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Review

Lateralization of auditory-cortex functions

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Abstract

In the present review, we summarize the most recent findings and current views about the structural and functional basis of human brain lateralization in the auditory modality. Main emphasis is given to hemodynamic and electromagnetic data of healthy adult participants with regard to music- vs. speech-sound encoding. Moreover, a selective set of behavioral dichotic-listening (DL) results and clinical findings (e.g., schizophrenia, dyslexia) are included. It is shown that human brain has a strong predisposition to process speech sounds in the left and music sounds in the right auditory cortex in the temporal lobe. Up to great extent, an auditory area located at the posterior end of the temporal lobe (called planum temporale [PT]) underlies this functional asymmetry. However, the predisposition is not bound to informational sound content but to rapid temporal information more common in speech than in music sounds. Finally, we obtain evidence for the vulnerability of the functional specialization of sound processing. These altered forms of lateralization may be caused by top-down and bottom-up effects inter- and intraindividually In other words, relatively small changes in acoustic sound features or in their familiarity may modify the degree in which the left vs. right auditory areas contribute to sound encoding.

Keywords: Hemispheric asymmetry; Brain lateralization; Auditory processing; Speech; Music; Planum temporale; Dichotic listening

Contents

1. Introduction

The cortical areas devoted to auditory processing in humans are located in the left and right temporal lobes in the middle and superior temporal gyri, and the associative areas expanding to the posterior sites of the temporal lobes. Since the original ideas and findings of Fechner [25] and Wernicke [118] in the late 19th century, the complementary roles of the left and right temporal lobes in auditory processing have traditionally been investigated by neuropsychological tests in brain-lesioned patients. More recently, also functional and structural brain imaging methods have been applied (see below). The majority of these studies have

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confirmed the predominant role of the left hemisphere in speech processing and, to a lesser extent, the predominant role of the right hemisphere in music processing. In the following, anatomical and functional evidence regarding the existence and degree of hemispheric asymmetry in auditory processing will be reviewed and discussed.

2. Anatomical constraints

A key problem in the literature on brain laterality has been the lack of correspondence between structural and functional measures of asymmetry. For instance, there are no anatomical areas in the visual cortex showing a right–left asymmetry, which could match functional asymmetry findings in vision (cf. Ref. [46]). Similarly, the functional difference between the left and right hands in most individuals has no structural correspondence in either the central or peripheral nervous systems, or in the appearance of the limbs.

The only accepted example of correspondence between structural and functional asymmetry in the brain is link between auditory processing, notably speech perception, and the larger left-hemisphere planum temporale (PT) area in the upper posterior temporal lobe (Fig. 1). More accurately, the PT is located in the superior temporal gyrus, between the Heschl's sulcus anteriorly and the end of the Sylvian fissure posteriorly (cf. Ref. [103]). It is an auditory association area involved in the processing of verbal and non-verbal stimuli (for a thorough and critical review, see Ref. [56]). In a recent review [113], it is proposed that this area ''is the epicentre of a mosaic of left-hemisphere language regions''. The structural asymmetry of the PT was first observed at autopsy [89,115] and later verified [29,32]. Pfeifer [89] also observed that there often were two Heschl's gyri on the right side but only one on the left side, an observation also later verified by the more modern MR technique (e.g., Ref. [70]).

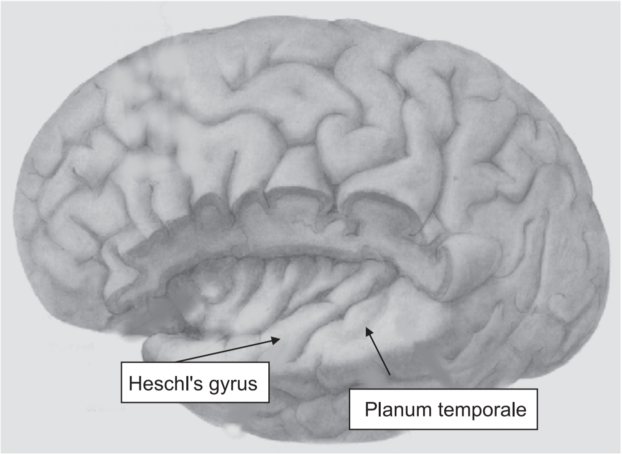


Fig. 1. The anatomical localization of the planum temporale in the upper posterior part of the temporal lobe, with the Heschl's gyrus outlines as the transverse gyrus just in front of the planum temporale. Adapted from Ref. [40].

Recently, the asymmetry of the PT has been extensively studied by using voxel-based morphometry (VBM) techniques. These techniques are based on segmentation of grey and white matter tissue from MRI, the segmentation revealing differences in grey matter concentration, or volume, for instance between groups of subjects [6]. Good et al. [34] found that the PT area was larger in the left hemisphere compared to the homologous right area in a large study based on 465 brains. The effect was particularly evident in males. This is supported in numerous other studies, which have used other morphometry techniques (e.g., Refs. [21,38,57,104]; see also Refs. [8,99] for reviews).

The PT with a left-larger-than-right asymmetry is also found in great apes [30,43,67]. This may provide evidence for a relation between the development of the PT and the ability to develop a sound-based language. That the great apes did not develop language may not have been because they lack the necessary neurocognitive foundations, but rather because they did not evolve the necessary supporting anatomy related to the vocal chords and the vocal trajectories. The findings that the great apes show a leftward asymmetry of the PT region similar to humans and the conclusion drawn from these studies with regard to language development was critically reviewed by Marshall [74] who commented on the findings by Gannon et al. [30]. According to him, in 17 out of 18 (94%) chimpanzees studied, the left PT was larger than the right. Since the findings by Geschwind and Levitsky [32] indicated that only 66% of the human brains that the examined showed a leftward PT asymmetry, we would be left with the conclusion that the species that did *not* develop language have a greater PT asymmetry than the species that did.

However, some concern should be kept in mind with regard to these structural data. First of all, the methods used in quantifying the PT area differ in their accuracy even between hemispheres, for instance, in taking account the folds and curvatures [55,99,119]. Second, the definitions of the areas included in the PT differ between investigations, partly caused by normal interindividual variability [70]. Consequently, depending on the particular study, PT asymmetry has been found in 64–82% of the brains (see meta-analysis by Shapleske et al. [99]). Perhaps, a more fundamental problem in the evidence based on anatomical constraints of the PT is that the posterior rami of the Sylvian fissure (which defines the posterior border of the PT) is often absent in the left hemisphere [92]. As pointed out by Jäncke and Steinmetz [56], the cytoarchitecture of the perisylvian region is complex and its intersubject variation has not been intensively studied in humans. One problem is how to define the exact borders of auditory association cortices in this region of the brain (e.g., Ref. [14]). Another problem is interindividual variation in frequency and location of the sulcal boundaries of Heschl's gyrus, which marks the anterior border of PT [70].

3. Brain functional evidence for hemispheric asymmetry

The earliest evidence for lateralized auditory functions by utilizing modern brain-imaging techniques was obtained by Mazziotta et al. [76]. During PET scanning, they presented their subjects with monaural and binaural verbal (detective story) material and non-verbal (single musical sounds, sound pairs and chord pairs) stimulation. While verbal stimulation activated more wide-spread areas in the left than in the right hemisphere, the opposite was true with non-verbal stimulation. In addition, the pattern of activity observed during tone-pair stimulation reflected the subjects' listening strategy: The subjects who reported to have listened to the sounds analytically or by using visual imagery showed stronger activation in the left hemisphere. In contrast, in the subjects who listened to the sounds without any specific strategies, stronger activation was observed in the right hemisphere. It should be noted, though, that due to small group sizes ($N=2-8$) and the use of between-subjects design, solid conclusions could not be drawn on the basis of the above-reviewed data alone.

More recently, the complementary roles of the left vs. right hemispheres in processing speech vs. music sounds, originally suggested by Ref. [76], have received further support. Using a within-subject design with verbal and music stimuli, Zatorre et al. [122] showed that the pattern of brain activation can also vary as a function of the task given to the subjects while keeping the stimulation constant. An instruction to "categorize the phoneme" led to more pronounced activity in the left hemisphere, whereas an instruction to "discriminate between the pitch contents" led to more pronounced right-hemispheric activity. However, the right-hemispheric activation was located in the frontal lobe, suggesting the importance of working-memory systems in the task specific to the music dimension rather than functional specialization of the right auditory areas for music sound processing.

Moreover, it has been shown that, under an instruction to detect a target word, dichotic presentation of contiguous sentences activated left-hemispheric areas were different from those activated during binaural presentation of the same material [37]. These areas, observed in fMRI recordings, were larger in the left than in the right temporal lobe and, additionally, located in the secondary auditory areas and in the PT. This difference between activated brain areas during dichotic versus binaural stimulus presentations can be explained by the task difficulty: during dichotic stimulation, the subjects receive two competitive, different messages via the left and right ear whereas during binaural stimulation, both ears are presented with the same message (see Section 4). In other words, dichotic stimulus presentations which forces a listener to on-line attend to two parallel messages (a common real-life situation) with different spatial sources but with possibly the same semantic content activates brain areas not seen in less demanding conditions.

Celsis et al. [17] did not engage their subjects in any behavioral task during fMRI recordings but rather instructed them to listen to binaurally presented stimuli with their eyes closed. The subjects were presented with three types of stimuli in different sequences: pure sinusoidal tones (frequent 500 Hz) intermixed with (1) rare 700 Hz sinusoidal or (2) rare 500 Hz square wave sounds, or (3) the syllable /ta/ intermixed with the syllable /da/. All sounds were 80 ms in duration, separated by 80 ms silence. The stimulation was presented in a block design, one block consisting either of four identical stimuli or of three identical and one different (rare) stimulus. When blocks with standards and deviants were contrasted with blocks with standards only, it was found that the frequency changes activated left posterior STG and the syllable changes activated the left inferior supramarginal gyrus (BA40).

