

7.4 The Forebrain Auditory System

For decades, the dominant species for research on the auditory forebrain has been the cat, but the focus has now clearly shifted to non-human primates. Although the subcortical auditory systems of monkeys and cats are largely similar, there are important differences in cortical organization (Kaas and Hackett 2000).

7.4.1 The Auditory Thalamus

The **medial geniculate body (MGB)** or **nucleus** is clearly visible on the inferior surface of the inferior thalamus. The MGB contains several divisions, the principal auditory relay nucleus is the **ventral** or **principal medial geniculate nucleus** (Winer 1984). The ventral division of the MGB is laminated. It receives the major ascending auditory projection from the also laminated central nucleus of the inferior colliculus. For both

nuclei, lamination is a structural correlate of precise tonotopic organization. In contrast, the dorsal and medial divisions of the MGB are not laminated and receive much less dense input from the inferior colliculus. The ventral medial geniculate nucleus projects via the auditory radiation to the tonotopically organized primary auditory cortex. The dorsal and medial sub-nuclei project to higher-order auditory cortical areas in the planum temporale, areas that do not have such a precise tonotopic organization as the primary auditory cortex.

7.4.2 The Acoustic Radiation

In 1882, Constantin von Monakow first described the origin of the acoustic radiation from the MGB in rabbit experiments. The classic studies in the human brain located the proximal part of the acoustic radiation just caudal to the thalamus, where it originates from the MGB, then passes through the sublenticular, posterior part of the internal capsule to curve around the inferior sulcus of the insula before reaching Heschl's gyrus

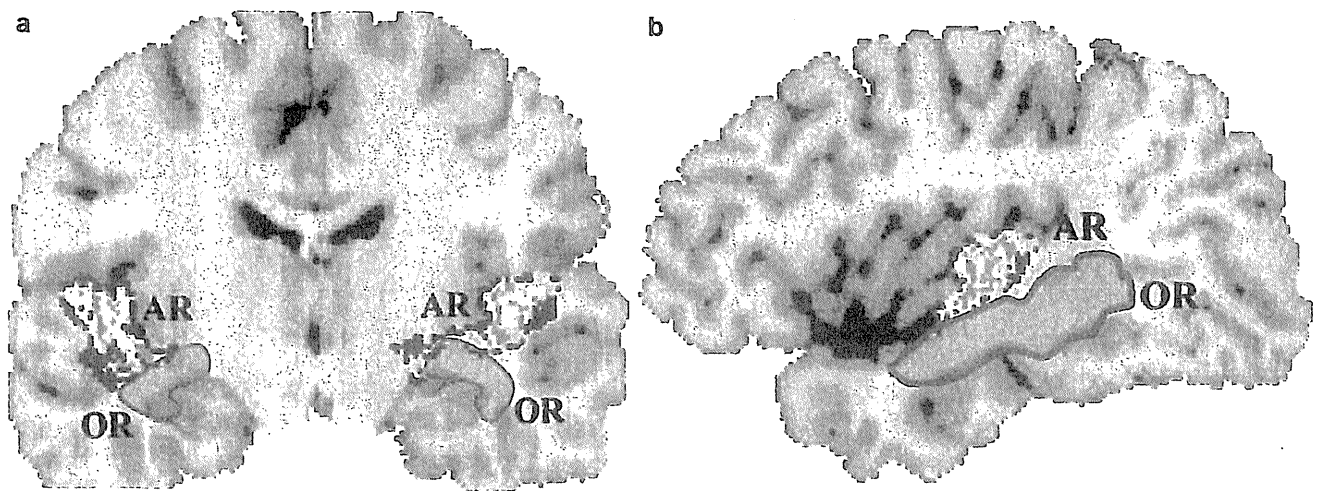


Fig. 7.10 The acoustic and optic radiations in coronal (a) and sagittal (b) probabilistic maps (after Rademacher et al. 2002). *Abbreviations:* AR acoustic radiation; OR optic radiation

(Dejerine 1895; Flechsig 1920; Pfeifer 1920). In a more recent study, Rademacher et al. (2002) showed the stereotaxic localization, intersubject variability and interhemispheric differences of the human acoustic radiation (Fig. 7.10). They showed that the location of the acoustic radiation varies considerably between individuals and hemispheres.

7.4.3 The Auditory Cortex: Sequential Levels of Auditory Processing

The **primary auditory cortex (A1)** is located on the transverse temporal or Heschl's gyrus in the temporal lobe of the cerebral cortex and corresponds to area 41. It is surrounded by secondary auditory areas (A2): caudally the caudomedial area, also known as the planum temporale, and rostrally, the rostral area. Geschwind and Levitsky (1968) demonstrated that the **planum temporale** is larger on the left side in the majority of the postmortem brains they examined. **Asymmetry** of the planum temporale may form the substrate for left hemispheric dominance for language-related auditory processes (Geschwind and Galaburda 1985; Dorsajnt-Pierre et al. 2006) and is correlated with handedness (Steinmetz et al. 1989, 1991).

Heschl's gyrus is located largely within the lateral sulcus (von Economo and Horn 1930; Fig. 7.11). The transverse temporal gyrus is often partially duplicated into a double, or occasionally triple convexity (Pfeifer 1920; Steinmetz et al. 1989; Penhune et al. 1996; Leonard et al. 1998; Morosan et al. 2001). The cytoarchitecture of the human auditory cortex has been described by Brodmann (1908, 1909), von Economo and Koskinas (1925), Galaburda and Sanides (1980) and, more recently by Hackett et al. (2001) and Hackett

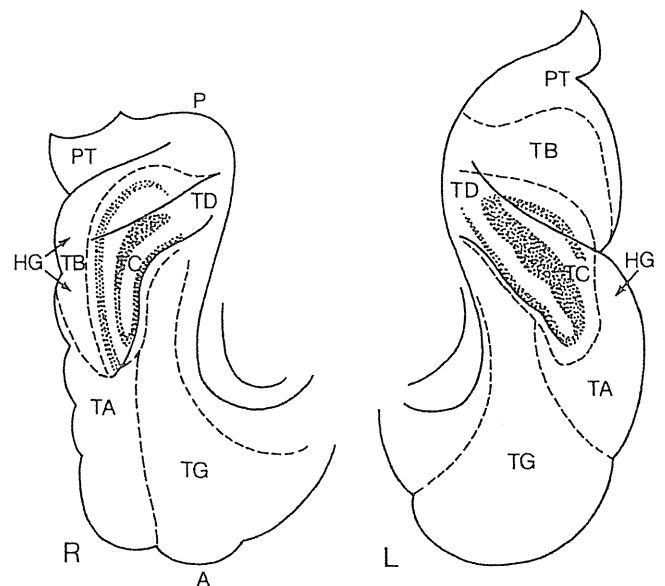


Fig. 7.11 The human auditory cortex. The primary auditory cortex is composed of two fields, TD and TC. On the right side (R), these occupy a double transverse temporal gyrus (Heschl's gyrus); on the left side (L), they correspond to a single Heschl's gyrus and a part of the more caudally situated planum temporale (PT). TD and TC are composed of markedly granular subareas (dotted in red) and less granular areas. Note the distinct right-left asymmetries with a larger planum temporale on the left side. *Abbreviations:* A anterior; HG Heschl's gyrus; P posterior; TA superior temporal area; TB magnocellular supratemporal area; TC transverse supratemporal area; TD intercalate supratemporal area; TG temporopolar area (after Brodal 1981)

and Kaas (2004) and Morosan et al. (2001) and Rademacher et al. (2001a, b). The primary auditory cortex was designated area 41 by Brodmann, TC by von Economo and Koskinas and

