites of multisensory convergence, in which the processing of auditory, visual, and somatosensory inputs occurs (Romanski et al, 1999; Kaas and Hackett, 2000; Ghazanfar and Schroeder, 2006).

The designation of an area as auditory or auditory-related depends on the establishment of a profile based on its anatomical and physiological characteristics. Although detailed information can be obtained experimentally from research animals, this is generally not the case for humans. This is the main reason why models of human auditory cortex are less well-developed than other species commonly used for research. Anatomical studies of humans are limited

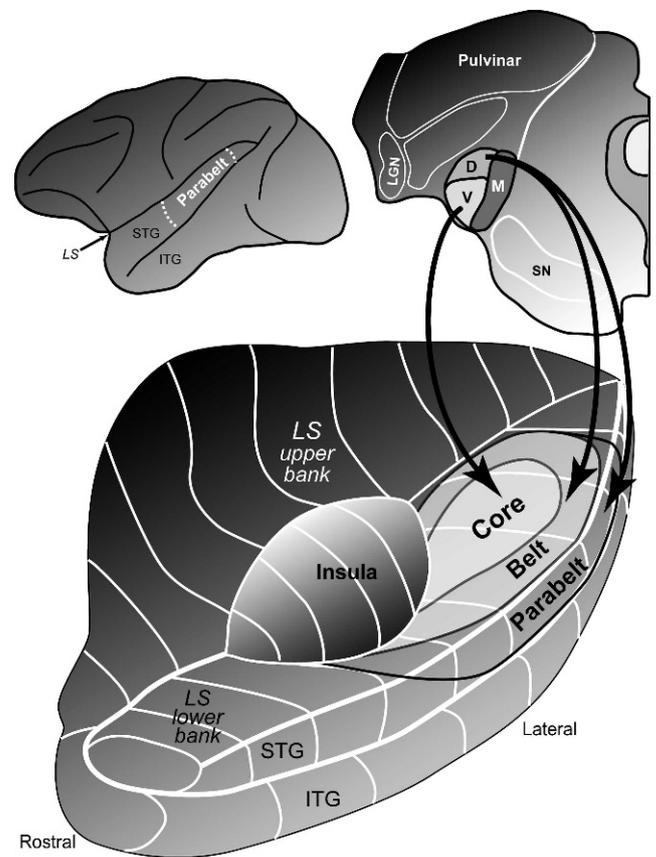


Figure 1. Schematic of the macaque monkey auditory cortex (left hemisphere), showing projections (arrows) to the core, belt, and parabelt regions from the medial geniculate complex. *Top left*, left hemisphere showing the location of the parabelt region of auditory cortex on the surface of the superior temporal gyrus (STG). *Top right*, coronal view through the posterior thalamus showing the three major divisions of the medial geniculate complex: D = dorsal; V = ventral; M = medial. *Below*, dorsolateral view of the lateral sulcus (LS), which has been graphically opened to show the location of auditory cortex on the lower bank. Other abbreviations: ITG = inferior temporal gyrus; LGN = lateral geniculate nucleus; SN = substantia nigra. Areas shown apply to both hemispheres.

to postmortem examination of the tissue and may take years to complete. Functional imaging and electrophysiological techniques are now widely used, but current technologies lack either the spatial or temporal resolution needed to reliably identify and distinguish one area of cortex from another. Thus, the need for studies to identify and characterize auditory and auditory-related areas in the human brain remains great. To some extent, advances can be achieved through comparative studies involving nonhuman primates, for which the organization of the auditory cortex is more certain. Although we do not expect the auditory cortex of humans and nonhuman primates to be identical, there is both direct and indirect evidence that the major features of nonhuman primate auditory cortex organization are conserved in humans.

