

Jeffery A. Winer  
Christoph E. Schreiner  
*Editors*

# The Auditory Cortex

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Photograph courtesy of Jane A. Winer

Jeffery A. Winer (1945–2008)  
Scholar, scientist, colleague, mentor, friend

## Preface

This volume is a summary and synthesis of the current state of auditory forebrain organization. We think it a timely contribution in view of the growing interest in this network as the arbiter for hearing, as a key element in the larger communications network that spans and links the parietal, temporal, and frontal cortices, and as a candidate for clinical intervention, whether through cochlear implants or more exotic upstream prostheses that, one day, may involve the forebrain more directly.

The present account differs from the available efforts (Aitkin 1990; König et al. 2005) in two significant ways. First, the medial geniculate body is included as a full partner since it has cooperative, reciprocal, and robust relations with the auditory cortex that suggest a partnership in which the exclusion of either structure detracts from a functional portrait of their interactions. Second, our aim has been systematic and synoptic, including as it does a wide range of species, methods, subsystems, physiological perspectives, and functional architectures. We look back on 100 years of the discipline of auditory forebrain studies with a view to framing a future agenda. As new methods emerge and as older approaches exhaust their potential, it seems appropriate to attempt a summing up and to forge a prospectus for future work. We cannot present a full theory of auditory forebrain organization since the field is still so new as a discipline; that task we must leave to a later, more mature volume that recognizes the distributed nature of forebrain operations in a more refined way than is now possible. Our goal is to provide an experimental foundation and a conceptual framework for the auditory forebrain useful to the discipline as a whole, and which one might consult as both a summary of work in progress and an invitation to explore further. This formidable task could not have been accomplished without the contribution of an expert cohort of collaborators on whose efforts this enterprise rests.

Several methodological and conceptual insights have converged to create the present, congenial atmosphere for this effort. The emergence of new functional approaches such as the tissue slice and its varieties has enabled the exploration of new neurochemical and synaptic vistas (Metherate and Hsieh 2004) and allowed a more formal and anatomical–physiological characterization of identified neurons (Verbny et al. 2006). Related advances include the important insights gleaned from large silicon electrodes that span the full cortical depth and reveal critical facets of interneuronal and laminar organization invisible to a single extracellular pipet (Atencio and Schreiner 2008). Such local circuits in the medial geniculate body and auditory cortex are the functional building blocks upon which the large-scale operations of spectral analysis, aurality, and frequency modulation are arrayed. How these several subsystems interact cooperatively as a network is among the most challenging questions for the future. Other powerful insights flowed from the ability to record from synaptically joined pairs of cells (Miller et al. 2001) contributing to a new perspective on the thalamocortical transformation (Winer et al. 2005). Understanding such transformations—tectothalamic, thalamocortical, corticocortical, and corticofugal—remains an enterprise for the future.

A second wave of insight arose from the neuroimaging domain, where positron emission tomography, functional magnetic resonance imaging, and magnetoencephalography each provided powerful documentation of the locus and density of activity in the living brain during specific tasks or after particular pathologies. This work not only defined the site of activation, but related measures such as 2-deoxyglucose provided the first full perspective on the limits of auditory-responsive cortex (Poremba et al. 2003).

Neuroanatomical and immunocytochemical approaches have provided credible maps of connectivity in the thalamocortical and corticocortical systems (Huang and Winer 2000; de La Mothe et al. 2006), documenting a vast web of forebrain long- and short-range circuits. The implementation of studies of lamina-specific interneuronal properties has provided valuable insights into these dynamic systems (Atencio et al. 2009). The corticothalamic and other corticofugal systems likewise are now construed as prospective dynamic players in regulating auditory cortical excitability rather than as feedback pathways (Winer et al. 2001). Combined physiological-connectional studies established the existence of specific pathways for sound localization and object identification (Rauschecker and Tian 2000).

The dramatic demonstration and ensuing exploration of widespread auditory forebrain plasticity (Kilgard and Merzenich 1998; Weinberger 1998) was a watershed and its implementation in the descending systems (Zhang et al. 2005) suggested a role for the corticofugal systems very different from earlier accounts that emphasized feedback. The auditory cortex now appears to be as concerned with the control of inferior colliculus excitability and plasticity and information processing as it is in the analysis of sound parameters and categorical perceptual analyses. Such findings were a linchpin in larger efforts to characterize the distributed auditory cortex as an entity that represents hearing in its largest and most inclusive sense (Winer and Lee 2007). The present volume can be construed as a multidisciplinary effort to further implement and instantiate that perspective.

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On a more individual basis we are especially grateful to our editor, Ann Avouris of Springer New York for her unfailing efforts to help us realize our vision. She was the ideal editor, providing timely and balanced counsel and reminding us with courtesy of the shortest path to our goal. David T. Larue used his graphics expertise to organize and perfect the many figures that are at the heart of this volume.

Each of us were beneficiaries of the aid and encouragement of our families, Jane M. Winer, Carol R. Galbraith, and Eileen G. Winer for Jeff, and Marcia Raggio and Christina Schreiner for Christoph. We are most thankful for their unfailing and loving support.

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## Chapter 1

# The Historical Development of Ideas About the Auditory Cortex

Edward G. Jones

### 1 Introduction: Early Theories of Brain and the Perception of Sound

The realization that auditory perception depended upon the cerebral hemispheres came to science and medicine rather later than that of the other principal sensations. Thomas Willis (1664, 1681) while recognizing the dependence of auditory perception upon the forebrain, felt that some aspects of the hearing sense, especially the appreciation of music, depended upon the cerebellum, a view that was to persist well into the eighteenth century and even beyond. Willis, knowing that the auditory nerves (his seventh pair of nerves) were concerned with hearing, and tracing them to the vicinity of the cerebellum, considered that “the impression of the sound or the Species admitted to the Ears . . . [is] carried inwardly towards the Cerebel and *sensorium commune*,” that is, to both the cerebellum and higher levels of the brain. Of the latter, he felt that the corpus striatum was the eventual arrival place. “Ideas of sounds conveyed also to the Cerebel; which forming there footsteps or tracts, impress a remembrance of themselves, from whence when afterwards the Species there laid up are drawn forth by the help of the vocal process, voices, like the sounds before admitted, and breaking forth in a certain ordained series, come to be made.” That is, the cerebellum maintains the beat and tempo of a series of sounds and permits them to be reproduced later, in this case mediated by the outgoing facial nerve, which Willis also saw as part of the auditory nerve arising from the vicinity of the cerebellum. “Hence it is usual, that musick or melody is soon learnt by some men, which afterwards they bring forth with exact Symphony . . . the Spirits moving within the Cerebel [being] disposed into peculiar Schemes; to which when they flow on

both sides into the vocal process of the auditory Nerve, they render as it were with a certain spontaneous voice, and like a Machine or Clock with the succession of Species, the measures or Tunes of the Instrument which they had drunk in at the ears.”

The realization that the cerebral cortex formed the substratum for sensation and motion starts to become implicit in many of the numerous anatomical studies devoted to charting the cerebral sulci and gyri in the latter part of the eighteenth and early part of the nineteenth century. By the time that Ecker (1869) wrote his *Die Hirnwindung des Menschen*, he could begin by saying “That the cortex of the cerebrum, the undoubted material substratum of our mental operations, is not a single organ, which is brought into play as a whole in the exercise of each and every psychical function, but consists rather of a multitude of mental organs, each of which is subservient to certain intellectual processes, is a conviction which forces itself upon us almost with the necessity of a claim of reason” (Translation by John Galton 1873). No friend to phrenology, then in its dying days, Ecker considered that uncovering the localization of “psychical functions” in the cortex of the cerebral hemisphere was destined to become one of the most important problems for anatomy and physiology and destined to bring about a revolution in psychology. Ecker’s work, which summed up in brief format the knowledge that had accumulated about the human cerebral sulci and gyri and provided a systematic nomenclature that remains in use today, came at a time when experimental studies that were to reveal the localization of the sensory and motor areas of the cerebral cortex were about to begin. A curious feature of his work, however, is his unusually superficial description of the gyri of the insula and temporal operculum. This stands in marked contrast to his detailed descriptions of the other gyri and sulci of the hemisphere. The discovery of Heschl’s gyrus had to wait until 1877 (Heschl 1877). Heschl’s gyrus is in fact two gyri, which Heschl himself called the anterior and posterior transverse temporal gyri.

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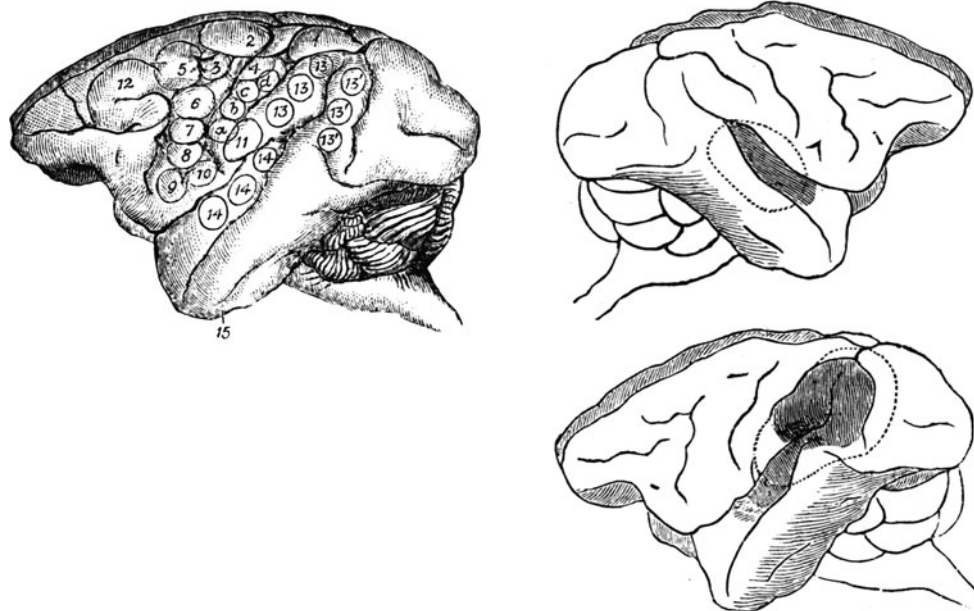


## 2 First Experimental Studies in Monkeys: David Ferrier

If Ecker was disdainful of phrenology, it was nevertheless an interest in cerebral localization derived from phrenology that induced Sir James Crichton Browne, the Director of the West Riding Lunatic Asylum to invite a young Scottish neurologist with time on his hands in London to come to Yorkshire and commence investigations of the cerebrum in animals using lesions and electrical stimulation. David Ferrier commenced his investigations by confirming and extending the studies of Fritsch and Hitzig (1870; Hitzig 1874) that had led to the identification of the motor cortex. By using Faradic rather than Galvanic stimulation, Ferrier (1873, 1876) was able to obtain a far more precise localization of the motor cortex than had Fritsch and Hitzig, and in a series of experiments on monkeys, dogs, cats, jackals, rabbits, guinea pigs, and rats, he demonstrated regions from which movements of comparable parts of the limbs could be obtained, and thus confirmed the presence of a similar motor map. All his experiments were carried out under ether or chloroform anesthesia and the level of current used was that which elicited a tingling sensation when the electrodes were applied to the tongue of the investigator! He also identified regions from which stimulation evoked movements, such as eye and head turning, that he considered to be reflex responses to sensory experiences, and thus to betoken the presence of specific sensory areas.