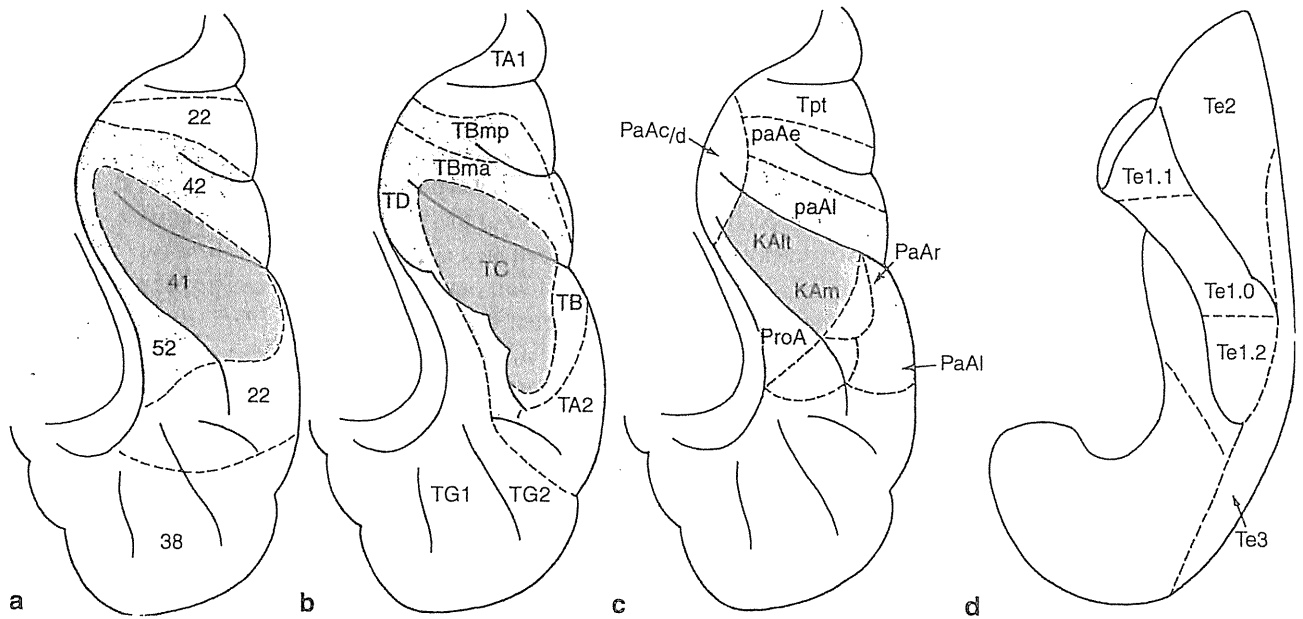


Fig. 7.12 Regional parcellation of the right human superior temporal cortex (rostral is below) according to (a) Brodmann, (b) von Economo and Koskinas, (c) Galaburda and Sanides and (d) Morosan and co-workers (after Hackett and Kaas 2004 and Morosan et al. 2001). In (a–c), core areas are shown in *red*, belt areas in *medium red* and parabelt areas in *light red*. Abbreviations: *KAlt*, *KAm* lateral and medial auditory

koniocortex; *PaAc/d*, *paAe*, *PaAl/paAl*, *PaAr* caudal/dorsal, external, lateral and rostral auditory parakoniocortex; *ProA* proauditory cortex; *TA1*, *TA2*, *TB*, *TBma*, *TBmp*, *TC*, *TD* subdivisions by von Economo and Koskinas; *Te2*, *Te1.0*, *Te1.1*, *Te1.2*, *Te3* subdivisions by Morosan and co-workers; *TG1*, *TG2* temporopolar subdivisions of von Economo and Koskinas; *Tpt* temporoparietal area; 22–52 Brodmann areas

KAm and *KAlt* (medial and lateral auditory **koniocortex**) by Galaburda and Sanides (Fig. 7.12a–c). *KAm* is the most medial and the most granular area, whereas the more lateral *KAlt* is less granular. Morosan et al. (2001) suggested three areas with well-developed layers IV, *Te1.1*, *Te1.0* and *Te1.2*, to represent the primary auditory cortex (Fig. 7.12d). There is considerable variability in size of the auditory koniocortex and its extent does not coincide with gyral or sulcal anatomy (Galaburda and Sanides 1980; Rademacher et al. 1993, 2001a, b; Hackett et al. 2001; Morosan et al. 2001). The human auditory koniocortex (area 41/TC/KA/Te) is homologous to the core area of the monkey auditory cortex. Based on parvalbumin staining, Wallace et al. (2002) suggested that Heschl's gyrus contains two core fields, partially surrounded by at least six belt fields that lie mostly on the superior temporal gyrus. In an fMRI study, Wessinger et al. (2001) showed that pure tones primarily activate the core and that more complex sounds activate belt areas.

The **primate auditory core area** is located in the centre of the superior temporal plane (Hackett et al. 2001; Fig. 7.13). In primates, a centrally located core region containing two or three subdivisions including the primary auditory area (*A1*), a surrounding belt of cortex with some seven divisions, and a lateral parabelt region comprised of at least two fields, have been described. In monkeys, the **core region** can be identified

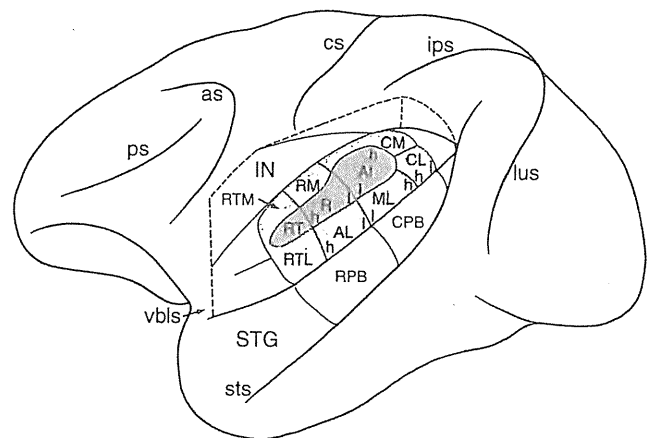


Fig. 7.13 Auditory and auditory-related cortices in macaque monkeys. Core areas (*A1*, *R*, *RT*) are shown in *red*, belt areas (*CL*, *CM*, *AL*, *RM*, *RTL*, *RTM*) in *medium red* and parabelt areas (*CPB*, *RPB*) in *light red*. Major sulci have been opened to show the extent of auditory-related cortex. Abbreviations: *A1* primary auditory area; *AL* anterolateral area; *as* arcuate sulcus; *CL*, *CM* caudolateral and caudomedial areas; *CPB* caudal parabelt area; *cs* central sulcus; *h*, *l* high and low frequencies; *IN* insula; *ips* intraparietal sulcus; *lus* lunate sulcus; *PL* posterolateral area; *ps* principal sulcus; *R* rostral area; *RM* rostromedial area; *RPB* rostral parabelt area; *RT* rostrotemporal primary auditory cortex; *RTL*, *RTM* lateral and medial rostromedial areas; *STG* superior temporal gyrus; *sts* superior temporal sulcus; *vbls* ventral bank of lateral sulcus (after Hackett et al. 2001)

on the basis of *specific* anatomical and physiological features. The region shows dense immunostaining for parvalbumin in layer IV, surrounded by a more lightly stained belt, which is flanked by a very sparsely stained parabelt (Jones et al. 1995; Kosaki et al. 1997). Parvalbumin staining also marks the human core auditory cortex in humans (Nakahara et al. 2000; Wallace et al. 2002; Chiry et al. 2003). In macaque, chimpanzee and human brains, Hackett et al. (2001) identified the auditory core from serial sets of adjacent sections processed for cytoarchitecture, myeloarchitecture, acetylcholinesterase and cytochrome oxidase. The position of the core region with respect to major sulci and gyri in the superior temporal region varied most in chimpanzee and human brains.

In monkeys, most neurons of the ventral division of the MGB project to the core cortex (Mesulam and Pandya 1973; Burton and Jones 1976; Luethke et al. 1989; Rauschecker et al. 1997). These **thalamocortical projections** terminate in layers IV and lower III in regular patches of higher density label, separated by areas of less dense labelling (Pandya and Rosene 1993; Hashikawa et al. 1995). In contrast, the medial and dorsal divisions of the MGB project to the core area diffusely. It seems likely that the human primary auditory cortex also receives dense thalamic input. This input explains the cochleotopic organization shown in this area by functional imaging, including magnetoencephalography (MEG) (Elberling et al. 1982; Hari et al. 1989; Pantev et al. 1995; Lutkenhoner and Steinstrater 1998), PET (Lauter et al. 1985; Ottaviani et al. 1997; Lockwood et al. 1999), fMRI (Wessinger et al. 1997; Scheich et al. 1998; Di Salle et al. 2001) and microelectrode mapping studies in epilepsy patients (Howard et al. 1996).

The human auditory koniocortex is surrounded rostrally, laterally and caudally by an area of **parakoniocortex** (Fig. 7.12). This region covers the lateral part of the transverse temporal gyrus, and extends rostrally and caudally over the superior temporal plane. The auditory parakoniocortex has been called area 42 by Brodmann and TB by von Economo and Koskinas. Galaburda and Sanides (1980) distinguished three regions: (1) a rostral auditory parakoniocortex (PaAr) on the rostral aspect of the superior temporal plane; (2) a lateral, internal auditory parakoniocortex (PaAl), lateral to A1; and (3) a caudal auditory parakoniocortex (PaAc), covering the caudal portion of the superior temporal plane and extending around the insula to the parietal operculum. In its turn, the parakoniocortex is surrounded by an extensive area of auditory cortex that covers the remaining of the superior temporal plane and the lateral surface of the superior temporal gyrus, except for its rostral pole. This region was described as area 22 by Brodmann (1909), as TA by von Economo and Koskinas (1925) and as external auditory parakoniocortex (PaAe) by Galaburda and Sanides (1980).