The surprising left-dominant pattern of activity evoked by pitch changes by Celsis et al. [17], traditionally considered as the faculty of the right hemisphere, might be explained by the rapid stimulation rate. The PT may be more tuned to the analysis of the acoustic content innate for speech information, such as fast changes in sound frequency or amplitude information. In several studies, the PT has been found to be equally activated by speech and non-speech sounds [9,11,24,124]. Symmetry of activation in the STG area is typically observed in these studies, asymmetry being observed only in more anterior and ventral areas, including the superior temporal sulcus (STS) area [10–12,24]. Binder et al. [11] have suggested that this may indicate that the 'classic' PT is likely to be involved in early auditory processing, while later language-related processing occurs in an extended, possibly, multimodal, area that also involves the STS and MTG.

Data by Hugdahl et al. [51] support these findings. Fig. 2 shows 15-O PET data obtained while subjects listened to consonant–vowel (CV) vs. musical instrument stimuli. The subject had to press a button whenever a predetermined target stimulus was detected among other stimuli of the same category. Three different CV syllables and music instruments sounds were presented in each block. Both stimulus types were contrasted against a baseline condition with simple tones that varied in pitch ("high", "medium", "low"). During the baseline condition, the subjects pressed the response button whenever a tone appeared, thus there was no discrimination requirement.

Note that, although Fig. 2 shows that the CV syllables activated areas ventral and anterior to the STG/PT, these activations were mainly bilateral. A left-sided asymmetry occurred first at +6 mm above the AC-PC midline, which is the inferior region of the STG/PT, and continued up to +18 mm, in the vicinity of the upper border of the STG in a Talairach and Tournoux normalized brain volume [105]. Since the STG/PT follows the slope of the Sylvian fissure, it could also be expected that activation, which is specifically related to this area would show up more posteriorly as the analysis is moved upwards through the STG/PT area. As Fig.

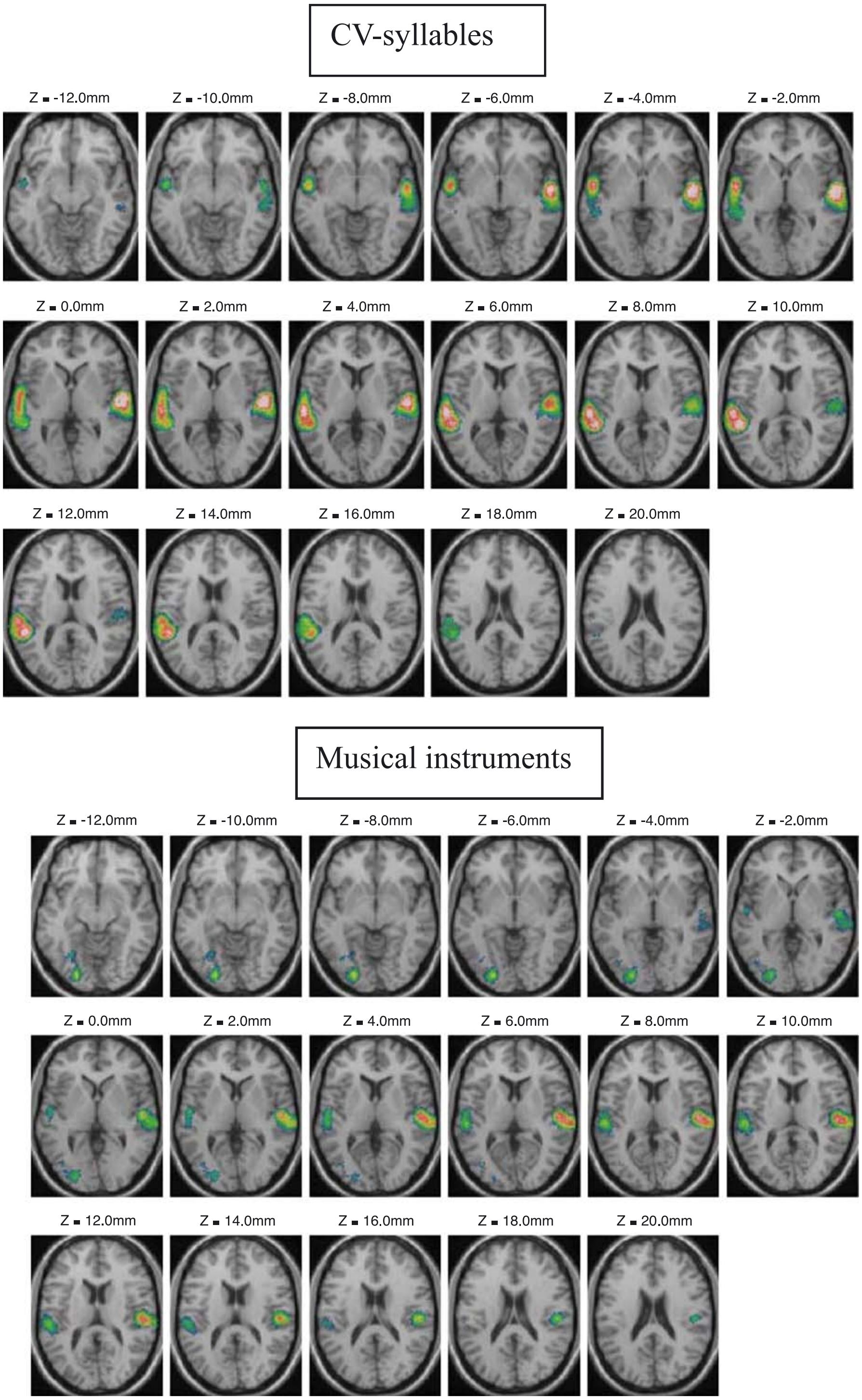


Fig. 2. Axial slices going from -12 to $+20$ mm below and above the AC-PC zero line, showing significant activation in the medial temporal gyrus/superior temporal sulcus to the upper surface of the superior temporal gyrus. Data were acquired during the subjects ($N = 12$) performed a dichotic-listening task with CV syllables (upper panel) and with music sounds (bottom panel). Data from Ref. [51]. Courtesy of Ian Law, Copenhagen University Hospital, Denmark.

2 illustrates, this posterior shift in activation clearly occurred to the CV syllables, while the activations to the music stimuli were unaffected by the slope of the Sylvian fissure.

However, it is important that activation differences between the hemispheres are tested formally for significant differences. This may be done by creating a template brain consisting of a "single hemisphere" by flipping or mirror-reversing the two hemispheres with regard to each other. Activation data could then be formally tested for significant differences between homologous voxels on the left and right side. The data displayed in Fig. 2 were further analyzed by using this technique. The resulting activations in Fig. 3

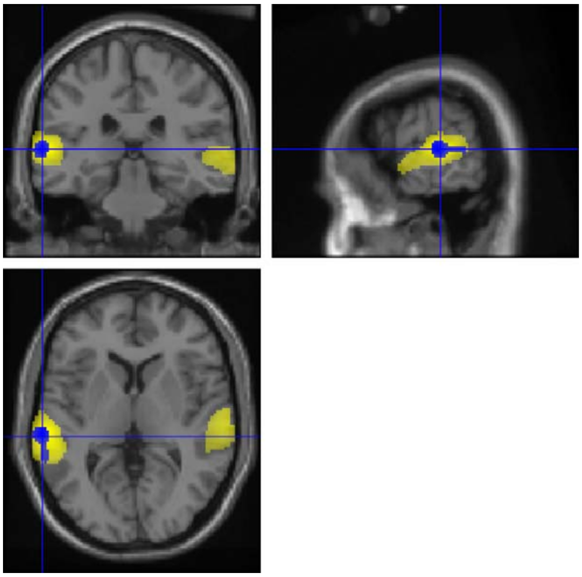


Fig. 3. Statistical hemisphere × stimulus interaction effect (blue) mapped together with main effect of stimulus (yellow). Data from Ref. [51]. Courtesy of Ian Law, Copenhagen University Hospital, Denmark.

show the statistical interaction between the hemisphere × CV syllable stimulus (blue) mapped together with the main effect of stimulus (yellow). A significant interaction effect can be observed, with a clear left-sided asymmetry to CV syllables.

The functional role of the left planum temporale for processing of speech sounds already in infancy was clearly demonstrated [23]. fMRI data was obtained in 2–3-month-old infants while they listened to a female voice reading from a children's book. There were significant activations in the left temporal lobe encompassing Heschl's gyrus, STG, STS and PT. This study is important since it shows for the first time that the human brain is asymmetrically organized for the processing of speech sounds already at the infant level, long before the child begins to speak and can understand when others are speaking.

Recently also the issue of the existence and magnitude of the STG and PT asymmetry underlying spatial processing has been revitalized [125]. In a PET study using free-field stimulation, the subjects had to indicate whether the sounds presented at different locations were the same or not. In one experiment, different sounds that varied in spatial locations were presented. The results showed significant activations in the PT area and in the left temporoparietal operculum. Interestingly, the right inferior parietal cortex was also activated when the subjects had to make explicit judgements of left–right localizations, as when deciding whether two sounds that were displaced 30° to the right and left were the same or different sounds. Thus, it seems that there may be different neural pathways for identifying a sound per se and its localization in auditory space, similar to the "what" and "where" systems identified in the visual modality (cf. Refs. [19,93,114]).

Corresponding right parietal cortex activation was observed for the perception of movement of sounds [36]. However, using a similar technique in which stationary stimuli presented via headphones were filtered so that they are perceived as moving sounds in different locations outside of the head, strongest activation in areas anterior of Heschl's gyrus in both the right and left hemisphere was obtained [117]. Thus, it is at present unclear exactly what areas that are activated when subjects perceive sound movements in space.

To briefly summarize, the traditional role of the left PT as an anatomical substrate to Wernicke's area is today questioned by more recent neuroimaging data, the bulk of the available evidence still pointing towards a specific role for the left PT in processing of phonologically relevant stimuli. It may turn out, however, that it is not the phonemes per se that causes neuronal activation in the PT region, but rather the specific temporal characteristics of, for instance, the stop-consonants.