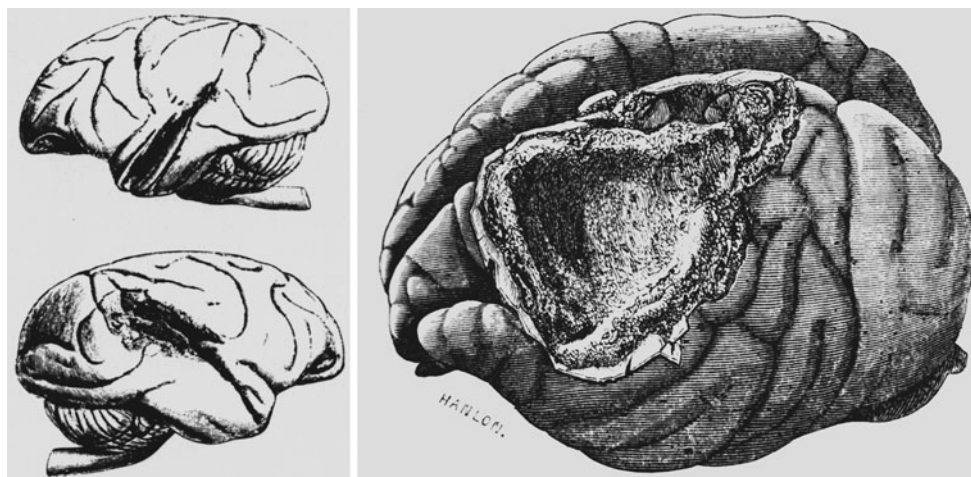
These observations led him to ablate various gyri or surface regions of the hemisphere in up to 25 monkeys (Ferrier 1875) in the search for specific losses of sensation. It was from these experiments that there emerged the first intimations of the existence of an auditory cortex.

Ferrier localizations were not always correct. He located the visual cortex, for example, in the angular gyrus since destruction of that gyrus led to “blindness in the opposite eye.” As discussed below, a deeply penetrating lesion, compounded by secondary infection, undoubtedly led him into this error, his lesions having severed the optic radiation. He was closer to the truth with his identification of the auditory region. He had located it in the first instance in the upper part of the superior temporal gyrus (called by him the superior temporo-sphenoidal convolution) by noting that electrical stimulation of that region caused monkeys to prick up the opposite ear and turn the head and eyes to the opposite side. Following bilateral lesions of the superior temporal gyri (Fig. 1.1), “the animal, though fully conscious and on the alert to everything attracting sight, failed to respond to auditory stimuli usually exciting active reaction and attention.” After unilateral lesions, “the animal continued to respond to auditory stimuli, turning its head if called to; . . . reactions, however, which did not ensue when the ear on the same side as the lesion was securely stopped with cotton wool.” Ferrier’s account of how he determined that his animals with bilateral lesions were indeed deaf bears quoting in full: “In



**Fig. 1.1** Figures from Ferrier (1876) illustrating his stimulation and ablation experiments in monkeys; from these, he located the auditory cortex in the superior temporal gyrus. *Left*: the locations of regions which when stimulated electrically gave rise to movements of different parts of the body. From regions labeled 14 he reported “pricking of

the opposite ear, head and eyes turn to the opposite side, pupils dilate widely.” *Right*: the locations of bilateral lesions that led to “loss of hearing in both ears, and loss of sight in the right eye.” The *dotted lines* indicate the extent of brain surface exposed by removal of part of the skull



**Fig. 1.2** *Left:* the extent of bilateral superior temporal lesions in one of Ferrier's monkeys, demonstrated at the *International Medical Congress* in 1881 and found to be profoundly deaf. From Ferrier (1886). *Right:*

the extent of the lesion in the second, hemiplegic monkey. From Ferrier et al. (1881)

order to avoid attracting its attention by sight, I retired behind the door and watched the animal through a chink, while it sat comfortably before the fire. When all was still I called loudly, whistled, knocked, &c., without attracting the animal's attention to the source of the sound, though it was sitting perfectly awake and looking around. On my cautiously approaching it, it remained unaware of my proximity until I came within the field of vision, when it started suddenly and made grimaces as if in terror or alarm. On repeating these tests when the monkey was sitting quietly along with a companion monkey whose powers of hearing were unquestionable, the companion invariably became startled at the sounds, and came peering curiously to ascertain their origin, while the other remained quite still. Ten hours subsequently I again repeated these various tests with the same results—results which justified the conclusion that whether the animal heard or not, it certainly gave no signs of hearing that which, in another animal, excited lively curiosity. Beyond this, without personal testimony from the subject of experiment, it is impossible to go, but I think that when the two sets of experiments are taken together,—*viz.*, the positive reactions to electric stimulation, and the absence of reaction to usual forms of auditory stimuli when the superior temporo-sphenoidal convolutions were destroyed,—the evidence of the localization of the centre of hearing in this region amounts to positive demonstration."

All of Ferrier's lesions in his first and largest series of monkeys were deeply penetrating and apparently heavily compromised by infection. They undoubtedly undercut the region on the supratemporal plane where we now know the primary auditory cortex to be located; and the presence of severe infection seems to have led Ferrier to kill the animals after relatively short survivals so that recovery of function could not be tested. By the time that he demonstrated his monkeys at the 1881 International Medical Congress in

London (Ferrier et al. 1881), he had obtained the assistance of the surgeon, Gerald Yeo, who made lesions in a group of monkeys by the newly introduced antiseptic method, with the result that animals could survive postoperatively for long periods free of infection. One of the monkeys that demonstrated by Ferrier at the Congress had survived for 6 weeks subsequent to a bilateral ablation of the superior temporal gyri (Fig. 1.2). The other was a monkey with hemiplegia as the result of a lesion of the pre- and postcentral gyri carried out some 7 months before. The brain of a third monkey that had been blind as the result of ablation of the angular gyri and, significantly, of the occipital lobes, was also shown. When the monkeys were demonstrated at King's College on August 3rd, Yeo confessed that he had had some earlier skepticism about cerebral localization but now admitted to being completely won over. As has often been described, the condition of the hemiplegic monkey led the French neurologist, Charcot, to exclaim: "It is a patient." The second monkey is described in the *Proceedings of the Congress* as "the one which had had the region of the superior temporo-sphenoidal convolution destroyed in both hemispheres 10 weeks previously. The animal was seen to be active and vigorous without the slightest sign of motor paralysis in any part of the body. Its vision was evidently perfect, the animal snatching eagerly at pieces of food offered it. That it was deaf, however, was demonstrated most clearly. While the two monkeys were on the floor together before the audience, Dr. Ferrier snapped a percussion cap in their immediate proximity, whereupon the hemiplegic monkey started with the most lively signs of surprise, whereas the other exhibited not the slightest indication whatever of hearing. This experiment was repeated several times with the same result. The animal was admitted to be perfectly deaf, and no other deficiency could be detected." Ferrier had thus demonstrated the general location of the

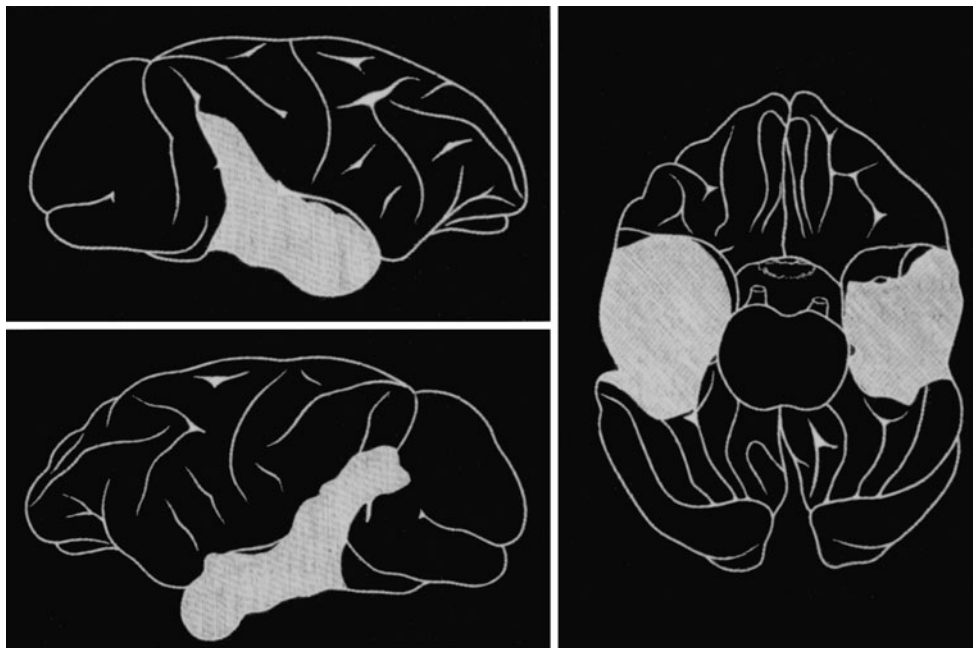
auditory cortex in the region of the upper part of the superior temporal gyrus. That success and Charcot's earlier poking fun at the English paradox of promoting fox hunting while enacting the most stringent of anti-vivisection laws, did not ensure Ferrier's protection from the hounds of righteousness and, within days, he was hauled off to Bow Street Magistrates Court and charged with cruelty to animals. Fortunately, it was proven that Yeo had performed the operations under general anesthesia and that he had the appropriate license, so Ferrier was acquitted, but not before he had been pilloried in the popular press and made a martyr by the medical establishment.