ORGANIZATION OF THE AUDITORY CORTEX OF MONKEYS

Models of auditory cortex organization have been developed for several mammalian species, including bats, cats, ferrets, mice, rats, and monkeys. Species differ with respect to the number of areas present, their relative position and arrangement, connections (inputs/outputs), and tonotopic organization. For example, the number of auditory areas identified ranges from 5–6 in rodents, 6–9 for cats and ferrets, 10–12 in monkeys, and over 30 in humans. Thus, there is a tendency to identify more auditory areas in larger brains. The number of areas is also thought to be equal in both hemispheres, although structural and functional asymmetries are common.

A common feature of organization is that a central primary, or *core region*, containing one or more areas, is adjoined by a variable number of secondary areas comprising a *belt region* (Fig. 1). The main source of thalamic inputs to the core areas is the MGv, whereas the MGD is the principal source of inputs to the belt areas. In nonhuman primates, the core-belt scheme has been extended to include a third region, known as the *parabelt region* (Morel and Kaas, 1992; Morel et al, 1993; Hackett et al, 1998; de la Mothe et al, 2006a). The parabelt region receives thalamic inputs from the MGD but is distinguished from the belt region in that it does not receive direct inputs from the core (Hackett et al, 1998). Information reaching the parabelt region from the core appears to be mediated by connections with the belt region, suggesting that there is a processing hierarchy within auditory cortex (i.e., core, then belt, then parabelt) (Kaas and Hackett, 1998).

Complicating the picture is the observation that each of the three major *regions* contains two or more interconnected areas, or subdivisions. Our model of the monkey auditory cortex contains three subdivisions of the core region, seven areas within the belt region, and two divisions of the parabelt region. Areas within each region are not identical, since each has a unique set of connections with the thalamus and other areas of cortex. Thus, some information is processed in parallel by two or more areas, and some is not. These connection patterns indicate that both serial and parallel processing is accomplished within the auditory cortical network (Rauschecker et al, 1997; Kaas and Hackett, 1998; Rauschecker, 1998; Kaas et al, 1999).

ORGANIZATION OF THE AUDITORY CORTEX OF GREAT APES AND HUMANS

Compared to monkeys, much less is known about the organization of the auditory cortex in the great apes and humans. As mentioned above, identification of auditory areas in these primates is mainly limited to

descriptions of architectonic features defined from postmortem and noninvasive physiology. Despite these limitations, however, a number of detailed anatomically based models have been produced (see Hackett, 2003). Early studies relied on analyses of cytoarchitecture or myeloarchitecture to identify areas. More recent studies have incorporated quantitative methods and the expression of enzymes, proteins, neurotransmitters, and receptors as additional means to characterize areas and provide insight into their functional properties (Ong and Garey, 1991; Rademacher et al, 1993; Hutsler and Gazzaniga, 1996; Rivier and Clarke, 1997; Clarke and Rivier, 1998; Nakahara et al, 2000; Hackett et al, 2001; Morosan et al, 2001; Wallace et al, 2002; Morosan et al, 2005; Sweet et al, 2005).

Although the details vary substantially across studies, a common finding has been the identification of a central core region flanked by belts of several nonprimary fields, similar to the pattern of organization found in monkeys and other animals (Fig. 2). In monkeys, the core region is elongated along the anterior-posterior axis of the temporal lobe. In apes and humans, the core occupies the posteromedial two-thirds of the TTG, which is oriented from posteromedial to anterolateral across the superior temporal plane (Hackett et al, 2001; Hackett, 2003). Therefore, the core region corresponds most closely to area 41 of Brodmann (1909).

An interesting and important aspect of the gross anatomy of the superior temporal lobe is that there is much greater variability in apes and humans, compared to monkeys. For example, the number of transverse temporal gyri varies between individuals and sometimes between hemispheres. The position of the core region also varies relative to those sulcal and gyral landmarks (Rademacher et al, 1993; Leonard et al, 1998; Hackett et al, 2001) and cannot be determined from inspection of the gross anatomy. Thus, precise localization of the core requires close inspection of the small-scale anatomical features, or architecture. In humans, the most common gyral configurations are a single or paired TTG, also referred to as a posterior duplication or bifid HG. In humans with a single TTG, the core occupies most of this gyrus and usually does not extend beyond its anterior and posterior sulcal boundaries. When the TTG is duplicated, or bifid, the core spans the intermediate sulcus to occupy portions of both gyri, usually favoring the anterior TTG.