4. Behavioral measures of hemispheric asymmetry

With the dichotic-listening (DL) technique, two different auditory stimuli are presented at the same time, one in each ear [63] (see Refs. [44,45] for reviews). The subject is free to report the stimuli heard, although often instructed to report only the item heard first or best (other procedures also exist in the dichotic-listening literature). A commonly used paradigm includes pair-wise combinations of CV syllables that are made up of the six stop-consonants and the vowel /a/. The result, better recall from the right ear (when controlling for hearing differences between the ears), is taken as a behavioral measure of left-temporal lobe processing superiority for phonological stimuli. This right-ear advantage (REA) is probably caused by the fact that although auditory input is transmitted to both auditory cortices in the temporal lobes, the contralateral projections are stronger and more preponderant, which may block the processing of the ipsilateral projections [15,63]. Thus, while reporting the stimuli, the subjects more rely on right-ear input which mainly entered the left auditory cortex.

The robustness of the right-ear advantage in DL studies of CV syllables is seen in Fig. 4 illustrating the distribution of number of correct reports from the left and right ear from 1466 subjects ranging in age from 7 to over 80 years, both males and females. Note the apparent normal shape for both distributions and the marked shift "to the right" for the right ear distribution, indicating a highly significant right-ear advantage. Thus, speech stimuli like CV syllables produce a reliable left hemisphere asymmetry advantage when measured from self reports like in the DL paradigm (the data are from Refs. [47,52].

The dichotic-listening REA has been validated with several methods. Fig. 5 shows the data of a study comparing

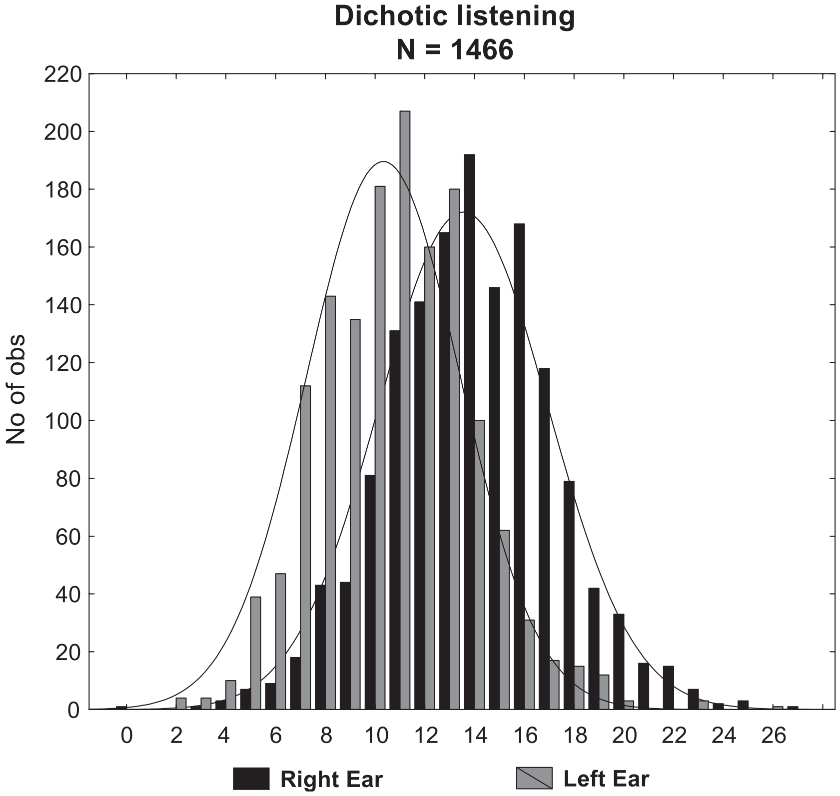


Fig. 4. Distribution of right and left ear scores in the CV syllable dichotic-listening test (1466 subjects). Black bars = right-ear score distribution; gray bars = left-ear score distribution. The data are from Refs. [47,52].

dichotic-listening performance and the Wada-test [49]. The Wada-test involves the administration of a sedative drug (e.g., sodium amytal or amobarbital) into the left or right hemisphere through a catheter into the carotid artery from the femoral artery [116]. By sedating one hemisphere at a time, and then testing for which cognitive functions are absent, it is possible for the clinical neuropsychologist to derive the hemisphere that houses, for instance, language. The Wada-test is the 'gold standard' for establishing hemisphere dominance in patients with epilepsy undergoing surgical removal of sclerotic brain tissue. The subjects in the present study were first tested with the Wada-test and thereafter with the dichotic-listening test [49]. The Wada-test results revealed that 10 subjects had left-hemisphere dominance for language, while 3 subjects had right-hemisphere dominance. Eight of the 10 subjects with language dominance in the left hemisphere showed a right-ear advantage on the dichotic-listening test. All three subjects with right-hemispheric language showed a left-ear advantage on the dichotic-listening test. In Fig. 5, individual scores from the left and right ear are plotted, respectively.

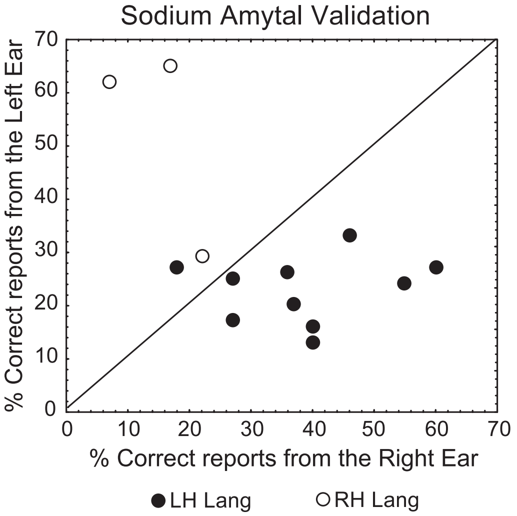


Fig. 5. Scatterplot of dichotic listening performance against Wada-test performance. The *x*-axis shows percentage of correct right-ear reports; the *y*-axis shows percentage of correct left-ear reports. Filled circles represent individuals with left hemispheric language functions and open circles represent individuals with right hemispheric language functions (as determined by Wada-testing). Data from Ref. [49].

The above-described evidence for the hemispheric lateralization of auditory processing was revealed either with behavioral or brain-imaging methods from subjects who were instructed to listen attentively or passively to the sound stimulation and, in most cases, also to indicate whether or not they perceived the sounds. Unfortunately, these paradigms set some limits to the level of generalization of the conclusions one can draw from the data: It has been argued that the right hemisphere has a predominant role in attentional control [39]. If this was a case, a paradigm which is free from confounds caused by attentional factors would be useful.

5. Mismatch negativity—a probe to auditory memory

An electromagnetic brain response termed mismatch negativity (MMN) can be recorded when the subject is presented with an infrequently presented deviant auditory stimulus, which differs from the frequently presented standard stimulus in one or several acoustic parameters [79]. Since the MMN is elicited even when the subject is performing a task unrelated to the stimulation under interest, such as reading a book or playing a computer game, it may be used to determine the involvement of the left vs. right hemisphere in sound processing prior to attentive control.

The presence of the MMN implies that the invariant parameters of the standard sound stimulus are neurally encoded and found to be discrepant with the parameters of the deviant sound. Thus, by recording the MMN, it is possible to objectively determine the degree of how much two neural sound representations differ from each other. In addition, since the MMN can be probed with event-related potential and magnetic evoked fields with excellent temporal resolution in the millisecond range, it MMN provides the researcher with a tool for determining the speed of sound-change discrimination. Moreover, the generator(s) of the MMN response are relatively well established. The MMN is generated mainly in the primary auditory cortex or in its immediate vicinity as evidenced by magnetoencephalographic (MEG) (e.g., Ref. [2]), positron emission tomography (PET) [110] and functional magnetic resonance imaging (MRI) [84–86] investigations. Additional source in the frontal lobe has been proposed [33,95]. Thus, MMN recordings offer a mean to specify the separate involvement of the left and right the auditory cortices in sound-change discrimination.

6. MMN and asymmetric processing of speech and music sounds

The functional roles of the left and right auditory cortices in speech and music sound processing were addressed in several studies by Näätänen and his colleagues. In the first study, subjects with Finnish or Estonian as their native language were instructed to watch and attend to a silent movie while they were presented with the phoneme /e/ as the standard stimulus and the phonemes /ö/ and /õ/ as the deviant stimuli [81]. The vowels /e/ and /ö/ exist in both the Finnish and Estonian languages, whereas /õ/ exists only in the Estonian language. However, the physical distance between /e/, /õ/ and /ö/ is linear due to the increasing frequency of the second formant along this continuum. Previously, the MMN response has been found to reflect the physical difference between the standard and deviant sound (see, for instance, Refs. [96,112]). Therefore, differential ERPs to these vowels especially with regard to their MMN to the vowel /õ/ would indicate modulation of the brain processes as a function of subjective long-term experience with a particular language. The results obtained confirmed the original hypothesis: the electrical MMN amplitude was smaller for /õ/ in the Finnish subjects compared with the Estonian subjects (Fig. 6). In subsequent MEG recordings, the MMN(m) enhancement in Estonian subjects was shown to result from enhanced neuronal activity in the left hemisphere. These findings were interpreted as evidence for the existence of long-term memory