Ferrier seems not to have performed any further lesion experiments on the cerebral cortex, although the three that he had described at the 1881 International Medical Congress were written up in Ferrier and Yeo (1884) and presented in the second edition of his *Functions of the Brain* (1886). He was not, however, to escape from controversy over his localization of the auditory cortex. He was able to dismiss the observations of Luciani and Tamburini (Luciani 1884), who had described an early loss but considerable recovery of auditory function subsequent to bilateral lesions of the perisylvian regions, on the grounds that they had been made on dogs rather than monkeys and the testing of auditory function was crude. His own method wasn't much better. A more serious attack came from quarters closer to home, when Edward Schäfer, in a series of papers published between 1887 and 1888, described monkeys operated on with aseptic techniques and with extensive bilateral lesions of the temporal lobes (Fig. 1.3) and that displayed no evidence of

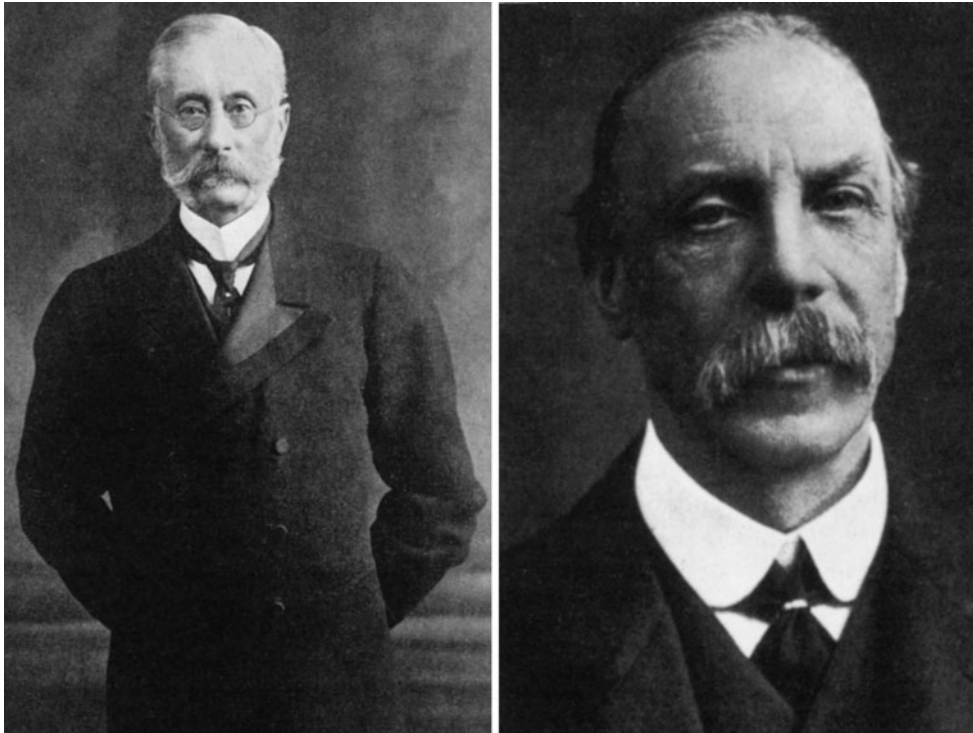
severe or sustained hearing loss (Schäfer 1888a, b; Horsley and Schäfer 1888; Brown and Schäfer 1888). The dispute between Ferrier and Schäfer was perhaps as bitter as any between two rather correct Victorian gentlemen (Fig. 1.4) could be, Ferrier responding with a further review of his own work in which he presented additional data from his and Yeo's experimental notebooks, along with a discussion of cases in the human literature associated with bilateral strokes affecting both superior temporal gyri. He concluded that Schäfer's lesions were too small and superficial. They probably were too superficial, unlike Ferrier's, not penetrating deeply enough to undercut the auditory cortex. Perhaps Victor Horsley, who made most of the lesions, had a lighter neurosurgical hand than Gerald Yeo. Schäfer wasn't silenced and fought back along much the same lines as had Ferrier. Eventually however, Ferrier seems to have won the day and most neurology texts subsequent to this era localized the auditory cortex in the superior temporal gyrus. Even Schäfer (1900) seems to have retreated. By 1905, Campbell (1905) was in little doubt that Schäfer's lesions did not penetrate deeply enough to undercut the transverse temporal gyri.

### 3 The Clinical Experience: Localization of Human Auditory Cortex in the Superior Temporal Gyrus

A typical illustration from the later nineteenth century (Fig. 1.5) shows where many neurologists believed the

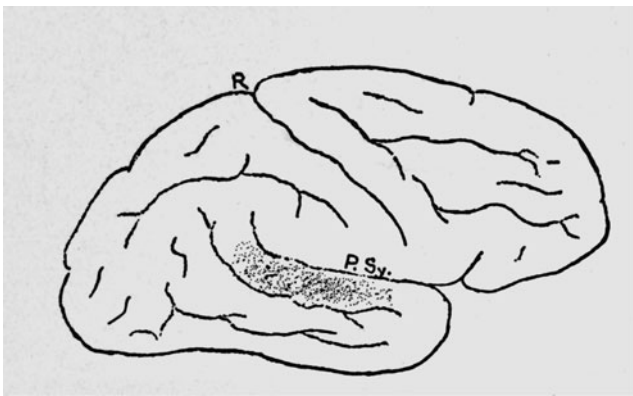


**Fig. 1.3** The brain of a monkey with almost total removal of both temporal lobes, who reportedly could even hear slight sounds soon after the operation. From Schäfer (1888a)



**Fig. 1.4** Sir David Ferrier (1843–1928) and Sir Edward A. Schäfer (later Sharpey-Schäfer) (1850–1935), who fought bitterly over the location of the auditory cortex in the superior temporal gyrus. From

*Biographical Memoirs of the Fellows of the Royal Society* (left) and from the *Quarterly Journal of Experimental Physiology* (right)



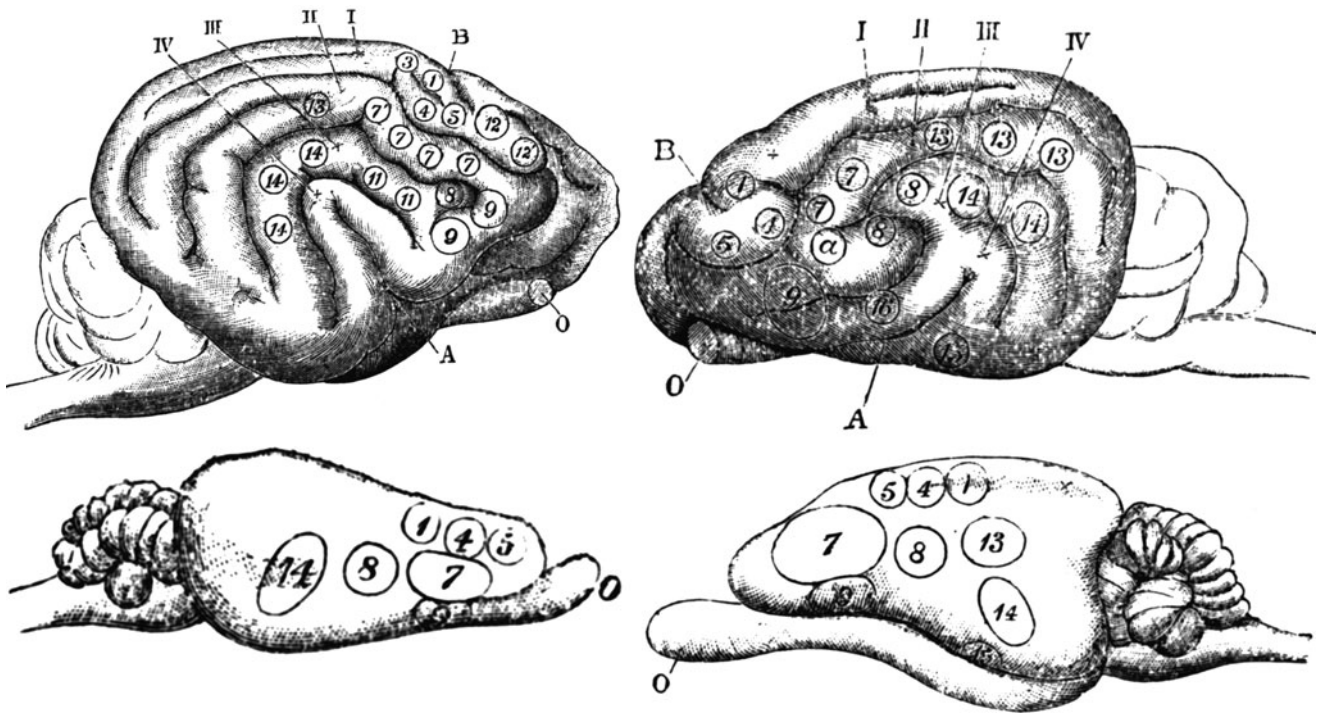
**Fig. 1.5** The location of the auditory cortex in the human superior temporal gyrus, as commonly understood by neurologists, from about 1880 to about 1900. From Gowers (1885)

human auditory cortex to be located (Wernicke and Friedlander 1883; Gowers 1885; Mills 1891; Dejerine and Dejerine-Klumpke 1895). Examination of postmortem brains from patients who had suffered from strokes that impaired hearing invariably revealed large lesions of the upper part of the superior temporal gyrus; these findings were taken to be confirmatory of Ferrier's original observations. Bilaterally symmetrical lesions were rare but, when reported, were usually associated with total deafness. In the case

reported by Wernicke and Friedlander (1883), there were bilateral gummata (abscess-like lesions of tertiary syphilis) in the upper parts of the superior temporal gyri. A case reported by Sérieux and Mignot (1901) had bilateral hydatid cysts; others such as those of Pick (1892), Anton (1899) and Mills (1891) were stroke cases with bilateral softening. Most neurologists, however, noted that lesions that impaired audition were also accompanied by alterations in the comprehension of language and extended into the temporal and parietal opercula and onto the insula.