Flanking the core region on the anteromedial and posterolateral sides of the TTG are two regions that appear to comprise at least part of a belt region. The anterior region, interposed between the core and circular sulcus of the insula, is a region with distinctive architecture that most closely corresponds to the medial belt region of monkeys and area 52 of Brodmann. The posterior region occupies part of the planum temporale (PT) adjacent to the TTG, and

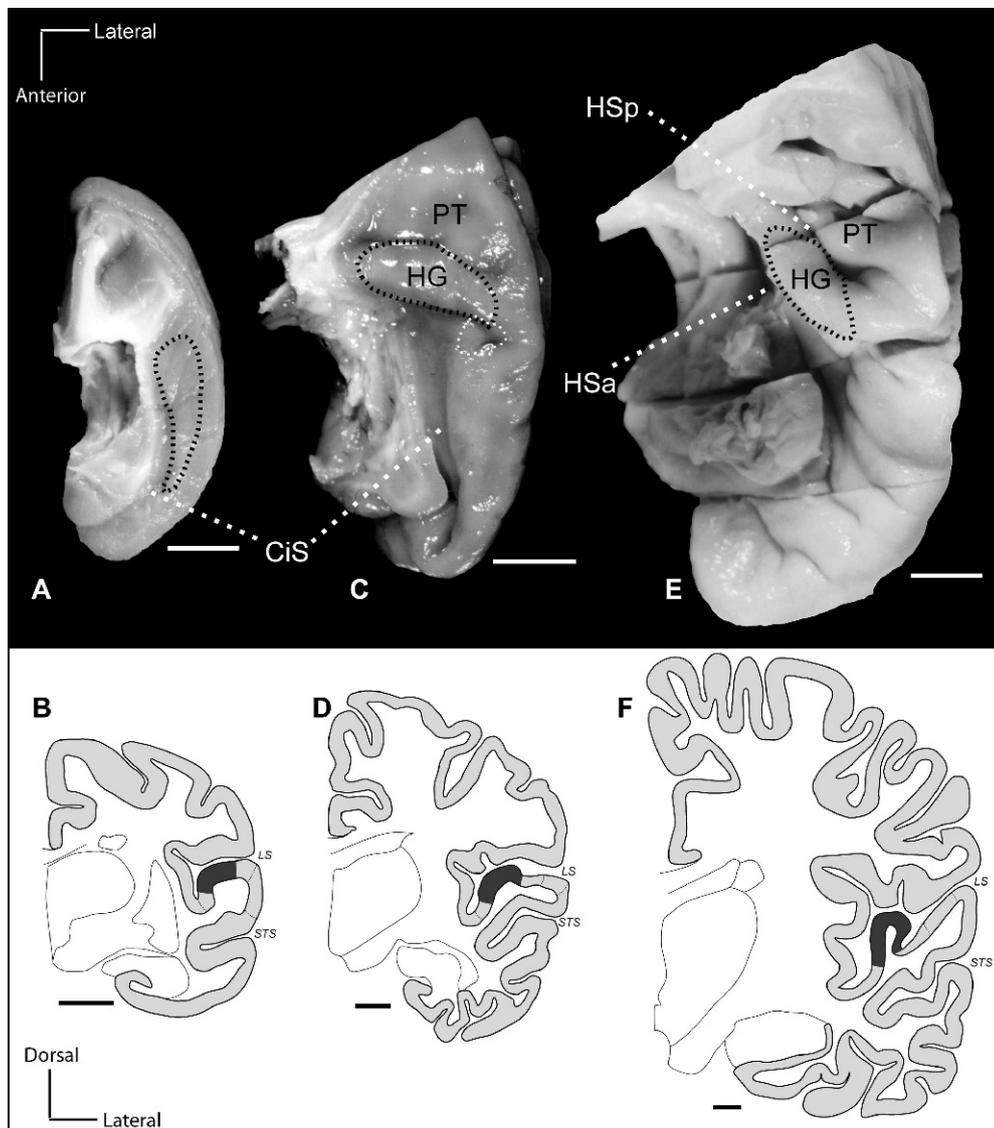


Figure 2. Location of auditory cortex in the macaque monkey (A, B), chimpanzee (C, D), and human (E, F). *Top*, dorsal views of the superior temporal plane in each species. The location of the core region is outlined by a dashed ovoid. The location of the transverse temporal gyrus of Heschl (HG) and planum temporale (PT) are labeled in the chimpanzee and human specimens. Scale bars: 5 mm. *Bottom*, schematics coronal sections through auditory cortex. Dark shading denotes location of the core region. Dashed lines mark approximate locations of belt and parabelt areas on the superior temporal gyrus (STG), which is bound dorsally by the lateral sulcus (LS) and ventrally by the superior temporal sulcus (STS). CiS = circular sulcus; HSa = anterior Heschl's sulcus; HSp = posterior Heschl's sulcus. Scale bars: 5 mm.

corresponds most closely to area 42 of Brodmann and the lateral belt of monkeys (Hackett, 2003; Sweet et al, 2005). Extending further posteriorly onto the PT are at least two other anatomically distinct regions. One or both may correspond to the parabelt of monkeys. According to Brodmann (1909), part of area 22 extends onto the PT from the STG to flank the posterior border of area 42. Though speculative, this portion of area 22 may therefore correspond to part or all of the parabelt region. In that case, much of the STG (area 22) has no clear homolog among monkeys, apes, and humans. At present, however, serious consideration of possible homologies is premature, as it is not yet clear how

many areas of cortex occupy the STG of humans or the great apes. Further research is needed to clarify these relationships. On the other hand, there is support for a system of organization in humans and chimpanzees in which a central core is flanked by belt or bands of areas, as found in monkeys and other mammals.

SIGNIFICANCE AND DIRECTIONS FOR FUTURE RESEARCH

Establishing the anatomical organization of auditory cortex is important for several reasons. One of the most important is that, with the exception of