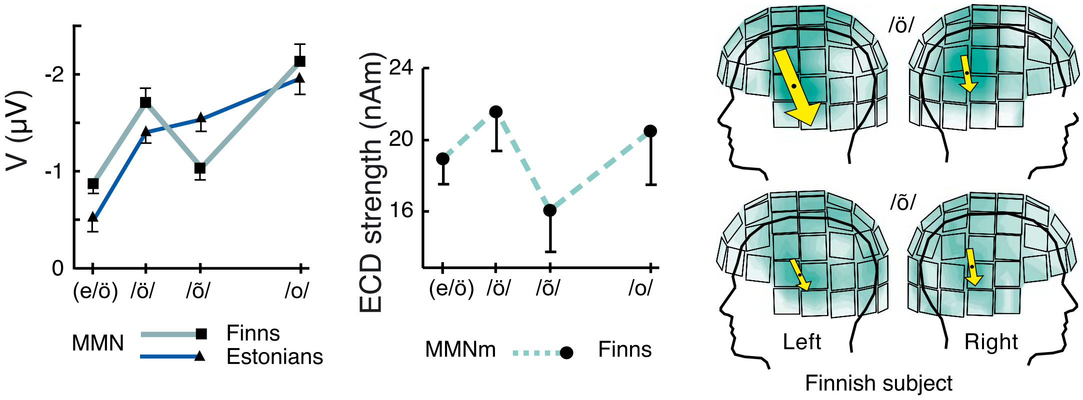


Fig. 6. Strengths of the electrically recorded MMN (left) and magnetically recorded MMNm (middle) elicited in adult subjects by four deviant vowels among standard /e/ vowel in Estonian vs. Finnish. There were 9–13 right-handed subjects in each of the recordings. From these vowels, /e-ö/ does not belong to either Estonian or Finnish, /ö/ and /o/ belong to both of them, and /õ/ only to the Estonian language. The MMN(m) amplitude was enhanced to /õ/ in Estonian subjects when compared to Finnish subjects, implying a presence of long-term memory traces for phonemes of the native language. The left-hemisphere dominance of the MMNm was demonstrated in MEG recordings with Finnish subjects (right). The size of the arrow illustrates the strength of the MMNm dipole in each hemisphere, the MMNm being elicited by /ö/ (upper panel) and /õ/ (lower panel). Adapted from Ref. [81].

traces for speech sounds specifically located in the left auditory cortex. In other words, since the strength of the MMN(m) was modulated by the familiarity of the vowels more than by their acoustical similarity (known to reflect the short-term memory contribution), a long-term contribution was postulated (see also [80]).

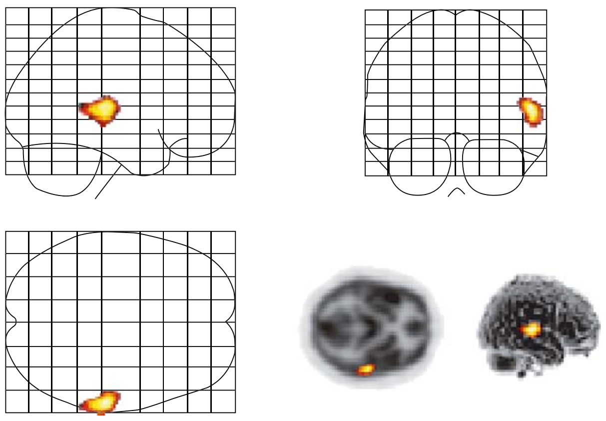
However, one might question whether the neural mechanisms behind a basic discrimination between two different sounds are similarly represented during automatic and attentive processing. To this end, Alho et al. [3] employed native English speakers in a whole-head MEG experiment in which CV syllables were presented in two separate conditions. In the first condition, the subjects were watching a silent video and in the second condition they were instructed to press a response key to the target (deviant) syllable whenever it occurred. It was found that the syllable discrimination elicited a stronger MMNm response in the left compared with the right hemisphere during both the video and discrimination conditions. This result suggests that the dominant role of the left hemisphere in speech-sound discrimination is not modified by conscious attention, despite the asymmetry of the neural networks underlying attentional control.

Furthermore, to determine whether the left and right auditory cortices are functionally specialized for pre-attentive encoding of phonetic vs. musical information, a whole-head MEG study was conducted. While watching a silent movie, the subjects were presented with frequent and infrequent phonemes (/e/ vs. /o/) or chords (A major vs. A minor) [109]. These phonetic and musical stimuli were matched in complexity as well as in the magnitude of the frequency change embedded in them. It was found that in both hemispheres, the source of the MMNm elicited by the infrequent sounds among phonemes and chords was located posteriorly to the source of the earlier P1m component which is known to be generated at or near the primary auditory area about 50 ms before the MMN(m). In addition, the MMNm source for a phoneme change was located superiorly to that of the chord change. These data, thus, indicate that there are distinct cortical areas specialized in representing phonetic and musical sounds in both hemispheres. In other words, the functional specialization does not only cover stimulus complexity as indicated by the previous study (comparing single tones vs. chords [2]) but also the informational content (phonetic vs. musical [109]). However, this specialization is not present prior to memory-related auditory processing as suggested by the dissociation between the P1m and MMNm data [109].

Tervaniemi et al. [109] also determined the left versus right hemispheric contribution to MMNm strength. The right hemisphere was more strongly activated by the chord change than the left hemisphere, whereas no such hemispheric dominance was found for the phoneme change. To further investigate this issue, a subsequent PET study was conducted [110]. In that experiment, the phoneme duration was prolonged from 200 to 400 ms to maximize the vowel-MMN elicitation [81] (see also Ref. [61]). During this study, the subjects were concentrating on a visually displayed word gender classification task. When sound sequences consisted of intermixed frequent and infrequent sounds, automatic phonetic processing was lateralized to the left hemisphere and musical to the right hemisphere (Fig. 7). This lateralization, however, did not occur in control blocks with one type of sound only (frequent or infrequent). The data thus suggest that automatic activation of lateralized neuronal circuits requires sound comparison based on short-term sound representations.

Most recently, the degree of the MMN(m) lateralization was probed with spectrally complex sounds in two rather different experimental paradigms. In the first one, the MMN was recorded during monaural stimulation (left vs. right) to infrequent changes in phonemes vs. spectrally rich sounds

Chord stimulation



Phoneme stimulation

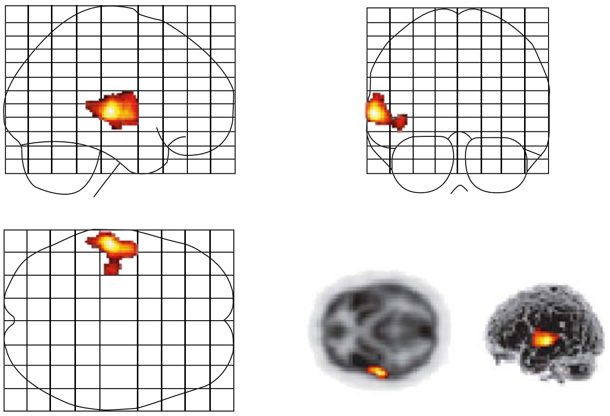


Fig. 7. Upper panel: Activated area in the right superior temporal gyrus during chord stimulation (subjects were 15 healthy adults without musical training). Lower panel: Activated area in the left superior and middle temporal gyri during phoneme stimulation. During both stimulations, the subjects concentrated on a word gender classification task in visual modality. Adapted from Ref. [110] and reprinted by permission of Wiley–Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

[59]. In general, the MMN to vowel changes was larger than to sound changes, and the duration-MMN was smaller than to frequency or frequency + duration changes. Most interestingly, the frequency-MMN to sounds delivered to the left ear was larger than to the sounds delivered to the right ear. Correspondingly, the duration-MMN was larger when the sounds were delivered to the right than to the left ear. Thus, the views about the predominant role of the right hemisphere in encoding frequency information and the left hemisphere in encoding temporal information were supported (cf. Ref. [124]). Yet, it should be noticed that, in contrast to several other studies with comparable findings, the sounds by Jaramillo et al. [59] were rather long (400 ms standard vs. 200 ms deviant).

Despite remarkable differences in methodology, the data obtained by Jaramillo et al. were replicated in a subsequent study by Mathiak et al. [75] in whole-head MEG recordings during a dichotic-listening task. While attending to a visual task or to detect the deviant sounds, the subjects were presented with standard (500–350 Hz) dichotic sound pairs intermixed with 2% and 4% frequency changes in the upper or lower of the sounds. The data indicated that, in general, the frequency changes to sounds delivered to the left ear evoked significantly larger MMNm than those delivered to the right ear. The magnitude of the frequency change or the task performed did not modulate this finding. Thus, taken together with the data by Jaramillo et al., these results give strong support for at least to the right-hemispheric dominance of the frequency-MMN.

To summarize: using relatively large variety of stimulation, the above-reviewed studies indicate the predominant role of the left auditory areas in phonetic as well as in duration discrimination. At the same time, they pinpoint the importance of the right auditory areas in pitch discrimination. Importantly, these data were obtained in experimental paradigms in which the subjects' focused attention towards the sounds is not required. Therefore, we can conclude that basic forms of brain asymmetry in audition exist even prior to the attentional control.

7. Vulnerability of lateralized sound processing

In the following, high-resolution EEG and whole-head MEG experiments with more elaborated stimulation will be introduced. The speech sounds were either presented during background noise or the sound material was manipulated to allow the determination of the effect of sound structure on hemispheric lateralization.

Rinne et al. [94] used 128-channel EEG recordings to determine the predominantly active hemisphere in sound discrimination by parametrically manipulating the complexity of the formant structure of a vowel. They presented subjects with phonemes, which either had a full formant structure or were filtered to consist of 75%, 50% or 25% of the formant frequencies. In the first condition, the subjects were reading a book. In the second condition, the subjects were asked to categorize the phonemes. The results indicated that when 75% or 100% of the formant information was present in the phoneme structure, the subjects were able to categorize the phonemes and, correspondingly, the MMN was predominantly larger in the left hemisphere. These data thus emphasize the role of sufficient amount of acoustic (phonetic) information in establishing the phonetic percept by the left-hemispheric neural networks.