#### 4 Experimental Studies in Other Animals: Cats, Dogs, Rabbits

Studies on dogs have already been mentioned. In them Fritsch and Hitzig had first localized the motor cortex and in these and other carnivores Ferrier had obtained what he thought was evidence of an auditory area which, when stimulated, elicited movements suggestive of the animal attending to a sound (Fig. 1.6). The area in the dog, cat, and jackal and the equivalent area in a rabbit are labeled "14" in the figure. With the success of his work on monkeys, Ferrier was to turn away from dogs and other non-primates for his later experimental studies and, in general, to discount recovery of



**Fig. 1.6** Results of Ferrier's electrical stimulation experiments in a jackal (*top left*), cat (*top right*), rat (*lower left*) and guinea pig (*lower right*). In each case, stimulation of the area labeled 14 resulted in

pricking of the ears and turning of the head to the opposite side. This area was therefore identified as the auditory cortex. From Ferrier (1876)

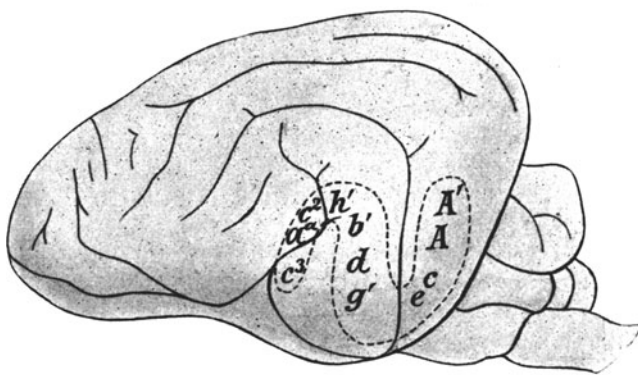
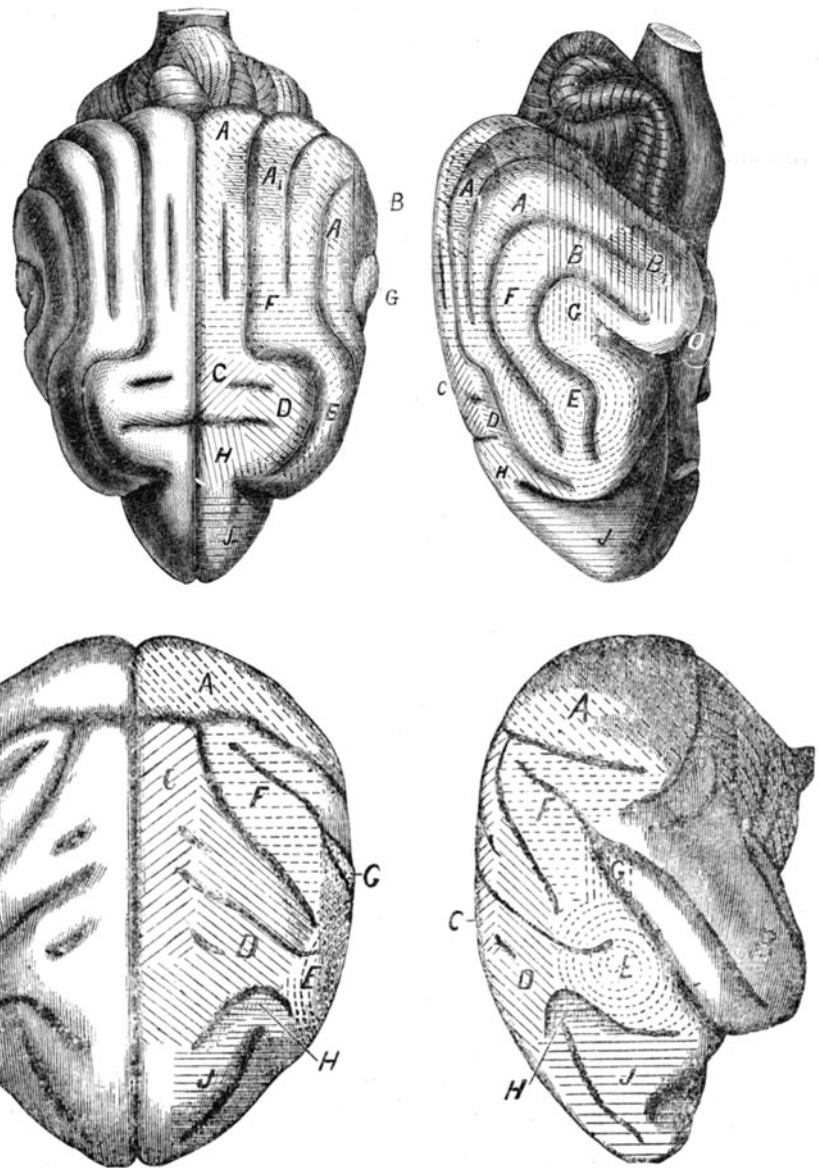
auditory function after lesions of the cerebral cortex in dogs and cats. Luciani and Tamburini (1879) and Luciani (1884) had bilaterally extirpated large regions of the sylvian and ectosylvian gyri in dogs and had observed an initial deafness and subsequently a significant loss of hearing acuity. Their method of testing hearing was to throw pieces of meat onto a tin plate. The German investigator, Hermann Munk (1881), had also observed a loss of hearing in dogs with bilateral lesions of the perisylvian region, localizing the principal focus at the ventral ends of the posterior ectosylvian and posterior suprasylvian gyri (Fig. 1.7) but noting that, to prevent any recovery of auditory function, it was essential to ablate much wider and deeper territories, perhaps extending to the hippocampus. To Munk, the key region in the posterior ectosylvian gyrus was a center for the comprehension of the meaning of sounds, likening the effects of its removal to something resembling psychic blindness. Clearly, these early investigators with their rather primitive means of testing auditory function were coming up against the capacity of animals to discriminate some aspects of sound without a cortex, so long as the inferior colliculus remains intact something that was demonstrated much later. For example, the auditory cortex is not essential for frequency discrimination, cats being able to perform this if the auditory midbrain is intact (Goldberg and Neff 1961). The cortex is, however, necessary for most aspects of sound localization (Whitfield et al. 1972; Heffner 1978). The ability of dogs to discriminate musical notes of different pitch after perisylvian region

lesions was examined in a preliminary way by Munk who felt that anterior lesions were associated with deficits in the discrimination of higher pitched sounds and posterior lesions with deficits in the discrimination of lower pitched sounds. A Russian student of Bechterew, Larionow (1899), followed up this observation by testing the ability of dogs to discriminate tones after small but penetrating lesions in the ventral ends of the posterior sylvian, posterior ectosylvian and posterior suprasylvian gyri (Fig. 1.8). The resultant map was a remarkable facsimile of the cochlea, with higher tones represented anteriorly and ventrally and lower tones represented posteriorly and dorsally. Perhaps Larionow's lesions penetrated different parts of the auditory radiation and thus interfered with the tonotopically organized thalamocortical projection to the primary auditory areas that we now know to be located more dorsally in the middle ectosylvian regions (see below). Larionow was an inventive man and tried to record responses to tuning forks of different pitches by placing a galvanometer on the surface of the dog's cortex. He may have been at least partially successful.

## 5 Anatomical Identification of Auditory Cortex

By this time, of course, terminations of the ascending auditory pathways in the medial geniculate nuclei had been demonstrated with the Marchi technique by Ferrier and

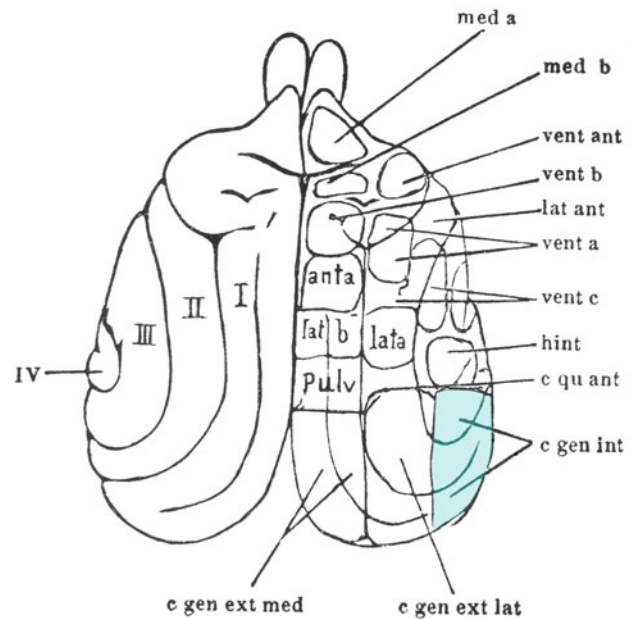
**Fig. 1.7** Functional areas of the cerebral cortex of the dog (*upper*) and monkey (*lower*) as located by Munk on the basis of experimental lesions. (A) Sehspähre or visual cortex. (B) Hörsphäre or auditory cortex. (C–J), Fühlspähre or somatic sensory cortex (C, hindlimb region, D; forelimb region; E, head region; F, eye region; G, ear region; H, neck region). From Munk (1881)