In primates (Fig. 7.13), anatomical and physiological studies defined a **belt area** surrounding the core rostrally, laterally and caudally (Pandya and Sanides 1973; Galaburda

and Pandya 1983; Morel and Kaas 1992; Morel et al. 1993; Hackett et al. 1998a). The area rostral and lateral to the belt is nowadays known as the **parabelt** (Morel et al. 1993; Hackett et al. 1998a). Both belt and parabelt areas differ from the core area in their pattern of thalamic input. The macaque belt area receives projections from only the medial and dorsal divisions of the MGB (Rauschecker et al. 1997), whereas the parabelt area is also innervated by these two divisions of the MGB but, moreover, by the medial division of the pulvinar (Trojanowski and Jacobson 1975; Burton and Jones 1976; Hackett et al. 1998b).

Ablation of the core of macaque auditory cortex eliminates responses to auditory stimuli in the adjacent belt region (Rauschecker et al. 1997), suggesting that input from the medial and dorsal geniculate nuclei is not sufficient to support auditory processing in the absence of direct projections from the ventral geniculate nucleus. Instead, information processing to the secondary auditory cortical areas appears to depend on transcortical projections that pass successively from core to belt to parabelt cortex (Jones and Powell 1970; Seltzer and Pandya 1978; FitzPatrick and Imig 1980; Luethke et al. 1989; Morel and Kaas 1992; Morel et al. 1993; Hackett et al. 1998a). Tardif and Clarke (2001) studied the intrinsic connectivity of human auditory areas with anterograde and retrograde labelling of the carbocyanine dye DiI. With DTI, the tracts connecting the Heschl's gyri via the corpus callosum have been studied (Hofer and Frahm 2006; Westerhausen et al. 2009). These interhemispheric connections are located more rostrally within the posterior callosal third than those connecting the posterior parts of both superior temporal gyri.

The idea of a two-stream, **what/where** organization of sensory cortex originated in the visual system (see Chap. 8). In rhesus monkeys, such a dichotomy has also been demonstrated for the cortical auditory projections (Rauschecker and Tian 2000). The **'where' (dorsal) pathway** is thought to link A1 via the caudomedial belt with the frontal eye field and parietal targets (Romanski et al. 1999; Fig. 7.14) that are implicated in *spatial processing*. The **'what' (ventral) pathway** is thought to represent a *pattern information* stream that originates in the anterior core and belt areas and influences targets within the temporal lobe. A similar **two-stream organization** may exist in the human auditory cortex (Griffiths et al. 2000; Alain et al. 2001; Maeder et al. 2001; Wessinger et al. 2001; Clarke et al. 2002). The right insula is activated by a moving sound image (Griffiths et al. 1994) and, conversely, a patient with a right hemispheric stroke causing atrophy of the right insula was unable to detect sound source movement by either phase or loudness cues (Griffiths et al. 1996). Subjects listening to stimulus movement stimulated by changes in binaural timing show maximal activity in the inferior parietal area, particularly on the right side (Griffiths et al. 1998; Weeks et al. 1999). These findings suggest: (1) that there is a transcortical passage of information from

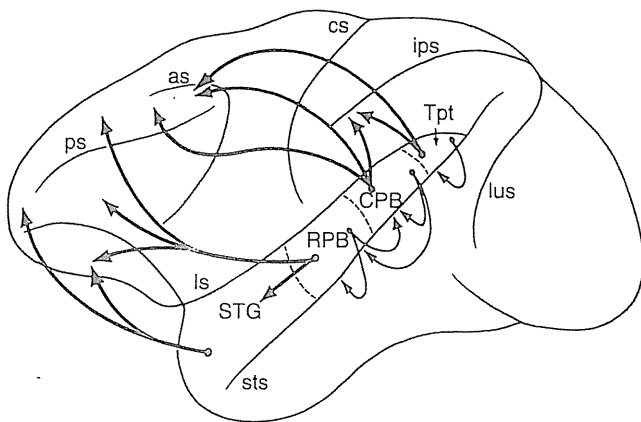


Fig. 7.14 Topography of auditory-related projections. Caudal (CPB) and rostral (RPB) subdivisions of the parabelt and the superior temporal gyrus (STG) project topographically to segregated regions of superior temporal, posterior parietal and prefrontal cortices. *Abbreviations:* as arcuate sulcus; cs central sulcus; ips intraparietal sulcus; ls lateral sulcus; lus lunate sulcus; ps principal sulcus; sts superior temporal sulcus; Tpt temporoparietal area (after. Hackett and Kaas 2004)

auditory koniocortex mediocaudalwards across the insula into the parietal lobe, during processing of information on sound source position and motion (see Hackett and Kaas 2004); and (2) a dominant functional role of the right hemisphere in sound localization.

In **functional imaging studies**, simple auditory tasks such as passive listening to white noise bursts, tones or consonant-vowel speech syllables, activate restricted areas within the lateral fissure on the superior temporal plane (Zatorre et al. 1992, 1994; Binder et al. 1994, 1997, 2000; Zatorre and Binder 2000). The extent of the activation varies from subject to subject and may spread rostralwards and caudalwards on the superior temporal plane. The area of activation is generally within and around the transverse temporal gyrus. With exposure of subjects to more complex stimuli such as passive listening to tone patterns, single words, pseudowords or narrative text, activity is not only present in the cortex of the superior temporal gyrus, but now foci of activation appear on the lateral aspect of the superior temporal gyrus in area 22/TA/PaAc (Binder et al. 1994). The human primary auditory cortex is functionally organized in a **tonotopic manner**. In a combined fMRI and DTI study, Upadhyay et al. (2007) showed that the connectivity pattern in the human primary auditory cortex is similar to that described in tonotopic mapping studies on macaque monkeys (Morel et al. 1993) and cats (Lee et al. 2004; Lee and Winer 2005).

In general, activity is **bilaterally equal**. With complex stimuli, language in particular, the question arises whether there is a right–left asymmetry in the response. Since handedness influences hemispheric lateralization, imaging studies of speech processing are normally restricted to neurologically normal right-handers. In them, there is a tendency for

greater activation of the left hemisphere during tasks that depend on word meaning. Left lateralization of speech characterizes both males and females (Frost et al. 1999). The functional significance of greater left hemispheric activity is implied by imaging studies of stroke patients after infarctions of the left perisylvian area (Weiller et al. 1995; Heiss et al. 1997; Mummery et al. 1999). Subjects who showed good recovery of speech perception had increasing activation of the left temporal cortex surrounding the infarct. Some indications for an **opposite asymmetry** in processing **musical stimuli** come from cases of pathology:

1. A patient with a **right** thalamic tumour experienced *distorted perception of music* but not of voices (Roeser and Daly 1974).
2. Cortical activity has been demonstrated in the right superior temporal lobe during *musical hallucinations* (Kasai et al. 1999).
3. A case of **amusia**, a form of auditory agnosia, was seen after an infarct involving the right insula (Griffiths et al. 1997b).

7.4.4 Auditory Disorders Related to Stroke

Disorders of auditory perception may follow strokes in the territory of the internal carotid arteries or of the vertebrobasilar system (Levine and Häusler 2001; Lechevalier et al. 2007; Kaga 2009), and appear as:

- **Auditory agnosia**, the impossibility of recognizing environmental sounds, words and music, which the patient, however, is said to hear
- **Pure word deafness**, the impossibility to understand spoken language to repeat or to write under dictation in the absence of other signs of aphasia
- **Cortical deafness**, the feeling of being deaf contrasting with the integrity of the tonal audiogram
- **Amusia**, auditory agnosia specific for music

The central disorders of auditory perception may result from lesions of either the right, the left or both cerebral hemispheres, usually involving parietotemporal cortical areas. **Cortical deafness** is characterized by bilateral abolition of the middle and late latencies of auditory potentials, caused by bilateral lesions of the primary auditory cortices. Such patients have the feeling of being deaf to all types of auditory stimuli, but often say they are *not* deaf, rather that they do not understand what is said to them. The term **subcortical deafness** is used to indicate an auditory disorder clinically identical to cortical deafness, but due to lesions in subcortical areas of the brain. It was first described by Le Gros Clark and Russell (1938). The ischaemic lesions involved the two external capsules and extended sufficiently downwards to interrupt the acoustic radiations, while sparing the auditory cortices. Recent cases were reported by Woods (1996), Levine and Häusler (2001) and Kaga et al. (2005; see *Clinical case 7.3*).

Since the pioneering studies of Ferrier (1875) and Henschen (1920), there has been a longstanding debate as to whether bilateral destruction of either the primary auditory cortex or the acoustic radiation results in *auditory agnosia*. In macaque monkeys, bilateral lesions of the primary auditory cortex apparently do not cause permanent deafness (Heffner and Heffner 1990). Less recovery of function in the human brain, compatible with the clinical diagnosis of auditory agnosia, may or may not have been caused by the inclusion of the surrounding auditory association areas (Lechevalier et al. 2007).