Shtyrov et al. [102] in turn kept the spectral sound complexity constant but manipulated the sound type and the speed of the non-speech sound onset. In other words, the stimuli were, in separate conditions, semisynthetic /pa/ vs. /ka/ and their non-speech equivalents with fast (25 ms) and slow (90 ms) transitions. In this whole-head MEG study, it was found that while speech-sound changes were more vigorously processed in the left hemisphere, no hemispheric dominance could be determined for the equally complex non-speech sounds with fast sound onset, chosen to match that of the speech sounds. In contrast, right-hemispheric dominance was observed when the stimuli were non-speech sounds with slow onset. These data suggest that not merely the presence of rapid transitions but also the quality of the spectral sound structure (phonetic vs. non-phonetic) deter-

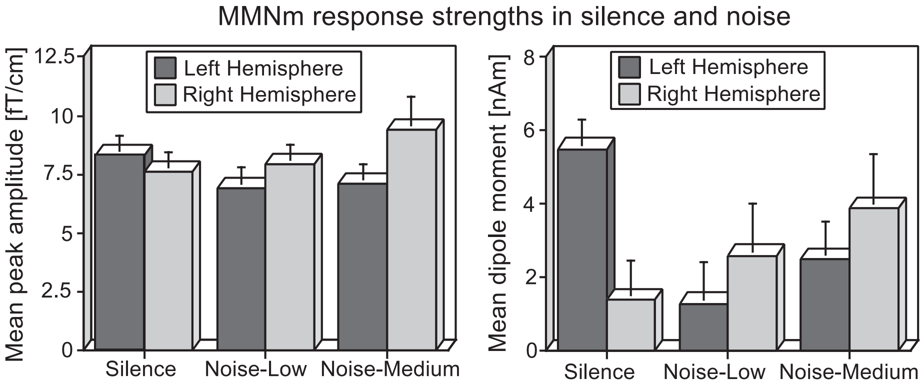


Fig. 8. MMNm peak amplitude strength (left) and dipole strength (right) elicited by /pa/ vs. /ka/ syllable change in silence as well as during soft and medium-level noise (average of 11 right-handed subjects). In silence, the MMNm was left-hemispheric dominant (black) while in the noisy background, it was right-hemispheric dominant (gray). Adapted from Ref. [100].

mine in which hemisphere the sound-change discrimination mainly occurs.

Moreover, Shtyrov et al. [100] determined the relative importance of left and right hemispheres on syllable processing in silence versus during a soft background noise. Their whole-head MEG experiment was inspired by behavioral studies in which the presence of noise was found to modulate sound processing and by the rarity of silent background in usual communication occasions despite their common use in experimental settings. The subjects, concentrated on watching a silent video, were presented with /pa/ (85%) and /ka/ (15%) syllables in silence and in low-level and medium-level noise (10 and 15 dB, respectively). The MMNm was larger in the left hemisphere during silence but larger in the right hemisphere during both levels of background noise (Fig. 8). In contrast, the dipole-moment analysis of the P1m and N1m responses revealed no effect of the noise on hemispheric lateralization [101]. The dipole moment of the P2m in turn was increased in the right hemisphere during low-level noise stimulation when compared with silent background.

Taken together, these data indicate that the existence of predominantly left hemisphere networks specialized in phonetic discrimination is relatively vulnerable to micro- or macro-level changes in the speech-sound environment, in other words, by the changes in sounds themselves or by their acoustic background.

8. Anomalous patterns of laterality

Over the last decades, several studies have reported that missing functional and anatomical hemispheric asymmetry might underlie some relatively common neurocognitive disorders. For instance, dyslexia has been related to difficulty in processing rapid temporal information even when phonetic information is not provided. Tallal and her colleagues (e.g., Refs. [4,26,106,107] have repeatedly shown that individuals with specific language impairment (SLI) and reading disorders have problems perceiving and processing rapidly occurring speech sounds, particularly the initial consonant-segments in simple consonant–vowel syllable stimuli. Moreover, several studies have over the last decade reported reduced STG/PT area on the left side in dyslexic children (e.g., Refs. [27,28,38,50,53,54,66]; see also Ref. [8] for a review). Considering that dyslexia involves a failure of phonological decoding [42,78,83], it is difficult to avoid a conclusion that the reduced PT asymmetry in dyslexics is related to their pitfalls in phonological processing.

Supporting the view emphasizing the importance of intact encoding of rapid (non-phonetic) sound information for reading ability, it was found that the MMN of adult dyslexic individuals did not differ from that of control subjects when it was elicited by a change in a within-pair interval of two 30-ms sinusoidal tones [64]. In contrast, their MMN was diminished when the sound pattern included four subsequent tones, the sound change taking place in the middle of the pattern. A subsequent study indicated that this selective difficulty in discriminating temporal changes among tone patterns in dyslexic subjects was caused by the sound following the sound change rather than by the sound preceding it [65]. This suggests that in dyslexic subjects, the formation of an auditory memory trace is especially vulnerable to rapid sound successions. Although no direct evidence for the deterioration of left-hemispheric functions was obtained so far, its existence would well explain the results.

Children with SLI are at risk for literacy problems that may overlap with the symptoms and signs of developmental dyslexia [69,108]. However, phonological decoding deficits are more prominent than comprehension deficits in dyslexia, whereas either comprehension deficits only or both deficits may be seen in individuals with SLI [13,71].

A key question with regard to the underlying mechanisms is the relation of SLI to brain structural and functional abnormality. With regard to structural brain measures, Ahmed et al. [1] reviewed the literature on structural brain anomalies in SLI, by means of MRI. They found that a positive family history of SLI seemed to go together with language deficiencies in children with SLI and brain abnormalities (see also Ref. [18]). Moreover, Kabani et al. [60] found that both adults and children with a family history of SLI showed structural abnormalities when comparing six children and five adults with a family history of SLI with an intact control group. They found also evidence for cortical atrophy in anterior regions in the adult sample, and an abnormal white-to-grey matter ratio in the children. Moreover, Gauger et al. [31] found that language areas in the left hemisphere, including the planum temporale and the pars triangularis (Broca's area), were smaller in 11 SLI children than in controls.

It has also been argued that schizophrenia is related to a left STG/PT area deficit, thus being connected to impaired language processing (e.g., Ref. [20]) and to auditory hallucinations (cf. Ref. [35]). Accordingly, several recent morphometry studies have also shown reduction in the left STG area in schizophrenic patients (see Ref. [21]). Also reduced functional and anatomical asymmetry of the auditory areas in schizophrenic patients when compared with healthy controls was obtained [111]. Interestingly, using fMRI, Lennox et al. [68] showed increased activation in the left STG/PT area in schizophrenic patients when experiencing hearing voices, which again relates the left STG/PT area to auditory speech processing. Finally, using a voxel-based morphometry technique [7] on MR images for analysis of group differences in grey matter volume in specified brain areas, it was revealed that schizophrenic patients have reduced grey matter volume in the left superior temporal gyrus, including the PT [82]. These same patients also show a reduction and sometimes absence of the REA in the dichotic listening test (cf. Ref. [73]), an expected result if these brain areas are critically involved in the processing of speech signals.

Interestingly, an altered hemispheric asymmetry has also been evidenced to cause highly respected forms of human cognition. Musicians with absolute pitch (ability to name a tone without a reference pitch) were found to have larger leftward PT asymmetry than musicians without AP [97] or non-musicians [123]. These anatomical findings received further support from MEG studies in which, the N1m was generated 1 cm posteriorly in the left than in the right auditory areas in AP subjects, non-musicians showing no such hemispheric difference [41]. However, most recent morphometric analyses of the AP musicians suggest that the phenomenon is more complex than originally assumed. Keenan et al. [62] found that instead of enlargement of the left PT in AP musicians when compared with non-AP musicians or non-musicians, their right PT was reduced in size, causing in part the larger PT asymmetry indices in AP musicians than in other subjects. The authors suggested that the right PT is pruned early in the neural development in AP musicians. It could be speculated that fewer right-hemispheric resources for pitch perception in AP musicians might cause additional involvement of the left PT, this, in turn, leading to use of advanced linguistic (categorization) strategies during pitch processing.

Taken together, the altered forms of hemispheric lateralization might underlie both deteriorated (dyslexia, schizophrenia) and advanced (absolute pitch) forms of human cognition. When it comes to the deteriorated forms of cognition, it remains open which forms of them are caused by altered lateralization, how early in individual developmental course those could be observed, and also whether neurocognitive rehabilitation could be used to remediate them.

9. Discussion

The above reviewed evidence, obtained from behavioral dichotic-listening studies as well as by high-resolution EEG, whole-head MEG, fMRI and PET investigations, suggests that speech sounds activate predominantly left-hemispheric neural networks and, correspondingly, musical sounds tend to activate right-hemispheric neural networks. This pattern of hemispheric asymmetry is relatively stable during both attentive and pre-attentive levels of processing, although the behavioral REA in dichotic listening is influenced by attentional demands (cf. Ref. [44]). These findings fit with the lesion data insofar that both expressive and receptive aspects of language function are more often affected after left-compared to right-hemispheric lesions, including BAs 44 and 42 [72]. For musical functions, the temporal (rhythmic) processing is predominantly left hemispheric whereas melodic as well as harmonic processing is based on intact right-hemispheric functions [22].

These findings, attributed to the “speech vs. music” domains, could also be discussed in terms of sound parameters optimally probing the hemispheric specialization under interest. For instance, when healthy subjects were presented with low-high pitch alternating sequences, their left auditory cortex displayed stronger activity during rapid pitch alterations while their right auditory cortex was more active during slow but small pitch alterations [121] (see also Ref. [124] for a review). This suggests that the left auditory cortex is tuned to process fast sound changes whereas the right auditory areas are more advanced to process tiny changes in pitch. Moreover, Jäncke et al. [58] found more pronounced left PT activity for syllables with voiceless than voiced initial consonant, which is congruent with such a view of hemispheric specialization. Thus, the left hemisphere predominantly processes sounds in a time scale of less than 50 ms, the critical time window determining the formant transition [9,90]. However, it seems that the presence of phonetic information is not necessary for such left-hemisphere dominant activity to occur.