Brodman's map, there is not a standard working model of the human auditory cortex from which to interpret data and test hypotheses of auditory processing. Models based on other species are informative but not wholly adequate. The expansion of the PT and STG in apes and especially humans is one of the most obvious differences in the gross morphology of the superior temporal lobe among primates. As these structural differences may underlie key differences in the capacity for speech and language, delineation of the anatomical substrates is essential. Anatomical variability and uncertainty is highly problematic for functional studies of auditory cortex in which the interpretation of results depends on accurate delineation of activated areas (Hall et al, 2003; Scott and Johnsrude, 2003). In imaging studies, activation patterns produced by auditory stimuli tend to spread across the core and belt regions, frequently without regard for anatomical borders. In electrophysiological studies (e.g., EEG, MEG), identification of the source is even less precise, and several sources may contribute to a given peak. Thus, it is generally not possible to accurately relate function to structure in such studies, given current technological limitations and our poor understanding of the underlying anatomy.

To overcome these limitations, advances are needed in at least two areas. The first is the establishment and acceptance of a working model of the human auditory cortex. A partial description of one such model was presented in this review and is the major focus of our research at Vanderbilt. This model could serve as the basis for interpreting imaging and electrophysiological data and for the testing of hypotheses about auditory processing. Some of these results would likely necessitate periodic refinements of the model, which would need to be flexible in that respect. The second advance is a means to accurately localize sources or relate activations to their anatomical substrates. Improvements in spatial resolution of functional imaging techniques have greatly improved our ability to resolve some of the prominent anatomical features that distinguish one area of cortex from another. Ideally, this would allow researchers to directly relate zones of significant activation to specific areas of auditory cortex identified in each subject. Ultimately, a more precise coupling between structure and function will provide more accurate and informative insights into the processing of sound by auditory cortex.

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