**Fig. 1.8** Results obtained by Larionow (1899) showing the distribution of tone centers in the brain of the dog. Lesions located at different points along the S-shaped trajectory result in a failure to respond to tones of different frequencies. Lower tones are represented posteriorly and higher tones anteriorly. From Bechterew (1911)

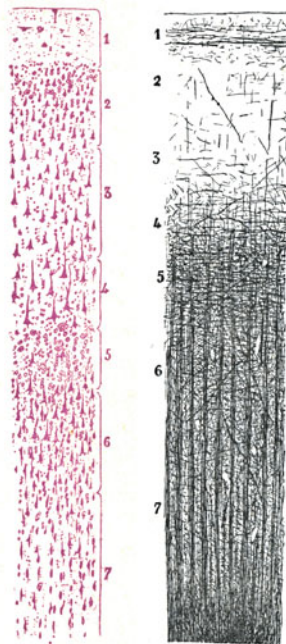
Turner (1894) and by Monakow (1895). A next step in localizing the auditory cortex was, therefore, to identify the region that received its thalamic input from the medial geniculate body. The first major studies with the retrograde degeneration technique of Gudden were carried out by Constantine von Monakow (1895) who found atrophy and fiber loss in the cat medial geniculate body after lesions of the posterior ectosylvian regions (Fig. 1.9). This was apparently a confirmation of the localization of the auditory cortex as identified by Munk.

With the beginnings of higher resolution studies of cortical histology by Santiago Ramón y Cajal, the first efforts at identifying a structural correlate of the auditory area were focused, not without reason, on the superior temporal gyrus. In the human brain (Fig. 1.10), Cajal (1900b) identified a region on the “anterior half of the first sphenoidal



**Fig. 1.9** *Left:* Constantine von Monakow (1853–1930). *Right:* summary of Monakow's experiments in cats in which he identified the thalamic nuclei projecting to different areas of the cerebral cortex on the basis of the retrograde atrophy that ensued from localized lesions

of the cortex. The *colored* region labeled c gen int was identified as the projection field of the medial geniculate body and was thus equated with the auditory cortex. From Monakow (1895)



**Fig. 1.10** The structure of the human anterior sphenoidal (superior temporal) gyrus as seen in Nissl (*left*) and Weigert (*right*) stains by Santiago Ramón y Cajal. From Cajal (1904, *left*, 1900b, *right*)

[superior temporal] gyrus" that he equated with the auditory region from his readings of Munk, Luciani, Ferrier and Monakow. Although repeatedly referring to the anterior part of the gyrus, Cajal's description makes it clear that

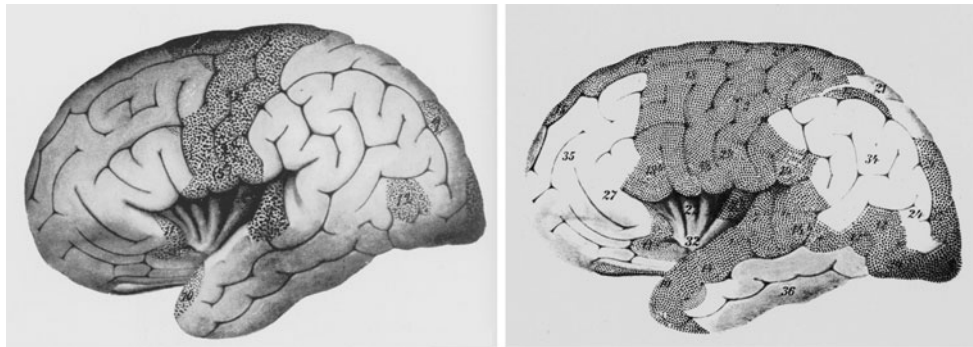
by this he meant the upper part of the gyrus where neurologists had localized the auditory area. Cajal's reading of Munk in particular left him in no doubt that the corresponding region of the canine cortex was a center for auditory perception. Other, more ventral areas of the dog's posterior ectosylvian regions were, according to Cajal, concerned with the comprehension of the significance of sounds, an interpretation of Munk's experiments that had involved deeply penetrating lesions. Monakow's findings on the degeneration of the medial geniculate body subsequent to temporal cortical lesions also impressed Cajal. Cajal studied both the human superior temporal cortex and that of the "central regions" of the posterior ectosylvian and suprasylvian gyri in the cat and dog with the Nissl, Weigert, and Golgi methods. After giving a detailed description, layer by layer and cell type by cell type, he sums up by saying that comparisons between the cortices of the human and of the two carnivores are not easy because of the great differences in cellular morphology present. But he stresses that what he interpreted as the auditory cortex in all three species was characterized by the presence of a distinct layer of granule cells containing a variety of types of cells with short axons, by the existence of cells resembling pyramidal cells and having a long axon projecting out of the cortex but devoid of an apical dendrite, and an excessive development of the deeper cortical layers. Noteworthy features were the greater abundance of cells with short axons and especially those of the tufted (i.e., double bouquet) type in the human and some special giant cells not

found in other areas were described in all layers. Cajal's auditory cortex in the human had 7 layers: plexiform or layer 1; layer of small pyramids or layer 2; layer of medium pyramids or layer 3; layer of giant pyramids or layer 4; layer of diminutive or granule cells or layer 5; layer of deep medium pyramids or layer 6; layer of fusiform cells or layer 7. Apart from the specific features mentioned above, this cortex had many similarities to the cortex of the postcentral gyrus but differed in its layering pattern from that of the precentral gyrus and of the visual cortex (Cajal 1899a, b, 1900a).

It is difficult to trace who first directed attention about the auditory cortex away from the superior temporal gyrus per se and onto the supratemporal plane. It may have been

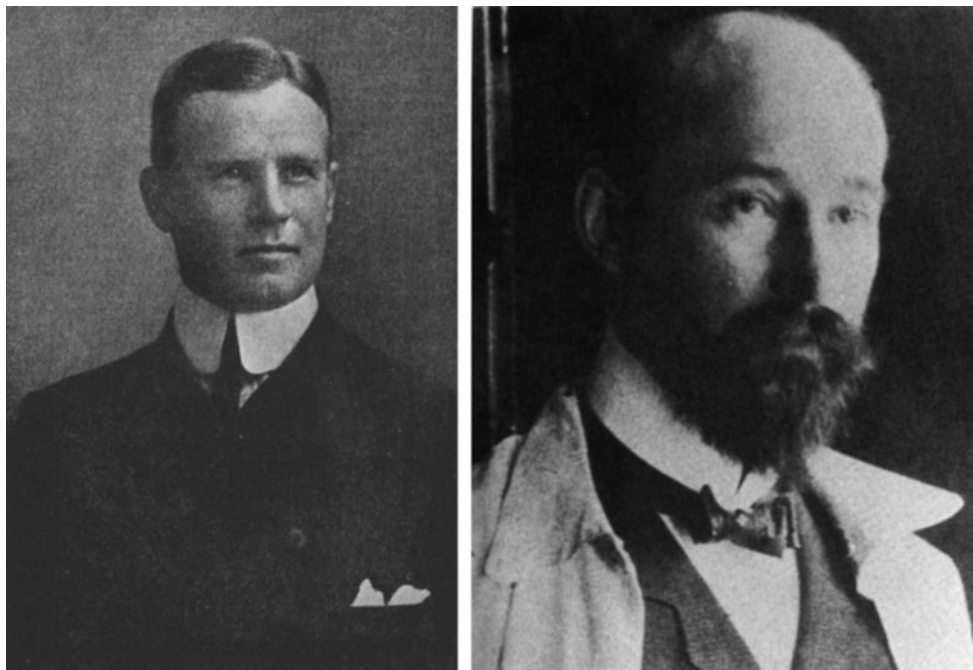
Flechsig (1898) who had recognized that a region corresponding mainly to the transverse temporal gyri (Heschl's gyrus) was the endpoint of fibers radiating into the hemisphere from the medial geniculate body and which, along with the visual and somatic sensory radiations, was the first to myelinate in the human embryo (Fig. 1.11). In the first of the great cytoarchitectonic studies of the human cerebral cortex, A. Walter Campbell (1905) and Korbinian Brodmann (1909) (Fig. 1.12), both located an area of granular cortex on the transverse temporal gyri that they thought corresponded to the region that Flechsig (1898) had identified.

Campbell found the fiber architecture of the transverse temporal gyri to be a more distinctive feature of the cortex



**Fig. 1.11** Paul Flechsig's location of the cortical areas of the human brain that show myelination before birth (*left*) and postnatally (*right*). An early myelinating field located on the anterior and anterior half of

the posterior transverse temporal gyri represents the primary auditory cortex. From Flechsig (1904)