It has also been argued that the processing of the initial formant transitions occurs in the left hemisphere, while the processing of CV syllables occurs in the right hemisphere, following their suggestion of short versus long processing time windows for the left and right hemisphere, respectively [90]. At the moment, this argument lacks, however, empirical support. It is also difficult to comprehend how such a qualitative difference in hemisphere functioning should occur when in fact the formant transition is an integral part of the perception of a CV syllable. It is doubtful that such critical information for the perception of a CV syllable, as the formant transition, is processed in one hemisphere, while the rest of the syllable is processed in the other hemisphere. Recent data by Pollmann et al. [91] also counteracts this argument. They studied performance on the CV syllables dichotic listening task in patients with either anterior or posterior corpus callosum lesions. The auditory fibers cross the corpous callosum in the posterior isthmus region. Thus an almost perfect right-ear advantage in patients with posterior lesions was predicted, if the left-ear stimulus could not be processed in the right hemisphere. The results clearly supported the prediction, with no reports at all from the left-ear stimulus in patients with more posterior lesions. Thus, in light of these findings, it is difficult to argue that CV syllables are exclusively processed in the right hemisphere.

Thus, the original question whether the left and right auditory areas are functionally specialized to process speech vs. music might be replaced by the question whether the left and right auditory areas are specialized to process rapid temporal changes vs. tiny changes in pitch. In other words, a model about domain-specific lateralization might be replaced by a parameter-specific lateralization model. Intrinsically, domain-specific and parameter-specific auditory processes overlap to large extent-speech sounds are full of rapid voice onsets and music is rich in melodic and harmonic (pitch) information flowing more slowly in time. However, this change in conceptualization would help understand also phenomena which previous domain-specific approach do not accommodate. For instance, emotional prosody, which is acoustically mainly determined by exaggerated pitch and intensity changes, is right-hemispherically determined [98].

Even if the principle of a parameter-specific lateralization model is accepted, the question remains whether and how the central nervous system (CNS) could perform such a parameter-specific computation of sound signals. Recently, Zatorre [120] and Zatorre et al. [124] suggested that the different degree of myelinization in the left vs. right hemispheres, leading into differential the speed of neural processing in the hemispheres, underlies behind their complementary functions. Although some anatomical evidence for this view is obtained (e.g., Refs. [5,88]), more evidence is required for before the authorization of the view.

In parallel, it should be noticed that according to the present evidence, the lateralization of sound processing is highly vulnerable. First, the ear dominance during a dichotic-listening task can be modified by simply changing the instruction to selectively focus attention to either the right or left ear, and to report only from that ear (top-down intraindividual effect). In majority of the dichotic-listening tests, the subject is given to report freely the syllable s/he heard. If the subject is instructed to selectively listen to the right/left ear, the results changed in a clear majority of the cases [16,44,48,77].

Second, the pattern of lateralization seem to be sensitive to several sound parameters as well as to sound familiarity. For instance, the MMN response evoked by a CV change is left-hemisphere dominant in silence but bilateral (or even right-hemispheric dominant) in background noise (bottom-up intraindividual effect) [100]. In such a case, continuous noise may activate up to a sufficient degree also the right-hemispheric mechanisms, which are specialized to encode slow transients [124]. Likewise, the MMN response evoked by a vowel is left-hemispherically dominant only if it belongs to the native language of the subjects (top-down interindividual effect) [81]. Here, it could be speculated that the long-term memory traces created by the vowels are activated. Of the vowels not belonging to the phonetic space of the native language, the formant changes are encoded as any other frequency change [81].

Third, interindividual differences in the degree of lateralization (as determined by the PT area) may underlie several neurocognitive anomalies such as dyslexia or schizophrenia and, surprisingly, also some special skills such as the absolute pitch may have their neural basis in altered forms of lateralization (bottom-up interindividual effect). Schlaug et al. [97] found that musicians with perfect pitch revealed stronger leftward PT asymmetry than non-musicians or musicians without perfect pitch. The results indicated that outstanding musical ability is associated with increased leftward asymmetry of cortex subserving music-related functions. Interestingly, reduction of PT leftward asymmetry is observed in dyslexic individuals [38,66]. This indicates that processing of pitch and phonemes share similar brain areas, since dyslexia involves impaired phonological decoding. A parameter-specific model may also be helpful in resolving some of the issues currently discussed or debated in the dyslexia literature. Dyslexia may not involve a functionally different form of lateralization as believed from the days of Orton [87]. He argued that dyslexia was caused by weakened left hemisphere suppression of the right hemisphere during reading, causing right hemisphere interference with the reading process. A parameter-specific model would, however, support more recent empirical evidence that dyslexia involves impairment in recognition and discrimination of rapidly changing sound transients [106,107], which goes along with MR data showing a reduction in grey matter volume in the auditory areas in the left hemisphere [66]. Following Zatorre's suggestion of differences in degree of myelinization in the left and right auditory areas, a parameter-specific model would suggest that an underlying cause of impaired sound discrimination is abnormal development of myelinization of left auditory cortex. This could also be directly empirically tested with modern MR diffusion techniques like diffusion tensor imaging.

The above-listed exceptions to the brain-lateralization literature in audition will hopefully lead one to reformulate the experimental paradigms used in comparing neurocognition of speech vs. music in electromagnetic and hemodynamic paradigms. According to our view point, without neglecting the practical limitations set by the methodologies in cognitive neuroscience, any experiment aiming to compare speech vs. music and/or left/right auditory functions should control and balance several variables. These variables include, at least, the acoustic sound properties, subjects' memory load during the experiment, and also their training in music and languages.

More specifically, first, the sound complexity in conditions under interest should be matched in acoustical terms. In this balancing, both temporal and spectral aspects should be kept in mind. However, the sounds should not loose their speech-quality/musicality. Second, the memory load given to the subjects during scanning should be comparable during speech/language vs. music/non-linguistic stimuli. In other words, both tasks should equally load semantic/acoustic and long-term/working/sensory memory systems. Third, the subjects' familiarity with the sound material should be carefully controlled taking into account also their linguistic and musical background, in other terms, their pre-existing long-term memory representations for the sound material.

To summarize, the data reviewed above provide strong evidence for the existence of the brain lateralization in audition but also for its vulnerability. Moreover, a model about domain-specific lateralization (speech/music) might need to be replaced by a parameter-specific lateralization model (fast temporal information/pitch information).

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References

[1] S.T. Ahmed, L.J. Lombardino, C.M. Leonard, Specific language impairment: definitions, causal mechanisms, and neurobiological factors, J. Med. Speech-Lang. Pathol. 9 (2001) 1–15.

[2] K. Alho, M. Tervaniemi, M. Huotilainen, J. Lavikainen, H. Tiitinen, R.J. Ilmoniemi, J. Knuutila, R. Näätänen, Processing of complex sounds in the human auditory cortex as revealed by magnetic brain responses, Psychophysiology 33 (1996) 369–375.

[3] K. Alho, J.F. Connolly, M. Cheour, A. Lehtokoski, M. Huotilainen, J. Virtanen, R. Aulanko, R.J. Ilmoniemi, Hemispheric lateralization in preattentive processing of speech sounds, Neurosci. Lett. 258 (1998) 9–12.

[4] K.C. Anderson, C.P. Brown, P. Tallal, Developmental language disorders: evidence for a basic processing deficit, Curr. Opin. Neurol. Neurosurg. 6 (1993) 98–106.

[5] B. Anderson, B.D. Southern, R.E. Powers, Anatomic asymmetries of the posterior superior temporal lobes: a postmortem study, Neuropsychiatry Neuropsychol. Behav. Neurol. 12 (1999) 247–254.

[6] J. Ashburner, K.J. Friston, Voxel-based morphometry—the methods, NeuroImage 11 (2000) 805–821.

[7] J. Ashburner, K.J. Friston, Why voxel-based morphometry should be used, NeuroImage 14 (2002) 1238–1243.

[8] A.A. Beaton, The relation of planum temporale asymmetry and morphology of the corpus callosum to handedness, gender, and dyslexia: a review of the evidence, Brain Lang. 60 (1997) 255–322.

[9] P. Belin, M. Zilbovicius, S. Crozier, L. Thivard, A. Fontaine, M.C. Masure, Y. Samson, Lateralization of speech and auditory temporal processing, J. Cogn. Neurosci. 10 (1998) 536–540.

[10] J.R. Binder, S.M. Rao, Human brain mapping with functional magnetic resonance imaging, in: A. Kertez (Ed.), Localization and Neuroimaging in Neuropsychology, Academic Press, San Diego, 1994, pp. 185–212.

[11] J.R. Binder, J.A. Frost, T.A. Hammeke, S.M. Rao, R.W. Cox, Function of the left planum temporale in auditory and linguistic processing, Brain 119 (1996) 1239–1247.

[12] J.R. Binder, J.A. Frost, T.A. Hammeke, P.S. Bellgowan, F. Springer, J.A. Kaufman, T. Prieto, Human brain language areas identified by functional magnetic resonance imaging, J. Neurosci. 17 (1997) 353–362.

[13] D.V.M. Bishop, C. Adams, A prospective study of the relationship between specific language impairment, phonological disorders and mental retardation, J. Child Psychol. Psychiatry 31 (1990) 1027–1050.

[14] H. Braak, On magnopyramidal temporal fields in the human brain-probable morphological counterparts of Wernicke's sensory speech region, Anat. Embryol. (Berl.) 152 (1978) 141–169.

[15] M.P. Bryden, An overview of the dichotic listening procedure and its relation to cerebral organization, in: K. Hugdahl (Ed.), Handbook of Dichotic Listening: Theory, Methods, and Research, Wiley, Chichester, UK, 1988, pp. 1–44.

[16] M.P. Bryden, K. Munhall, F. Allard, Attentional biases and the right-ear effect in dichotic listening, Brain Lang. 18 (1983) 236–248.

[17] P. Celsis, K. Boulanouar, B. Doyon, J.P. Ranjeva, I. Berry, J.L. Nespoulos, F. Chollet, Differential fMRI responses in the left posterior superior temporal gyrus and left supramarginal gyrus to habituation and change detection in syllables and tones, NeuroImage 9 (1999) 135–144.