Tanaka et al. (1991) differentiated three clinical syndromes of auditory agnosia: (1) *disconnection syndromes*, destroying the acoustic radiation and causing auditory agnosia (*prephonemic deficit*); (2) *cortical lesions* of the left superior temporal lobe may result in pure word deafness (*linguistic deficit*) and (3) unilateral or bilateral *temporoparietal* or *subcortical lesions* have been documented in patients with non-verbal auditory agnosia (*deficit to environmental sounds*). Lesions occurring peripherally to the MGB (*prethalamia*) may cause hearing loss and those bilaterally located centrally to the MGB (*postthalamia*) may result in auditory agnosia. Small lesions of the MGB may be related to auditory hallucinations (Fukutake and Hattori 1998). *Pure word deafness* may be the result of left or bilateral temporal lesions, possibly due to disconnection as suggested by Liepmann and Storch (1902). Recent cases were reported by Kaga et al. (2000; see *Clinical case 7.4*) and Levine and Häusler (2001).

Disorders of music perception following cerebral damage can be divided into two categories (Lechevalier et al. 2007):

1. *Multimode perceptive disorders* affecting more or selectively musical sounds, but with verbal and environmental sound difficulties
2. A *pure amusia*, where only music perception is affected (for *congenital amusia* see Ayotte et al. 2000)

In both monkeys and humans, neurons in **core areas** respond strongly to narrow-band sounds such as tones, whereas neurons in **belt areas** respond better to more complex sounds such as noise (Wessinger et al. 2001; Rauschecker and Tian 2004; Tian and Rauschecker 2004; Bendor and Wang 2006). Within the core areas, two mirror symmetric **tonotopic maps** sharing a low-frequency border have been identified, corresponding to A1 and the rostral field R (Formisano et al. 2003; Bendor and Wang 2006). In monkeys, a third core area (RT) has been found that lies rostral to R (Kaas and Hackett 2000; Hackett and Kaas 2004). Kaas and Hackett postulated that each core area is connected to medial and lateral neighbouring belt areas (see Fig. 7.14), with additional belt areas located on the rostral and caudal ends of the core. Three of these lateral belt areas (caudal-lateral, middle-lateral and antero-lateral) have been mapped

electrophysiologically and possess similar mirror tonotopic maps to those of their adjacent core (Rauschecker and Tian 2004; Tian and Rauschecker 2004). In an fMRI study, Patterson et al. (2002) identified a specific region in the lateral part of Heschl's gyrus that was preferentially activated by temporally regular sounds with a **pitch**. They determined that only lateral Heschl's gyrus, a non-primary auditory region rostralateral to the primary auditory cortex, responded to the temporal regularity of pitch of the acoustic stimuli. Other imaging studies (Penagos et al. 2004; Schneider et al. 2005) have confirmed these findings.

Musical perception is not a uniform competence in the general population. Some patients will have had musical training, others not. Peretz (2001) estimated that 5–10% of individuals are completely unable to distinguish the pitches of two notes of music or to memorize the smallest musical tone. Geschwind and Galaburda (1985) suggested that rightward deviation from the usual pattern of cerebral asymmetry may be associated with increased giftedness for talents for which the right hemisphere is assumed to be important. With MR morphometry, Schlaug et al. (1995) presented evidence for structural brain asymmetry in musicians. Musicians with **perfect pitch** revealed stronger leftward asymmetry of the planum temporale than non-musicians or musicians without perfect pitch. This suggests that outstanding musical ability is associated with increased leftward asymmetry of the cortex subserving music-related functions.

Neuropsychological studies in epileptic patients who underwent a unilateral temporal cortectomy have contributed to our knowledge of the localization of musical functions (Liégeois-Chauvel et al. 1998). A right temporal cortectomy was found to disturb melodic perception as well as the perception of pitch intervals, whereas a left-sided lobectomy did not disturb perception of the intervals. These data underline the key role of the superior temporal gyrus in discrimination of melodies. Cortectomy of the posterior part of T1, including the planum temporale, the lateral part of Heschl's gyrus and Brodmann area 22, is more striking for the processing of pitch and variations of rhythm than cortectomy of the rostral part of T1. Disorders of the perception of rhythm and metre (recognition of a cadence of march or waltz) can be dissociated. The right and left rostral parts of T1 would be implicated in the processing of metre. Griffiths et al. (1997b) reported a patient with lesions of the middle and posterior temporal areas and the insula of the right hemisphere. The patient complained of not being able to appreciate music. Neuropsychological testing showed a deficit of musical perception without disturbance of the perception of noises, environmental sound and speech sounds. His ability to detect continuous changes of sound frequency was preserved. However, a disturbance in the analysis of rapid sequences of notes seemed to be the basis of his musical perception deficit. Neuroimaging studies have revealed that rhythm perception

activates area 44 and that detection of pitch changes relies on the left cuneus and precuneus (Platel et al. 1997, 2003).

Auditory hallucinations are observed in brain stem (Ross et al. 1975; Cambier et al. 1987; Fisher and Tapia 1987; Griffiths 2000) and temporal lobe (Lechevalier et al. 1985) strokes. Cambier et al. (1987) reported five purely auditory observations of *hallucinosis* (hallucinations, regarded by the

patient as abnormal), four of which were attributed to paramedian strokes of the pons and one to an infarct of the dorsolateral mesencephalon. Auditory hallucinations following temporal lobe lesions are unusual and have specific characteristics (Liepmann and Storch 1902; Lechevalier et al. 1985; Augustin et al. 2001; Evers and Ellger 2004; Sacks 2007; see *Clinical case 7.5*).

Clinical Case 7.3 Auditory Agnosia Caused by Bilateral Lesions Restricted to the Auditory Radiations

Bilateral lesions of the auditory radiations are rare (Tanaka et al. 1991; Woods 1996; Kaga et al. 2005; see **Case report**).

Case report: Kaga et al. (2005) reported a patient with auditory agnosia due to bilateral lesions of the auditory radiations. A 43-year-old male patient experienced mild left temporal hemiplegia due to a right putaminal haemorrhage. He recovered completely but hypertension persisted. When he was 53 years old, he had a left putaminal haemorrhage and

went into a coma. After recovering from the coma and the right hemiplegia, he could hear but could not discriminate speech sounds. Brain CT and MRI demonstrated small bilateral lesions restricted to the auditory radiations (Fig. 7.15a, b). Pure-tone audiograms recorded 1 and 4 years after the second haemorrhage are shown in Fig. 7.15c, d. MEG demonstrated the disappearance of middle latency responses and AEP studies showed a very small Pa peak. In contrast, a positron emission tomographic study showed a marked bilateral increase in blood flow in the auditory cortex in response to both click and monosyllable stimuli. This may be due to activation of the auditory cortex via non-specific pathways.

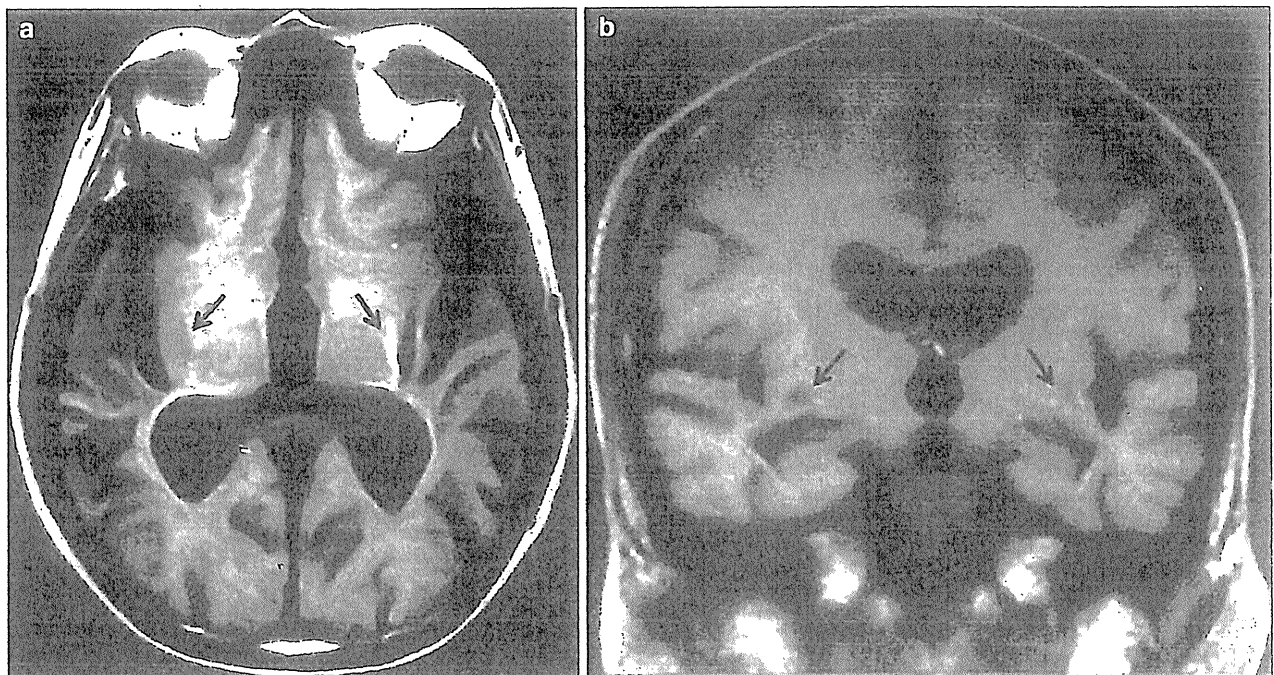


Fig. 7.15 Auditory agnosia caused by bilateral lesions restricted to the auditory radiations. In the axial (a) and coronal (b) MRIs, the auditory radiations are bilaterally damaged (arrows) by small brain

infarcts. Pure-tone audiograms recorded one (c) and four (d) years after the second haemorrhage (from Kaga et al. 2005)