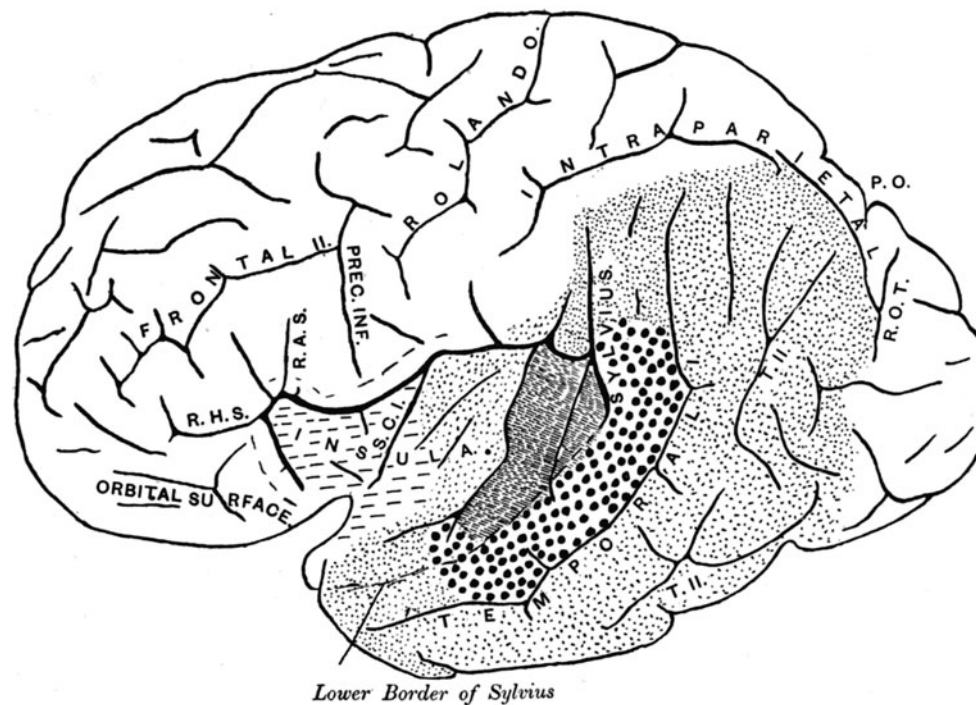


**Fig. 1.12** Alfred Walter Campbell (1868–1937, *left*) and Korbinian Brodmann (1868–1918, *right*). From the *Medical Journal of Australia* (*left*) and *World Neurology* (*right*)



here than the cytoarchitecture, noting that the outstanding features of this type of cortex are the many large fibers entering in a radial fashion from what he took to be the auditory radiation, the existence of a pronounced stria of Kaes which is the transverse band of myelinated fibers in our layer II, and a general wealth of fibers in all layers. It is interesting to read Campbell's description of his approach to the study of cellular lamination: "It is possible to distinguish three types, but the topical variations in cell lamination are not equivalent in degree to the differences in fiber-arrangement, also the intervening gradations are by no means abrupt: hence the extent and limits of these types of lamination are by no means easy to define; however, I may say that the following description has been built up on a particularly full and careful examination of the lobe, and above all things I would mention that judgments concerning the size, number, and general disposition of cells in various parts have been based not upon mere microscopic inspection, but upon the comparative results given by a great number of camera lucida drawings made at various magnifications. This statement is necessary because experience gained in this work has proved to me over and over again that the eye cannot be trusted to make reliable comparisons, especially when the matter concerns the relative magnitude, or the number of given cells in different sections: accordingly when any doubt has existed

on these points I have always settled the matter by making a drawing; and tedious as this procedure undoubtedly is, it is a very necessary, indeed an essential, safeguard in work of this description" (Campbell 1905). The chief distinguishing features of the cellular architecture of the cortex on the transverse temporal gyri were "a general rich supply of cells," prominent giant pyramidal cells in the external pyramidal layer (our layer III), and a thick stellate cell layer (our layer IV), the cells being divided into columns by radial fasciculi of fibers. The extent of this cortex "corresponds exactly with the area mapped out by fiber-arrangement." In some brains the area "is completely concealed, in others it is found peeping over the lip of the [Sylvian] fissure on to the free surface of the first temporal convolution" (Fig. 1.13). Campbell, in reviewing the neurological literature, was convinced that clinical distinctions could be made between cases of deafness, pure word deafness, amusia, and psychic deafness but he could find little pathological data to support the localization of causative lesions other than broadly in the upper part of the superior temporal gyrus and surrounding regions. The lesions in reported cases were simply too extensive. In trying to identify the primary auditory cortex, he was more impressed by the myelogenetic studies of Flechsig (1898) and of Cécile and Oskar Vogt (1902) which had clearly shown the auditory radiation emanating from the



**Fig. 1.13** Campbell's drawing of the human cerebral hemisphere with the Sylvian fissure opened out to reveal the audito-sensory area (*shaded*) confined to the transverse temporal gyri, the audito-psychic area (*large*

*dots*) on the exposed surface of the upper two thirds of the superior temporal gyrus, and the common temporal cortex (*small dots*). From Campbell (1905)

medial geniculate body of human fetuses and its termination beneath the two transverse temporal gyri, particularly the anterior gyrus. Marchi-based studies of degenerating fibers or studies of the secondary atrophy following cortical and subcortical lesions in stroke patients also helped to relate the outflow tract of the medial geniculate body to the transverse temporal gyri (Monakow 1895; Dejerine and Dejerine-Klumpke 1901). Campbell briefly describes atrophy more or less restricted to the transverse temporal gyri in the brain of a 40-year old man who had been deaf from birth. In comparing the architecture of the area that he had described on the transverse temporal gyri with that of the visual cortex, Campbell concluded that this “restricted transverse temporal area is the part of the temporal lobe on which auditory stimuli first impinge.” He named the area the *audito-sensory area* and, in a typically Edwardian railway analogy, he called it “the arrival platform of auditory stimuli.” Its bilateral destruction should lead, therefore, to total deafness. He pointed out, however, that this could not be definitively determined from the case studies that had been described because the lesions were far too large to have the requisite localizing value. Because unilateral lesions involving the transverse temporal gyri were usually reported to be accompanied by “a dulling of the sharpness of hearing” rather than unilateral deafness, he was inclined to believe that the auditory pathways providing the input to the *audito-sensory area* were bilateral.

Following on from his identification of “*psychic areas*” around the primary visual and somatosensory cortical areas, Campbell was led to search for a comparable “*audito-psychic*” area adjoining the *audito-sensory area*. This he identified in a “*skirt area*” located lateral to the *audito-sensory area* on the exposed surface of the superior temporal gyrus (Fig. 1.13) and possessing many structural similarities to the *audito-sensory area*. It differed, however, in that the large, deeply placed oblique fibers and the giant cells were less prominent, and the radial fasciculi were more prominent (Figs. 1.14 and 1.15).

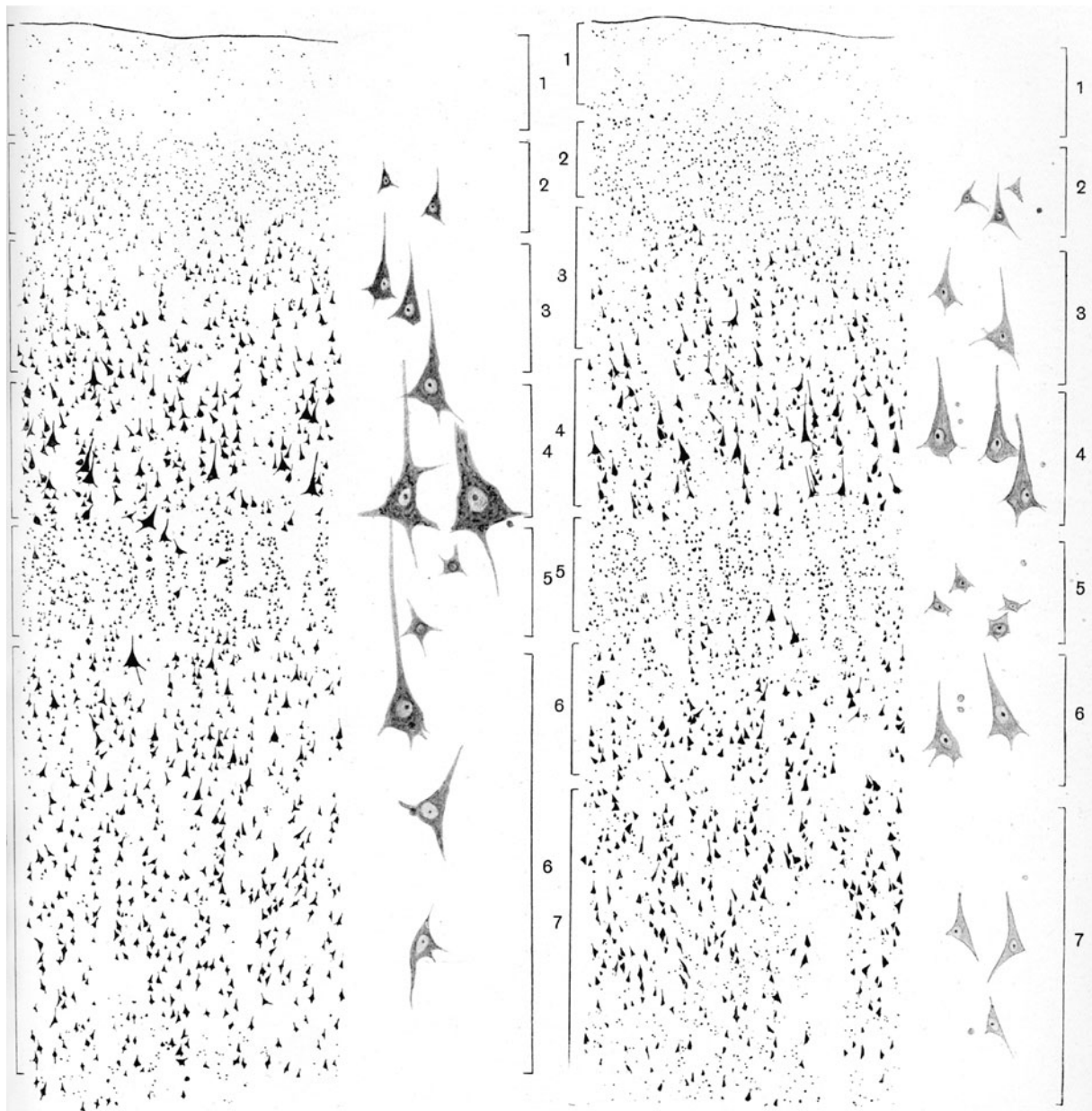
Brodmann (1909), also influenced by Flechsig, outlined in the human an area 41 which he called “the internal (anterior) transverse temporal area,” corresponding “approximately but not precisely to the anterior transverse gyrus.” It extended into the circular sulcus medially where it was sharply demarcated from a parainsular area that he numbered area 52 (Fig. 1.16). A second area, area 42, called “the external (posterior) transverse temporal area,” formed an arc around area 41 posteromedially, posteriorly and laterally, coming to the surface of the superior temporal gyrus lateral to area 41. Brodmann was never very explicit about the details of the cytoarchitecture of these three areas, although his context makes clear that area 41 was the area of smallest cells and highest granularity while area 42 was somewhat less granular. Areas 41, 42, and 52 were later

named areas TC, TB, and TD respectively, by Economo and Koskinas (1925) (Fig. 1.17).