[18] M. Clark, E. Plante, Morphology of the inferior frontal gyrus in developmentally language disordered adults, Brain Lang. 61 (1998) 288–303.

[19] S. Clarke, A. Bellmann Thiran, P. Maeder, M. Adriani, O. Vernet, I. Regi, O. Cuisenaire, J.P. Thiran, What and Where in human audition: selective deficits following focal hemispheric lesions, Exp. Brain Res. 147 (2002) 8–15.

[20] T.J. Crow, Schizophrenia as a failure of the hemispheric dominance for language, Trends Neurosci. 20 (1997) 339–343.

[21] T.J. Crow, Schizophrenia as the price that *Homo sapiens* pays for a language: a resolution of the central paradox in the origin of the species, Brain Res. Rev. 31 (2000) 118–129.

[22] S. Dalla Bella, I. Peretz, Music agnosias: selective impairments of music recognition after brain damage, J. New Music Res. 28 (1999) 209–216.

[23] G. Dehaene-Lambertz, S. Dehaene, L. Hertz-Pannier, Functional neuroimaging of speech perception in infants, Science 298 (2002) 2013–2015.

[24] J.F. Démonet, F. Chollet, S. Ramsay, D. Cardebat, J.L. Nespoulos, R. Wise, A. Rascol, R. Frackowiak, The anatomy of phonological and semantic processing in normal subjects, Brain 115 (1992) 1753–1768.

[25] G.Th. Fechner, Über die ungleiche Deutlichkeit des Gehörs auf linkem und rechtem Ohr, Berichte über die Verhandlungen der Könighlich Sächsischen Gesellschaft der Wissenschaften zu Leipzig Math.-Phys, Cl. Bd. 12., Hirzel, Leipzig, 1860, pp. 166–174.

[26] R.H. Fitch, S. Miller, P. Tallal, Neurobiology of speech perception, Annu. Rev. Neurosci. 20 (1997) 331–353.

[27] L.M. Foster, G.W. Hynd, A.E. Morgan, K. Hugdahl, Planum temporale asymmetry and ear advantage in dichotic listening in developmental dyslexia and attention-deficits/hyperactivity disorder (ADHD), J. Int. Neuropsychol. Soc. 8 (2002) 22–36.

[28] A.M. Galaburda, G.F. Sherman, G. Rosen, F. Aboitz, N. Geschwind, Developmental dyslexia: four consecutive patients with cortical anomalies, Ann. Neurol. 18 (1985) 222–233.

[29] A.M. Galaburda, J. Corsiglia, G. Rosen, G. Sherman, Planum temporale asymmetry, reappraisal since Geschwind and Levitsky, Neuropsychologia 32 (1987) 853–868.

[30] P.J. Gannon, R.L. Holloway, D.C. Broadfield, A.R. Braun, Asymmetry of chimpanzee planum temporale: humanlike pattern of Wenicke's brain language area homolog, Science 279 (1998) 220–222.

[31] L.M. Gauger, I.J. Lombardino, C.M. Leonard, Brain morphology in children with specific language impairment, J. Speech Lang. Hear. Res. 40 (1997) 1272–1284.

[32] N. Geschwind, W. Levitsky, Human brain: left–right asymmetries in temporal speech region, Science 161 (1968) 186–187.

[33] M.H. Giard, F. Perrin, J. Pernier, P. Bouchet, Brain generators implicated in the processing of auditory stimulus deviance: a topographic event-related potential study, Psychophysiology 27 (1990) 627–640.

[34] C.D. Good, I. Johnsrude, J. Ashburner, R.N.A. Henson, K.J. Friston, R.S.J. Frackowiak, Cerebral asymmetry and the effects of sex and handedness on brain structure: a voxel-based morphometric analysis of 465 normal adult brains, NeuroImage 14 (2001) 685–700.

[35] M.F. Green, K. Hugdahl, S. Mitchell, Dichotic listening during auditory hallucinations in schizophrenia, Am. J. Psychiatry 151 (1994) 357–362.

[36] T.D. Griffiths, G. Rees, A. Rees, G.G.R. Green, C. Witton, D. Rowe, C. Büchel, R. Turner, R.S.J. Frackowiack, Right parietal cortex is involved in the perception of sound movement in humans, Nat. Neurosci. 1 (1998) 74–79.

[37] R. Hashimoto, F. Homae, K. Nakajima, Y. Miyashita, K.L. Sakai, Functional differentiation in the human auditory and language areas revealed by a dichotic listening tasks, NeuroImage 12 (2000) 147–158.

[38] E. Heiervang, K. Hugdahl, J. Stevenson, A.I. Smievoll, L. Ersland, A. Lund, A. Lundervold, H. Steinmetz, Planum temporale, planum parietale, and dichotic listening in dyslexia, Neuropsychologia 38 (2000) 1704–1713.

[39] K. Heilman, T. Van Den Abell, Right hemisphere dominance for attention: the mechanisms underlying hemispheric asymmetries of inattention (neglect), Neurology 30 (1980) 327–330.

[40] L. Heimer, The Human Brain and Spinal Cord, Springer-Verlag, New York, 1994.

[41] Y. Hirata, S. Kuriki, C. Pantev, Musicians with absolute pitch show distinct neural activities in the auditory cortex, NeuroReport 10 (1999) 102–999.

[42] T. Høien, I. Lundberg, Dyslexia: From Theory to Intervention, Kluwer Academic Publishers, Dordrecht, NL, 2000.

[43] W. Hopkins, L. Mariono, J.K. Rilling, L.A. MacGregor, Planum temporale asymmetries in great apes as revealed by magnetic resonance imaging (MRI), NeuroReport 9 (1998) 2913–2918.

[44] K. Hugdahl, Dichotic listening: probing temporal lobe functional integrity, in: R.J. Davidson, K. Hugdahl (Eds.), Brain Asymmetry, MIT Press, Cambridge, MA, 1995, pp. 123–156.

[45] K. Hugdahl, Brain lateralization: dichotic listening studies, Elsevier's Encyclopedia of Neurosciences, 2nd ed., 1999, pp. 276–279.

[46] K. Hugdahl, Lateralization of cognitive processes in the brain, Acta Psychol. 105 (2000) 211–235.

[47] K. Hugdahl, Dichotic listening in the study of auditory laterality, in: K. Hugdahl, R.J. Davidson (Eds.), The Asymmetrical Brain, MIT Press, Cambridge, MA, 2002, pp. 441–477.

[48] K. Hugdahl, L. Andersson, The "forced-attention paradigm" in dichotic listening to CV-syllables: a comparison between adults and children, Cortex 22 (1986) 417–432.

[49] K. Hugdahl, G. Carlsson, P. Uvebrant, A.J. Lundervold, Dichotic listening performance and intracarotid amobarbital injections in children/adolescent: comparisons pre- and post-operatively, Arch. Neurol. 54 (1997) 1494–1500.

[50] K. Hugdahl, E. Heiervang, H. Nordby, A.I. Smievoll, H. Steinmetz, J. Stevenson, A. Lund, Central auditory processing, MRI morphometry and brain laterality: applications to dyslexia, Scand. Audiol. 49 (1998) 26–34.

[51] K. Hugdahl, K. Brönnick, S. Kyllingsbaek, I. Law, A. Gade, O.B. Paulson, Brain activation during dichotic presentation of consonant–vowel and musical instrument stimuli: a ^{15}O-PET study, Neuropsychologia 37 (1999) 431–440.

[52] K. Hugdahl, G. Carlsson, T. Eichele, Age effects in dichotic listening to consonant–vowel syllables: interactions with attention, Dev. Neuropsychol. 20 (2001) 445–457.

[53] G.W. Hynd, M. Semrud-Clikeman, Dyslexia and brain morphology, Psychol. Bull. 106 (1987) 447–482.

[54] G.W. Hynd, M. Semrud-Clikeman, A.R. Lorys, E.S. Novey, D. Eliopulos, Brain morphology in developmental dyslexia and attention deficits disorder/hyperactivity, Arch. Neurol. 47 (1990) 919–926.

[55] A. Ide, C. Dolezal, M. Fernandez, E. Labbe, R. Mandujano, S. Montes, P. Segura, G. Verschae, P. Yarmuch, F. Aboitiz, Hemispheric differences in variability of fissural patterns in parasylvian and cingulate regions of human brains, J. Comp. Neurol. 410 (1999) 235–242.

[56] L. Jäncke, H. Steinmetz, Anatomical brain asymmetries and their relevance for functional asymmetries, in: K. Hugdahl, R.J. Davidson (Eds.), The Asymmetrical Brain, MIT Press, Cambridge, MA, 2002, pp. 187–230.

[57] L. Jäncke, G. Schlaug, Y. Huang, H. Steinmetz, Asymmetry of the planum parietale, NeuroReport 5 (1994) 1161–1163.

[58] L. Jäncke, T. Wüstenberg, H. Scheich, H.J. Heinze, Phonetic perception and the temporal cortex, NeuroImage 15 (2002) 733–746.

[59] M. Jaramillo, T. Ilvonen, T. Kujala, P. Alku, M. Tervaniemi, K. Alho, Are different kinds of acoustic features processed differently for speech and non-speech sounds? Cogn. Brain Res. 12 (2001) 459–466.

[60] N.J. Kabani, D. MacDonald, A. Evans, M. Gopnik, Neuroanatomical correlates of familial language impairment: a preliminary report, J. Neurolinguist. 10 (1997) 203–214.

[61] K. Kasai, H. Yamada, S. Kamio, K. Nakagome, A. Iwanami, M. Fukuda, K. Itoh, I. Koshida, M. Yomoto, K. Iramina, N. Kato, S. Ueno, Brain lateralization for mismatch response to across- and within-category change of vowels, NeuroReport 12 (2001) 2467–2471.

[62] J.P. Keenan, V. Thangaraj, A.R. Halpern, G. Schlaug, Absolute pitch and planum temporale, NeuroImage 14 (2001) 1402–1408.