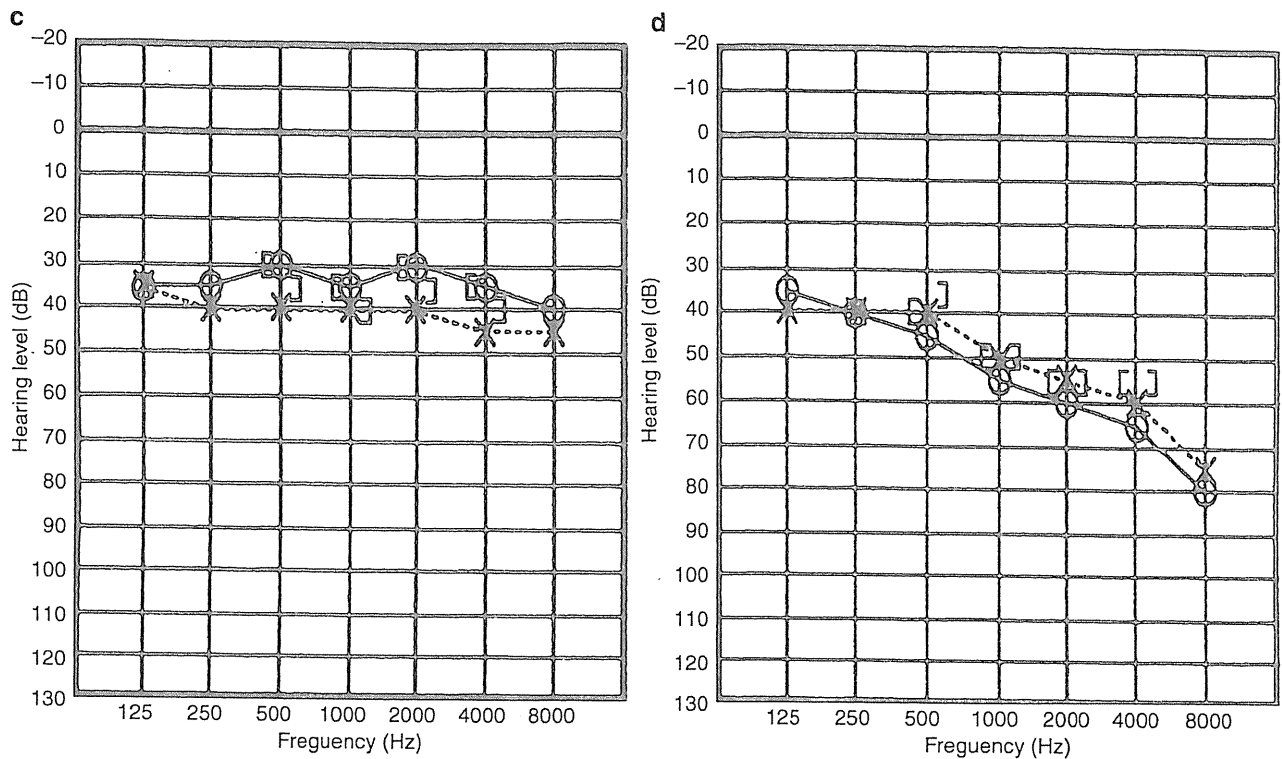


Fig. 7.15 (continued)

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Clinical Case 7.4 Neuropathology of Auditory Agnosia Following Bilateral Temporal Lobe Infarction

Severe auditory deficits due to bilateral lesions of the primary auditory cortex or the auditory radiations is very rare. The resulting hearing problem is referred to as *auditory agnosia* or *cortical deafness*. Kaga et al. (2000) reported a patient who came to autopsy (see **Case report**).

Case report: Kaga's case of auditory agnosia due to bilateral lesions of the auditory cortex was first diagnosed in 1975 when the patient was 37 years old. He was admitted to hospital for examination following his second cerebrovascular accident. MRI of the lesions on admission is shown in Fig. 7.16a, b. A comprehensive follow-up examination of auditory function was periodically conducted until his sudden death 15 years later. His brain was studied neuropathologically. Initial pure-tone audiometry revealed moderate

sensorineural hearing loss in the right ear and mild sensorineural hearing loss in the left ear. Repeated pure-tone audiometry revealed that bilaterally thresholds became progressively poorer over time. Speech audiometry of both ears consistently revealed that the patient was unable to discriminate any monosyllabic words. In general, speech and hearing tests demonstrated that he could not comprehend spoken words but could comprehend written commands and gestures. Neuropathological examination of the brain revealed a total defect and neuronal loss of the superior temporal gyrus, including Heschl's gyrus, and total gliosis of the MGB (MGB; Fig. 7.16c, d). In the right hemisphere, subcortical necrosis, gliosis in the centre of the superior temporal gyrus and partial gliosis of the MGB were found (Fig. 7.16c, e). These data support the clinical observations of imperception of speech sounds, music and environmental sounds, which may be due to progressive degeneration of both MGBs.

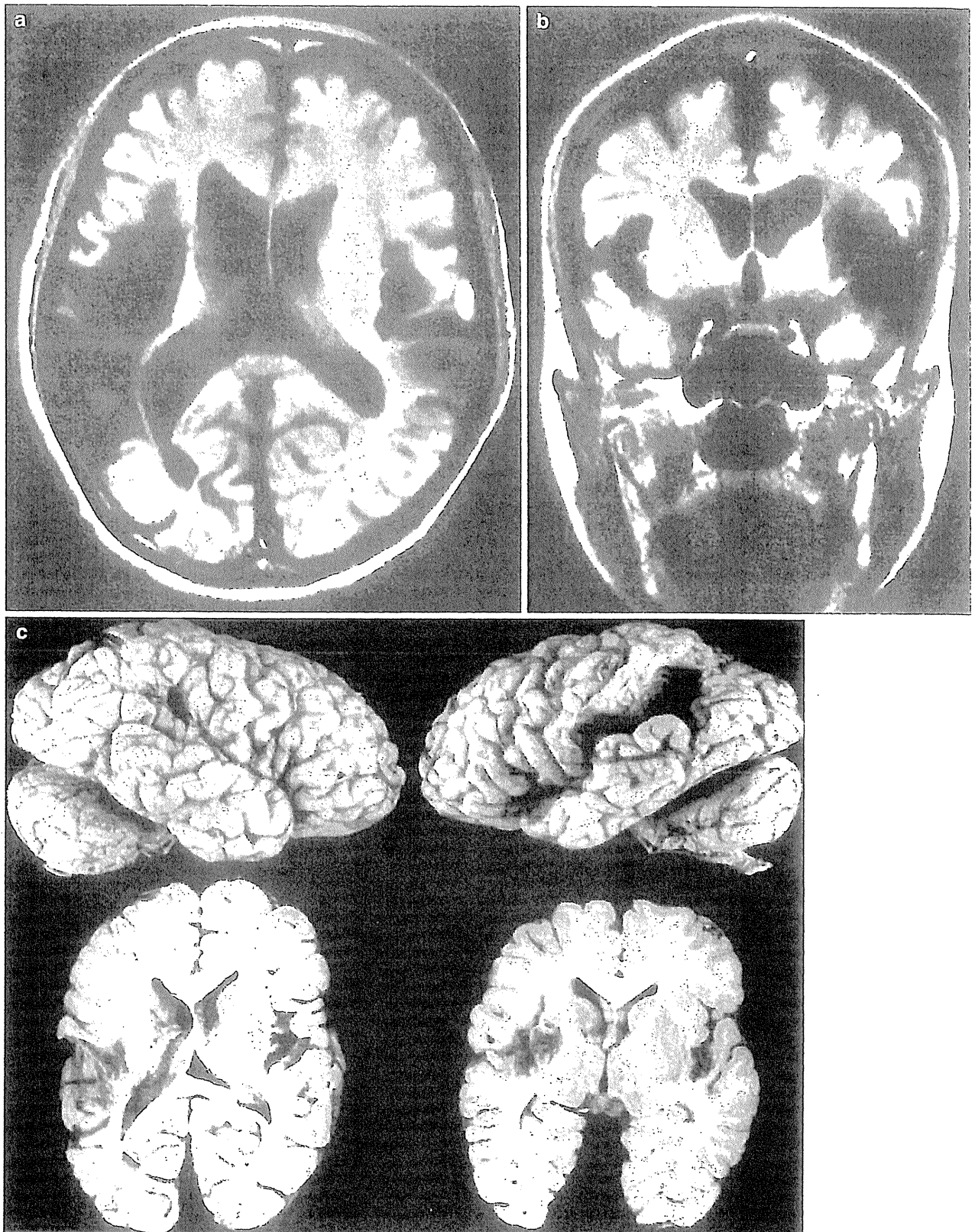


Fig. 7.16 Auditory agnosia following bilateral temporal lobe infarction. (a, b) Axial (here the left side is on the left) and coronal (here the left side is on the right) MRIs showing a large infarct in the left hemisphere and a small infarct in the right hemisphere including the auditory cortex. (c) Lateral views of the brain and two horizontal sections in which the auditory cortex is present. In the right hemisphere, a small

infarct is present in the upper part of the lateral sulcus, whereas in the left hemisphere extensive infarction can be seen in Broca's area, the superior temporal gyrus and the supramarginal gyrus. (d, e) HE-stained sections of the medial geniculate body (MGB). In the left MGB, neurons have been completely replaced by glial cells (d), whereas in the right MGB (e) there is partial neuronal preservation (from Kaga et al. 2000)