Campbell went on to locate an “*audito-sensory area*” and a surrounding “*audito-psychic area*” in comparable locations in the brains of a chimpanzee and an orangutan, but he was uncertain about the location of a homologous primary auditory sensory area in cats, dogs, or pigs (Figs. 1.18 and 1.19). The apes were the species that Grünbaum and Sherrington (1902, 1903) had used for mapping the motor cortex by electrical stimulation. Campbell was then working at the Rainhill Asylum, on the outskirts of Liverpool, where Sherrington had his laboratory in Liverpool University. He was undoubtedly influenced by the ablation studies of Munk (1881) although his area “*ectosylvian a*,” which he thought might correspond to the human auditory sensory area, is located on one or both of the two sylvian gyri anterior to where Munk had located the center of his auditory cortex (Fig. 1.19). Brodmann (1905), impressed by a lack of anything resembling typical *koniocortex* in the temporal cortex of monkeys and many other species (Figs. 1.20 and 1.21), considered either that animals lacked a specialized auditory cortex or that the human auditory fields (his areas 41, 42, and 52) represented specialization for functions additional to audition. Perhaps this is not surprising, given that the human auditory cortex when visualized in Nissl stains (Fig. 1.22) lacks the intense granularity of the postcentral somatic sensory and the primary visual areas. As Brodmann put it: “. . .the cell and fiber architecture, so very characteristic of both transverse gyri in man, is lacking in all other animals. To put it another way, a human structural zone in which Flechsig locates the cortical end-station of the auditory pathway, the auditory [cortex], is completely absent in animals, even in monkeys that otherwise possess a very similar cortical structure to man.”

## 6 New Experimental Studies in Animals

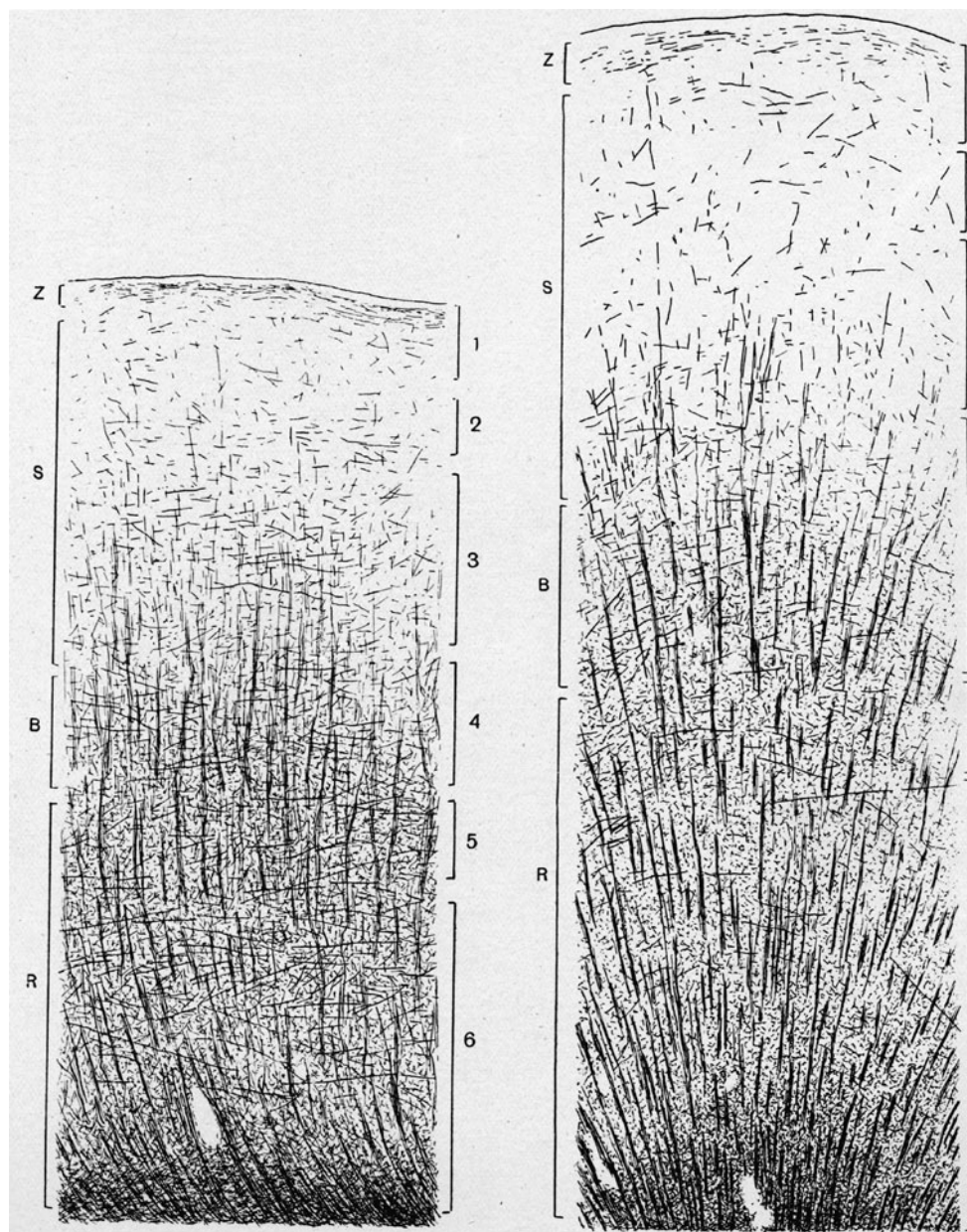
Brodmann’s view held for many years, and when A. Earl Walker (1937) discovered an area of granular cortex connected with the medial geniculate nucleus and located on the posterior part of the supratemporal plane in the macaque monkey (Fig. 1.23), there is a note of mild surprise in his description, even though Stephan Polyak (1932) had already traced degenerating fibers with the Marchi technique from the posterior part of the thalamus to the supratemporal plane (Fig. 1.24). Once Walker (1937) had recognized the location of what he thought must be the primary auditory cortex in the region to which Polyak had traced the putative auditory radiation, he could lesion it and observe not only the occurrence of retrograde degeneration in the heart of the



**Fig. 1.14** Campbell's drawings of cells and cell lamination in the audito-sensory area (*left*) and the audito-psychic area (*right*) of the human brain. From Campbell (1905)

medial geniculate body, but also the systematic movement of the locus of degeneration with lesions in different locations of the auditory cortex, implying a topographically ordered geniculo-cortical projection. Wilfrid Le Gros Clark (1936) had similar, although less detailed, findings. Later, Ades and Felder (1942), in delineating the cortical region from which evoked potentials could be recorded in response to click stimuli, confirmed Walker's location of the primary auditory cortex on the supratemporal plane of the monkey but found that it fell within a much wider area that was activated by click stimuli (Fig. 1.25).

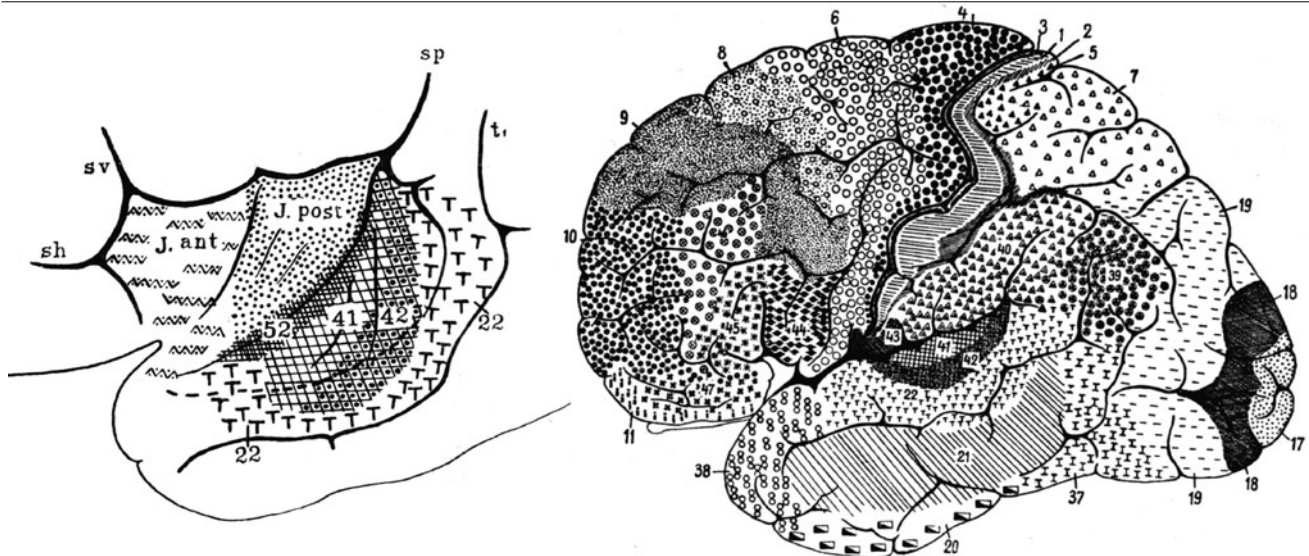
In cats, as noted above, Monakow had observed retrograde degeneration in the medial geniculate body after ablations of the posterior sylvian and ectosylvian regions, and Mettler (1932) later observed retrograde degeneration in the medial geniculate nucleus after dorsal ectosylvian lesions as well, while Woollard and Harpman (1939) traced Marchi-stained degenerating fibers to middle ectosylvian and sylvian gyri after lesions of the medial geniculate body. Retrograde degeneration was also described in the medial geniculate complex after temporal lesions in rats (Waller 1934; Waller and Barris 1937). The first investigation of the area of the



**Fig. 1.15** Campbell's drawings of fiber patterning in the audito-sensory (*left*) and audito-psychic (*right*) areas of the human cortex. From Campbell (1905)

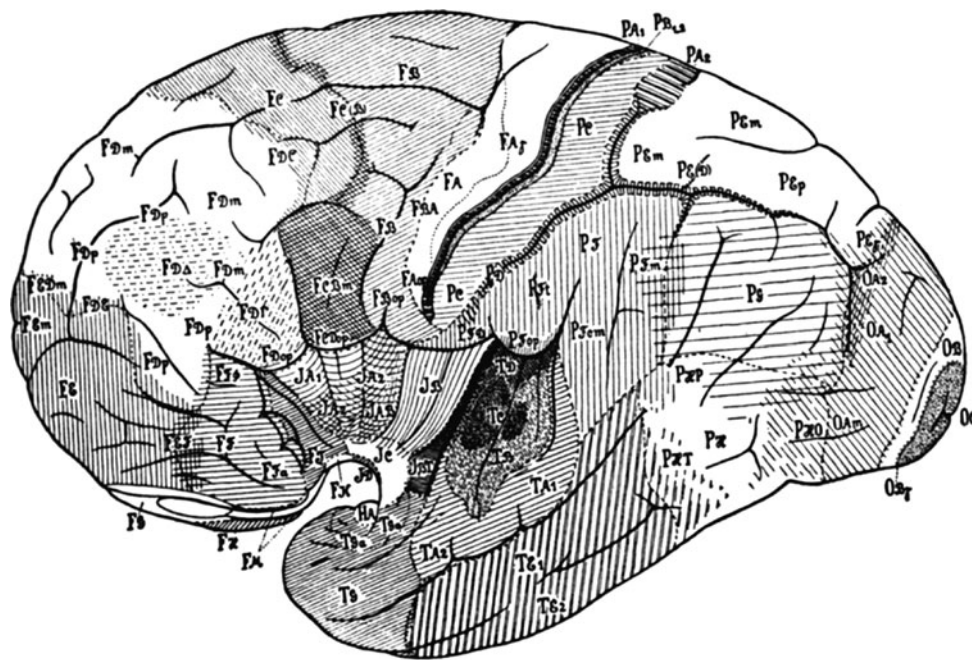
cat cortex in which evoked potentials could be recorded in response to auditory stimuli was made by Kornmüller in 1937 and was found anterior and dorsal to the region delineated by Munk as that which was essential for auditory perception (Fig. 1.7). Bremer and Dow (1939), in applying the click-evoked potential method for the first time in the cortex (Fig. 1.26), mapped out a larger region, the dorsal part of which, equivalent more or less to what we now call area AI, had a cytoarchitecture that was granular and typical of sensory cortex. An area virtually identical to the granular area of Bremer and Dow was also mapped using click-evoked

potentials by Ades (1941). Much earlier, the same region had been delineated by Cécile Vogt as the zone of earliest and heaviest myelination in the developing cat brain (Fig. 1.27). Waller (1934) made relatively small lesions in the region defined by Bremer and Dow and in certain areas around it and examined the distribution of retrograde degeneration in the thalamus (Fig. 1.28). With lesions largely restricted to the granular area of Bremer and Dow, he observed retrograde degeneration in what we would now regard as the ventral nucleus of the medial geniculate nucleus. With lesions located ventrally and posteriorly, degeneration was mainly



**Fig. 1.16** Brodmann's drawings of the insular region and upper surface of the superior temporal gyrus (*left*) and of the lateral aspect of the human cerebral hemisphere (*right*) showing areas 41 and 42, which are called the internal or anterior and the external or posterior transverse

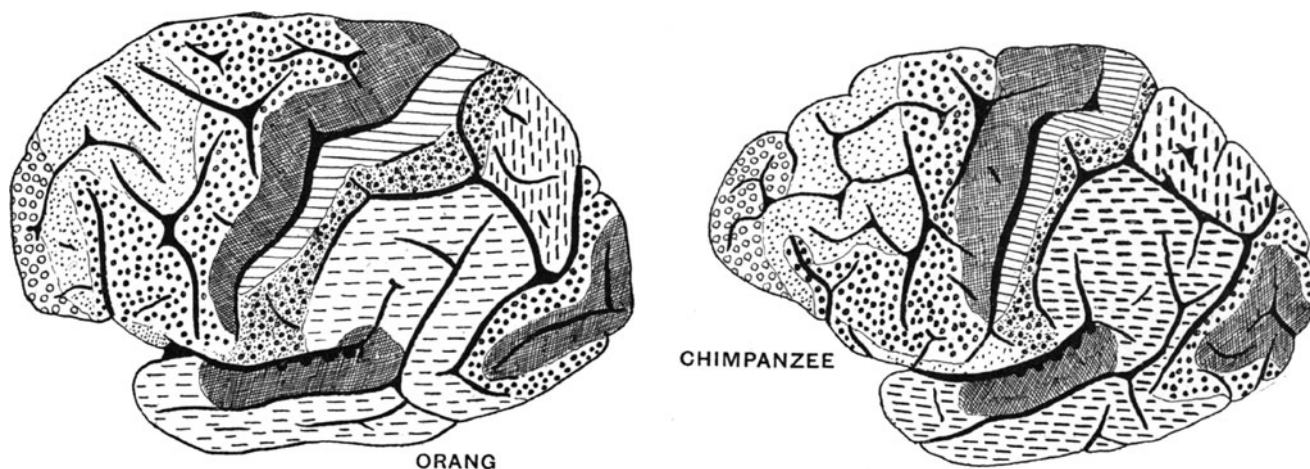
temporal areas, respectively. Area 52 is the parainsular area and area 22 the cortex on the exposed surface of the superior temporal gyrus. From Brodmann (1909)



**Fig. 1.17** Map of the cytoarchitectonic areas of the human cerebral cortex by Economo and Koskinas (1925). Te and Ts are the two transverse temporal areas of Brodmann and Campbell. From Economo and Koskinas (1925)

in what we would now call the dorsal and medial nuclei. These studies were forerunners of the concerted investigation made by Rose and Woolsey on the plan of organization of the cat auditory cortex and its thalamic connections (Rose 1949; Rose and Woolsey 1949, 1958; Woolsey 1961). The in-depth studies of Rose and Woolsey (Fig. 1.29) were to provide the first detailed parcellations of the auditory cortex.

Woolsey and Walzl (1942; Walzl and Woolsey 1946; Woolsey 1971a, b) had extended the studies of Bremer and Dow and Ades in the cat by recording surface evoked potentials in response to electrical stimulation of small bundles of nerve fibers leaving different parts of the cochlea. By this means, they could demonstrate that, within an area corresponding approximately to the granular area outlined by Bremer and Dow, the apex of the cochlea, and thus low



**Fig. 1.18** Campbell's maps of the orangutan and chimpanzee cortex. The audito-sensory area is represented by a row of *large dots*. The *hatched* region lateral to it is the audito-psychoic area. From Campbell (1905)

tones, was represented posteriorly and the base, and thus high tones, was represented anteriorly. This area they called the first auditory area or AI. They also noted that with increased intensity of stimulation, a much wider area could be activated and that the part of this wider area lying ventral to the primary area showed a cochleotopic representation that was a mirror image of that in the AI area. This area they called the second auditory area or AII (Fig. 1.30). Almost contemporaneously, Ades (1943) showed a similar region of click-evoked responses extending over the middle and posterior ectosylvian gyri. Responses in the posterior ectosylvian area could also be evoked by applying strychnine to the surface of the middle ectosylvian “primary area,” so the auditory responsiveness of the “secondary area” was thought to be dependent on corticocortical projections from the primary area.

## 7 Entering the Modern Era: Multiple Cortical Fields, Tonotopicity, and Thalamocortical Projections

The next steps in the delineation of the cat's auditory cortex came in the combined anatomical and physiological studies of Rose and Woolsey. In 1949, Rose subdivided the cat auditory cortex regions into a central, moderately granular area, coincident with the anterior half to two-thirds of the first auditory or AI field as delineated with the evoked potential method by Woolsey and Walzl (1942), and several surrounding areas with different cytoarchitectonic characteristics (Fig. 1.31). The AII area was reduced by Rose to only the anterior half of the original AII field, the posterior parts of both it and the old AI now being subsumed into a posterior ectosylvian or EP field virtually identical to the

secondary auditory field of Ades (1943). The surrounding areas were later mapped with the evoked potential method by Woolsey and his co-workers, further subdivided, and most of these areas were demonstrated to contain complete and independent representations of the cochlea (Fig. 1.32) (Woolsey 1958, 1964). Rose and Woolsey (1949) were able to show that destruction of the AI area resulted in retrograde degeneration in the anterior part of the medial geniculate complex, in a region corresponding to what we now call the ventral nucleus. They also found that lesions of different parts of AI led to degeneration in different parts of the nucleus in a manner that implied a cochlear representation within it, and a cochleotopic projection on the cortex (Fig. 1.33). They further confirmed this by showing that electrical stimulation of fibers from the apex or base of the cochlea in the cat resulted in evoked potentials in lateral or medial aspects of the ventral nucleus, respectively (Rose and Woolsey 1958), and that electrical stimulation at progressively more medial sites in the ventral nucleus led to evoked potentials at progressively more anterior sites in AI (Woolsey 1964).

The first single unit responses to pure tone stimuli were recorded from cat AI area by Erulkar et al. (1956), the locations of high and low tone-responding units being located anteriorly and posteriorly, respectively, confirming the electrical stimulation results of Woolsey and Walzl. Woolsey and his colleagues continued to map tonotopically organized evoked potentials in cat auditory regions (Woolsey 1959, 1960, 1964, 1971a). The culmination of several years of intensive work first appeared in the 1961 map (Fig. 1.32), where the AI field is embraced anteriorly, dorsally and posterodorsally by a “suprasylvian fringe” area, the apical cochlear representation of which has been taken from the old AII field which has become restricted to a region between the anterior and posterior ectosylvian sulci, and the posterior