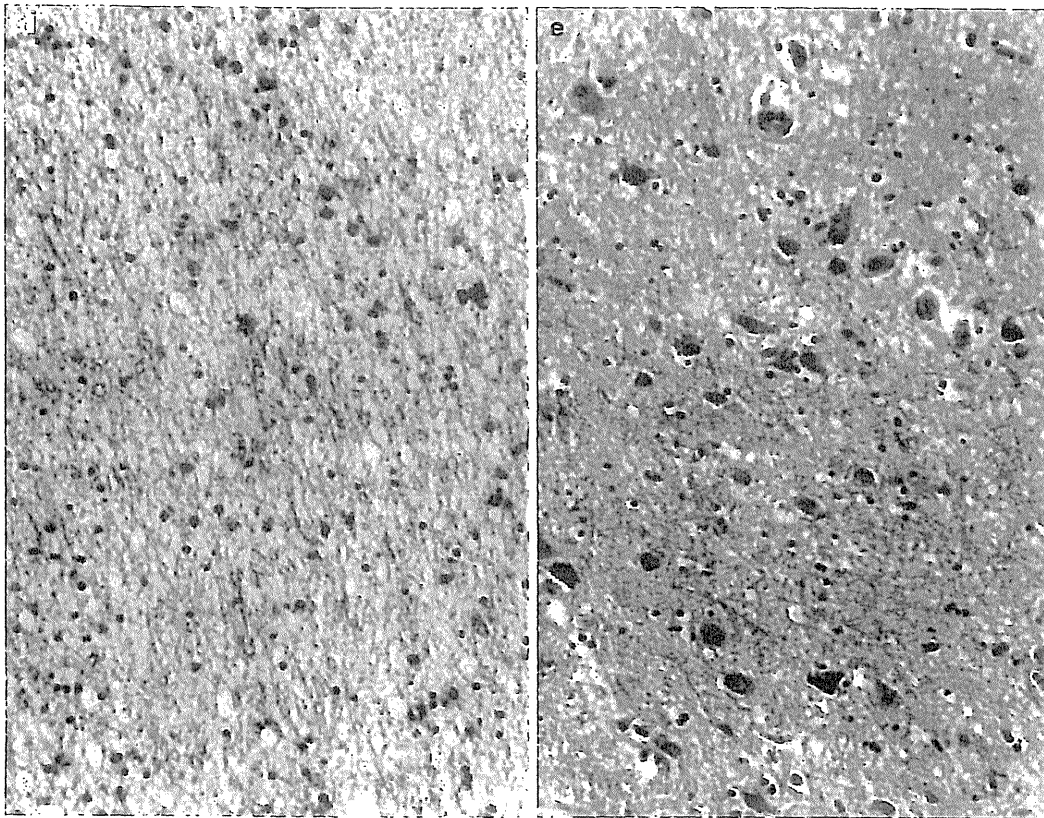


Fig. 7.16 (continued)

Selected Reference

Kaga K, Shindo M, Tanaka Y, Haebara H (2000) Neuropathology of auditory agnosia following bilateral temporal lobe lesions: a case study. *Acta Otolaryngol* 120:259–262

Clinical Case 7.5 Auditory Hallucinations Following a Metastasis in Heschl's Gyrus

Case report: A 64-year-old patient presented with word-finding difficulties. He suffered from coronary sclerosis with exercise-induced angina pectoris but he had no previous neurological complaints. On neurological examination, there were no focal signs but his speech was non-fluent with word-finding difficulties and suboptimal comprehension. On hospital admission, he repeatedly complained of *auditory hallucinations*, consisting of incomprehensible

words and sounds. On MRI, a contrast-enhancing lesion was found in the left gyrus of Heschl (Fig. 7.17) that appeared to be part of a more lobular contrast-enhancing in the left parietotemporal region with surrounding oedema. The auditory hallucinations disappeared on treatment with dexamethasone. A biopsy showed that the tumour was a gemistocytary astrocytoma for which he was treated with radiotherapy and temozolamide.

This case was kindly provided by Peter van Domburg (Department of Neurology, Orbis Medical Centre, Sittard, The Netherlands).

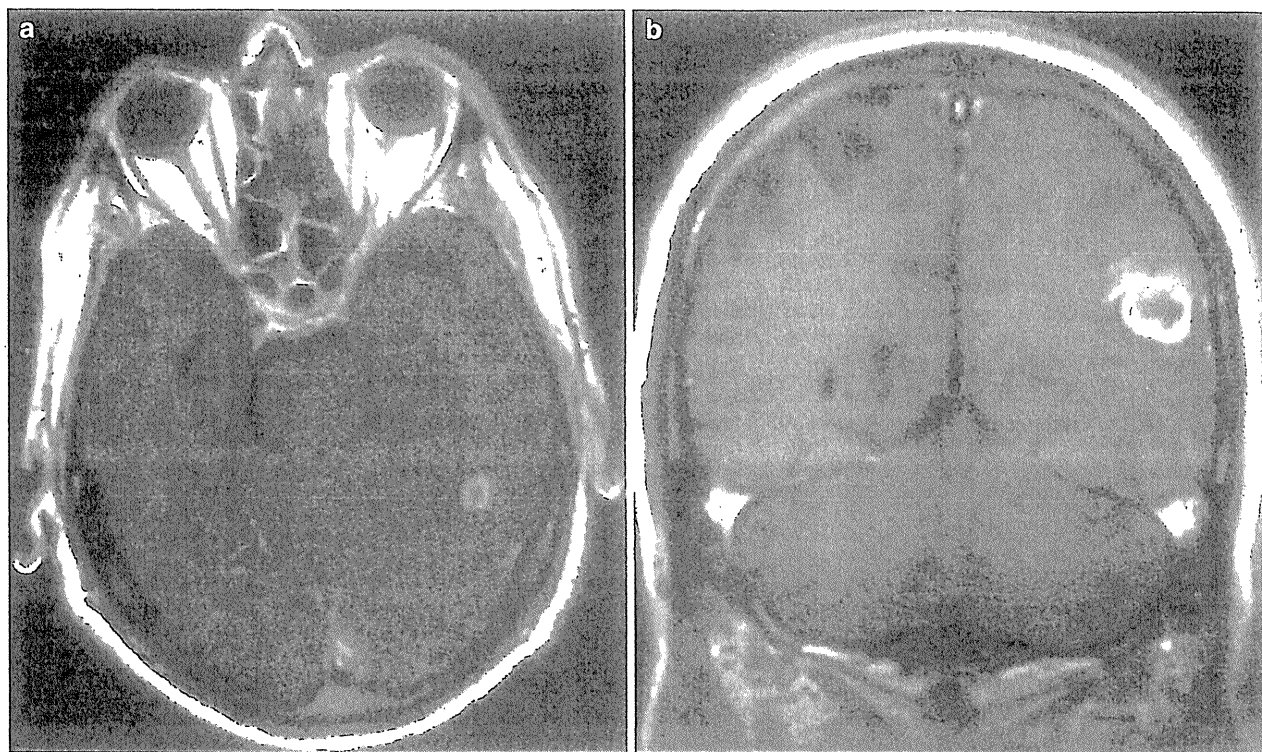
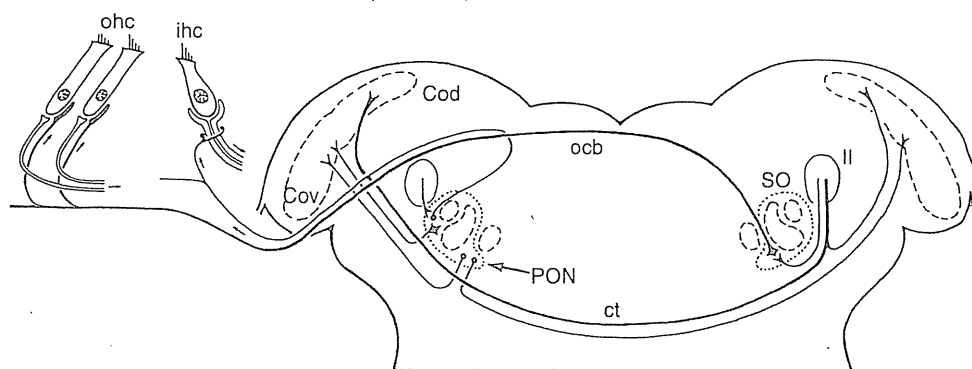


Fig. 7.17 T1-contrast MRIs of a metastasis in the left gyrus of Heschl that caused auditory hallucinations (courtesy Peter van Domburg, Sittard)

Fig. 7.18 Efferent control of the cochlea. *Abbreviations:* *Cod*, *Cov* dorsal and ventral cochlear nuclei; *ct* corpus trapezoidum; *ihc* inner hair cells; *ll* lateral lemniscus; *ocb* olivocochlear bundle; *ohc* outer hair cells; *PON* periolivary nuclei; *SO* superior olivary complex (after Nieuwenhuys 1984)



7.5 The Descending Auditory System

Parallel with the pathways from the organ of Corti to the auditory cortex, there is an uninterrupted chain of neurons conducting impulses in the opposite, descending direction. The final link in this **descending auditory system** is formed by the **olivocochlear bundle** of Rasmussen, which originates in the **peri-olivary nuclei** around the superior olivary

nucleus (Fig. 7.18). Most of the fibres of the olivocerebellar bundle decussate in the tegmentum. They enter the vestibular nerve and join the cochlear nerve via the vestibulocochlear anastomosis (Schuknecht 1993) to terminate in the inner and outer hair cells of the organ of Corti. The human olivocochlear system has been identified with acetylcholinesterase histochemistry (Schuknecht et al. 1959) and choline acetyltransferase immunohistochemistry (Moore et al. 1999; Moore and Linthicum 2004).

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二つの耳の不思議



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私のテーマは、「二つの耳の不思議」です。

まず、耳を考えるには、「地球は水と空気の惑星である」ということを考えることから始めます。太陽と水があつて生命が生まれて植物の光合成により酸素が生じ、いろいろな動物が発生し進化してきました。空気の中でコミュニケーションをするには、空気を振動させる声とそれを聞く耳が必要で、空気は、音速が秒速340メートルですが、水はその5倍、骨の中はその10倍、鉄はその15倍も速く伝わります。空気の中の音の速度は大変遅いのです。「音は振動である」と言い出したのは、今から2500年前、ギリシャのピタゴラスです。ピタゴラスというと、学校で「ピタゴラスの定理」を習ったと思いますが、今考えても、こういう定理をよく当時発見したものであると感心します。ピタゴラ

スは、音は空気を震わすものであることを見抜きました。

ここで、動物の二つの耳と進化や方向感、カクテルパーティ効果やステレオ、最近の耳の病気とその治療、最後にヘレン・ケラーの言葉などを紹介します。

動物の進化は、水があり太陽によって生命活動が生まれて始まりました。最初は魚類で水の中にかいませんでした。進化の順序を辿ると、次は、カエルなどの両生類ですが、水と空気の中の両方を行ったり来たりしています。次は、蛇などの爬虫類です。爬虫類の中には恐竜もいます。その次に、空を飛ぶ鳥が現れます。最後は哺乳類で私たち人類も含まれ、空気を吸いコミュニケーションをして生きています。

耳介は頭の左右にあります。パラボラアンテナのように音をキャッチして、外耳道を通り鼓膜を振動させ、「蝸牛」という渦を巻いたところにある感覚細胞で音を分析してその電気信号を脳に伝えます(図1)。

図1 両耳のしくみ

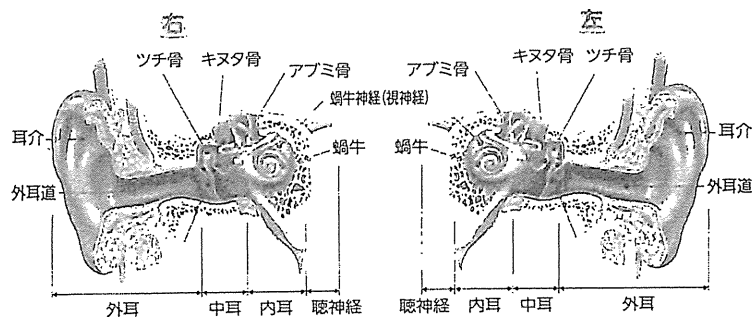
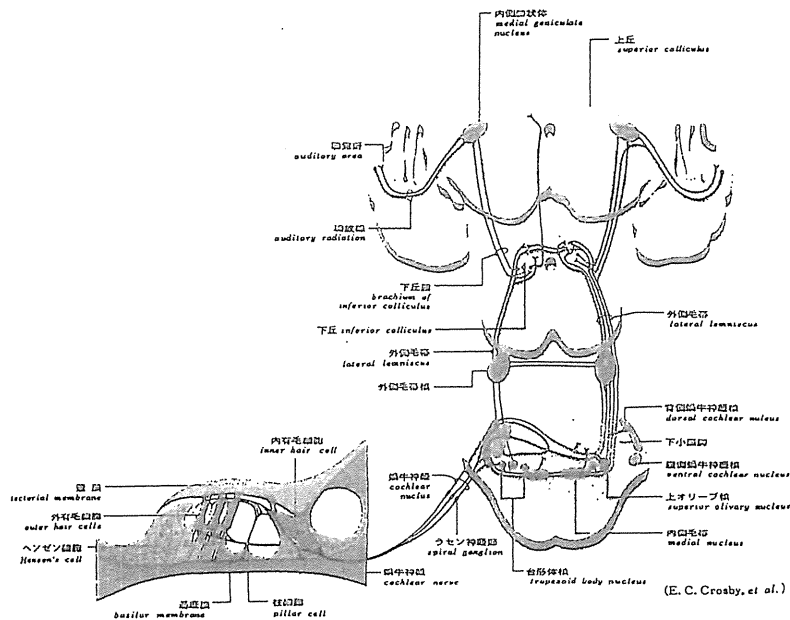


図2 脳の中で2つの耳に届いた音を分析してわかるしくみ



この渦巻きの中には、パイプオルガンのような毛のある感覚細胞が並んでいて、音が来るとパイプオルガンのパイプのような形をした毛が動き、両耳から脳に入っていきます。そして、脳幹という場所で初めて二つの耳の信号は一緒になり、大脳皮質まで神経を5回も替えてやっとたどり着きます。その間、「今来た音はどっちから来たか」、「人の声は何を言っているか」ということを、何度も分析をしてわかっていくしくみになっています(図2)。

動物の目と耳の位置は、それぞれ随分違います。形やサイズも違います。私は学生に、「なぜ人間の耳はどのような音でも聞く必要があるのだろうか」、「象みたいに耳はなぜ大

きくならなかったのだろうか」とよく尋ねますが、同じ哺乳類でも随分違います。動物の特徴は、耳を動かすことができます。相手の動物や木の音がどこから聞こえるかを、耳を動かして聞くことができます。基本的に人はできませんが、まれにできる人おりますが役には立てておりません。

聴覚と視覚を比較すると、役割が随分違います。聴覚は、360度どこから音が聞こえても大雑把にわかります。例えばここに敵がいて、動く音や鳴き声が聞こえると、「この方向らしい」と気付き、「本当にそうか」と目で見て、「ここにいる」と確認します。「どのぐらい離れているか」、「逃げるか襲うか」、そのように判断するために両方の感覚は非常に違う特徴を持ちながら共同作業をして、私たちの行動を助けています。

フクロウには耳に見えるようなものがありますが、これは耳ではなくて単なる飾りのようなものです。その横を探してみると小さな穴があつて、それが短い外耳道と言えます。私たちの耳は左右の耳が同じ高さにあります。フクロウは少し上下に差があり、音に対しての精度が大変強く、上下左右の音の方向がわかります。これは、フクロウだけにある性能です。では、人も手術でそのようにずらせたら便利だと思ふ人がいるかもしれませんが、そのようなことを希望する人はいません。

空を飛ぶユニークな動物はコウモリですが、これは鳥ではなく哺乳類です。特徴的な哺乳類で、のどを震わせると私たちに聞こえない超音波が生み出され、この音が相手にぶつかって反射波が生じま

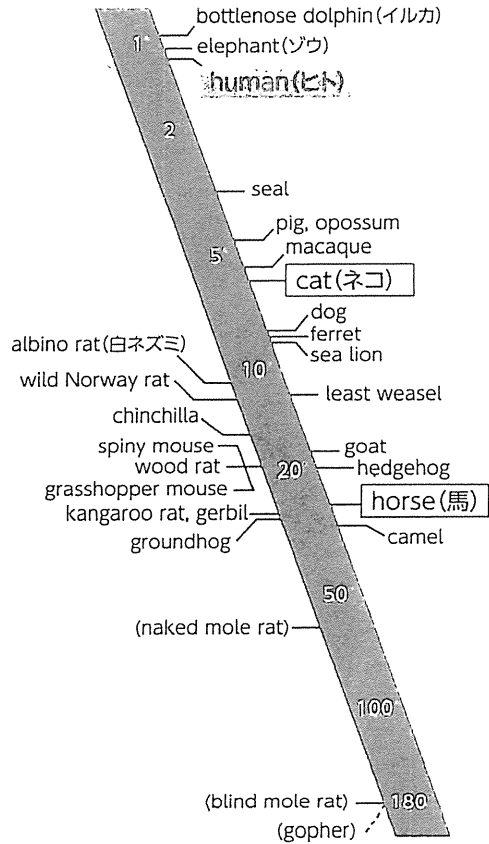
す。それを耳で聞いて分析して「ここにいる」ということがわかるので、夜飛んでもネズミや物体を同定ができるわけです。これは、レーダーや水中ソナーなどと同じです。

次に、「方向感」について二つの耳の役割を説明します。二つの耳を使って敵の位置を音で知る、逃げる、襲う、それから鳴き声でコミュニケーションをします。人の場合は、言語を身につけて言葉で会話をするようになります。私たちはどのような音の方向がわかるのでしょうか。音には高い音と低い音があります。図3に示すように、左耳にたどり着いた音は、右耳よりも早く、かつ強く聞こえます。

これは、神経細胞一個の反応時間よりもっと短い反応ですから、神経がシステムになって初めて分析できる極めて高度な感覚で、このようなわずかな差は両耳の時間

差、音圧差などでわかります(図3)。ですから、正中に音源があると差がないので真ん中だとわかり、横に音源があると差が生じるので、目をつぶっていても音がこちらにあるということがわかります。では、哺乳類はみんな音に敏感かというと、実はそうではありません。図4は、アメリカのヘフナー先生の

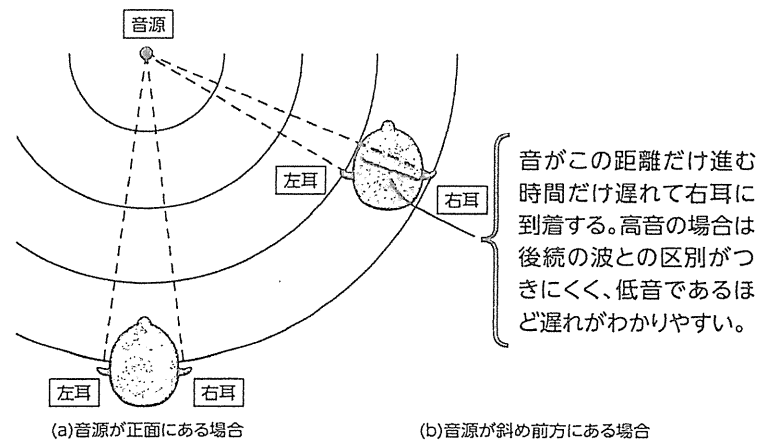
図4 哺乳類の音源定位の閾値



100msecあるいは400msecのノイズバーストによる反応

(Heffner RS, et al:1994より)

図3 音源の方向を知る両耳の効果



(a)音源が正面にある場合

(b)音源が斜め前方にある場合

研究で非常に有名なものですが、「ピー」という音を使っているいろいろな動物に聞かせました。その結果を、それぞれの動物が音の方向を何度ずらすとわかるかを角度で示しました。人は、象やイルカと同じように1度程度の差でわかりますが、猫は人よりも少し鈍く6度ぐらいです。さらに馬は20度です。競馬でも両方の目を横にそれないようにやっていますが、音に関しては鈍感なので、恐らく、馬は目を生かして行動していると思われれます。

次に、音の方向について話します。花火がドンと遠くで鳴ると、どこで鳴っているか近くにいるとわかりますが、遠くにいるとなかなかわかりません。花火は低音なので両耳に届く時間の差でわかりますが、距離も重要であるということです。風鈴は音が高いので、両耳の音圧差でわかります。家中でも近くにあると聞いて方向がわかりますが、少し離れるとどこからかわかりません。電子音も同じで、どこで鳴っているかわからないことがあります。それは、距離が離れていて音が小さいからです。電子音は、音圧差でわかります。

さて、小さな音は非常に弱くても両耳では聞こえますが、片耳では少し強くないと聞こえません。電子音がどこで鳴っているかわからないとき、その音は10ないし20デシベルという小さな音と思われれます。

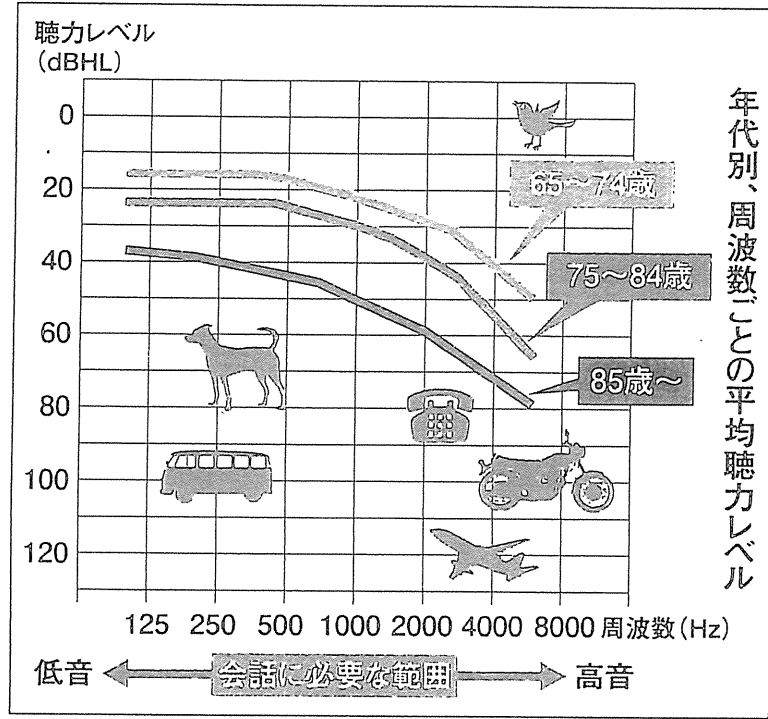
私がマイクに話しかける声は、50から60デシベルと大きい音です。また、ジェット機や新幹線、ロックコンサートなど、うるさい音があります。新幹線は、今、時速270キロで走っていますが、音速に近いためすごい騒音が生じます。どんなに速くても440キロが限界だそうです。日本の技術では現在よりもっと速く走らせることができます。しかし、騒音を伴うために周辺の住民から反対運動が起きるといふことで、今ぐらいになっています。周囲に何も無い大平原を走るのであれば、440キロでも可能でしょう。

最近、話題になっているものに、プリウスというトヨタ(自動車)のハイブリッド車があります。これは、「音が小さくて近づいて来たことがわからないので、非常に危険だ」と言われています。この前、私も実際に運転してみました。低速では電気自動車なので、電機のモーターは本来音が小さいのです。しかし、少しスピードを速くするとエンジンに変わりますから、普通の自動車と同じぐらいのさくなってきました。モーターのときだけ確かに音が低いので、音が静かになれば、周りの人は車が来たことがわからなくて危ないということになります。

次に、目に障害がある人たちはほかの感覚が鋭いかについて、「盲目の演奏家と聴覚」というテーマで述べます。

第13回ヴァン・クライバーン国際ピアノコンクールで辻井伸行というピアニストが優勝したニュースは、多くの皆さんが知っていると思います。日本にはほかに、バイオリニストの川島成道、和波た

図6 老化と聴力



成長とともに鋭く、老化とともに鈍感になる

音、高音はバイオリンの高い音だと思ってください。この図の見方は、「失われたものがゼロ」ということは「正常」ということで、「20」失われた、「40」失われた、「60」失われた、「80」失われた」ということになります。

真中の線は後期高齢者のグループ（75〜84歳）ですが、耳の正常な成人よりもひどく悪いことがわかります。ただ、85歳以上になると、60代の人と同じ人もいれば、もっと悪い人もいて、この範囲が大変広いのです。いずれにしろ、音の方向を感じる力が弱くなるの

かよし、昔は琴でも有名な宮城道雄がいました。彼らは、本当に私たちよりも聴覚が鋭いのかという謎がありました。検査をしてみると実際に鋭いことがわかりました。

図5は私どもの研究ですが、時間差を見るテストで、14歳から15歳の子どもたちを調べました。正常な子どもたちは、左右に一定の振幅差がつきます。しかし、目の見えない子どもたちはこの振幅が非常に小さくて、それをグラフで表すと、音の方向の時間差に対して1.5倍鋭いことがわかります。音圧差についてはそれほど変わりませんが、実は、時間差というものは時間分解能という聴覚の本質と関係があり、その本質的な能力に対して大変なことがわかってきます。

音の方向がわかるということは、生活上は大変重要ですが、子どもは成長とともに10歳ぐらいで大変方向感が鋭くなり、60歳代になると、だれでも加齢変化のため少しずつ悪くなります。次に聴力についてです。図6の横軸は音の周波数で、低音は太鼓のような

図5