[63] D. Kimura, Functional asymmetry of the brain in dichotic listening, Cortex 3 (1967) 163–168.

[64] T. Kujala, K. Myllyviita, M. Tervaniemi, K. Alho, J. Kallio, R. Näätänen, Basic auditory dysfunction in dyslexia as pinpointed by brain-activity measurements, Psychophysiol. Spec. Rep. 37 (2000) 262–266.

[65] T. Kujala, S. Belitz, M. Tervaniemi, R. Näätänen, Auditory sensory memory disorder in dyslexic adults, Eur. J. Neurosci. 17 (2003) 1323–1327.

[66] J.P. Larsen, T. Høien, I. Lundberg, H. Ødegaard, MRI evaluation of the size and symmetry of the planum temporale in adolescents with developmental dyslexia, Brain Lang. 39 (1990) 289–301.

[67] M. LeMay, Asymmetries of the brains and skulls of nonhuman primates, in: S.D. Glick (Ed.), Cerebral Lateralization in Nonhuman Species, Academic Press, New York, 1985, pp. 223–245.

[68] B.R. Lennox, S.B.G. Park, I. Medley, P.G. Morris, P.B. Jones, The functional anatomy of auditory hallucinations in schizophrenia, Psych. Res. 100 (2000) 13–20.

[69] L. Leonard, Facilitating linguistic skills in children with specific language impairment, Appl. Psycholinguist. 2 (1998) 89–118.

[70] C.M. Leonard, C. Puranik, J.M. Kuldau, L.J. Lombardino, Normal variation in the frequency and location of human auditory cortex landmarks. Heschl's gyrus: Where is it? Cereb. Cortex 8 (1998) 397–406.

[71] C.M. Leonard, L.J. Lomabrdino, K. Walsh, M.A. Eckert, J.L. Mockler, L.A. Rowe, S. Williams, C.B. DeBose, Anatomical risk factors that distinguish dyslexia from SLI predict reading skill in normal children, J. Commun. Disord. 35 (2002) 501–531.

[72] M. Lezak, Neuropsychological Assessment, 4th ed., Oxford Univ. Press, New York, 1994.

[73] E.M. Løberg, K. Hugdahl, M.F. Green, Hemispheric asymmetry in schizophrenia: a "dual deficits" model, Biol. Psychiatry 45 (1999) 76–81.

[74] J.C. Marshall, Planum of the apes: a case study, Brain Lang. 71 (2000) 145–148.

[75] K. Mathiak, I. Hertrich, W. Lutzenberger, H. Ackermann, Functional cerebral asymmetries of pitch processing during dichotic stimulus application: a whole-head magnetoencephalographic study, Neuropsychologia 40 (2002) 585–593.

[76] J.C. Mazziotta, M.E. Phelps, R.E. Carson, D.E. Kuhl, Tomographic mapping of human cerebral metabolism: auditory stimulation, Neurology 32 (1982) 921–937.

[77] T.A. Mondor, M.P. Bryden, The influence of attention on the dichotic REA, Neuropsychologia 29 (1991) 1179–1190.

[78] R.D. Morris, K.K. Stuebing, J.M. Føetcher, S.E. Shaywitz, G.R. Lyon, D. Shankweiler, L. Katz, D.J. Francis, Subtypes of reading disability: variability around a phonological core, J. Educ. Psychol. 90 (1998) 347–373.

[79] R. Näätänen, Attention and Brain Function, Lawrence Erlbaum Publishers, Hillsdale, NJ, 1992.

[80] R. Näätänen, The perception of speech sounds by the human brain as reflected by the mismatch negativity (MMN) and its magnetic equivalent (MMNm), Psychophysiology 38 (2001) 1–21.

[81] R. Näätänen, A. Lehtokoski, M. Lennes, M. Cheour, M. Huotilainen, A. Iivonen, M. Vainio, P. Alku, R.J. Ilmoniemi, A. Luuk, J. Allik, J. Sinkkonen, K. Alho, Language-specific phoneme representations revealed by electric and magnetic brain responses, Nature 385 (1997) 432–434.

[82] G.F. Neckelman, K. Specht, A.I. Smievoll, A. Lundervold, L. Ersland, R. Barndon, H. Gundersen, J. Iversen, A. Lund, B. Rund, K. Hugdahl, Left temporal lobe reduction in grey matter in schizophrenia: an MRI voxel-based morphometry study, Poster presented at the VIII Annual Meeting of the Organization for Human Brain Mapping, Japan, 2002.

[83] R.K. Olson, J.J. Gillis, J.P. Rack, J.C. DeFries, D.W. Fulker, Confirmatory factor analysis of word recognition and process measures in the Colorado Reading Project, Read. Writ. 3 (1991) 235–248.

[84] B. Opitz, A. Mecklinger, A.D. Friederici, D.Y. von Cramon, The functional neuroanatomy of novelty processing: integrating ERP and fMRI results, Cereb. Cortex 9 (1999) 379–391.

[85] B. Opitz, A. Mecklinger, D.Y. von Cramon, F. Kruggel, Combining electrophysiological and hemodynamic measures of the auditory oddball, Psychophysiology 36 (1999) 142–147.

[86] B. Opitz, T. Rinne, A. Mecklinger, D.Y. von Cramon, E. Schröger, Differential contribution of frontal and temporal cortices to auditory change detection: fMRI and ERP results, NeuroImage 15 (2002) 167–174.

[87] S. Orton, Reading, Writing, and Speech Problems in Children, Norton, New York, 1937.

[88] V.B. Penhune, R.J. Zatorre, J.D. MacDonald, A.C. Evans, Interhemispheric anatomical differences in human primary auditory cortex: probabilistic mapping and volume measurement from magnetic resonance scans, Cereb. Cortex 6 (1996) 661–672.

[89] R.A. Pfeifer, Pathologie der hörstahlumg und der cortikalen hörsphere, in: O. Bumke, O. Förster (Eds.), Handbuch der Neurologie, Springer-Verlag, Berlin, 1936.

[90] D. Poeppel, Pure word deafness and the bilateral processing of the speech code, Cogn. Sci. 25 (2001) 679–693.

[91] S. Pollmann, M. Mærtens, D.Y. von Cramon, J. Lepsien, K. Hugdahl, Dichotic listening in patients with splenial and nonsplenial callosal lesions, Neuropsychology 16 (2002) 56–64.

[92] J. Rademacher, V.S. Caviness, H. Steinmetz, A.M. Galaburda, Topographical variation of the human primary cortices: implications for neuroimaging, brain mapping and neurobiology, Cereb. Cortex 3 (1993) 313–329.

[93] J.O. Rauschecker, B. Tian, Mechanisms and streams for processing of "what" and "where" in auditory cortex, Proc. Natl. Acad. Sci. U. S. A. 97 (2000) 11800–11806.

[94] T. Rinne, K. Alho, P. Alku, M. Holi, J. Sinkkonen, J. Virtanen, O. Bertrand, R. Näätänen, Analysis of speech sounds is left-hemisphere predominant at 100–150 ms after sound onset, NeuroReport 10 (1999) 1113–1117.

[95] T. Rinne, K. Alho, R.J. Ilmoniemi, J. Virtanen, R. Näätänen, Separate time behaviors of the temporal and frontal mismatch negativity sources, NeuroImage 12 (2000) 14–19.

[96] M. Sams, P. Paavilainen, K. Alho, R. Näätänen, Auditory frequency discrimination and event-related potentials, Electroencephalogr. Clin. Neurophysiol. 62 (1985) 437–448.

[97] G. Schlaug, L. Jäncke, Y. Huang, H. Steinmetz, In vivo evidence of structural brain asymmetry in musicians, Science 267 (1995) 699–701.

[98] S.K. Scott, A.W. Young, A.J. Calder, D.J. Hellawell, J.P. Aggleton, M. Johnson, Impaired auditory recognition of fear and anger following bilateral amygdala lesions, Nature 385 (1997) 254–257.

[99] J. Shapleske, S.L. Rossell, P.W. Woodruff, A.S. David, The planum temporale: a systematic, quantitative review of its structural, functional and clinical significance, Brain Res. Rev. 29 (1999) 26–49.

[100] Y. Shtyrov, T. Kujala, J. Ahveninen, M. Tervaniemi, P. Alku, R. Ilmoniemi, R. Näätänen, Noise-induced shift in hemispheric lateralization of speech processing, Neurosci. Lett. 251 (1998) 141–144.

[101] Y. Shtyrov, T. Kujala, R.J. Ilmoniemi, R. Näätänen, Noise affects speech-signal processing differently in the cerebral hemispheres, NeuroReport 10 (2000) 2189–2192.

[102] Y. Shtyrov, T. Kujala, S. Palva, R.J. Ilmoniemi, R. Näätänen, Discrimination of speech and of complex non-speech sounds of different temporal structure in the left and right cerebral hemispheres, NeuroImage 12 (2000) 657–663.

[103] H. Steinmetz, J. Rademacher, Y. Huang, H. Hefter, K. Zilles, A. Thron, H.J. Freund, Cerebral asymmetry: MR planimetry of the human planum temporale, J. Comput. Assist. Tomogr. 13 (1989) 996–1005.

[104] H. Steinmetz, J. Volkmann, L. Jäncke, H.J. Freund, Anatomical left–right asymmetry of language-related temporal cortex is different in left-handers, Ann. Neurol. 29 (1991) 315–319.

[105] J. Talairach, P. Tournoux, Co-planar Stereotaxic Atlas of the Human Brain. 3-D Proportional System: An Approach to Cerebral Imaging, Georg Thieme Verlag, Stuttgart, 1988.

[106] P. Tallal, Auditory temporal perception, phonetics, and reading disabilities in children, Brain Lang. 9 (1980) 182–198.

[107] P. Tallal, M. Piercy, Developmental aphasia: impaired rate of non-verbal processing as a function of sensory modality, Neuropsychologia 11 (1973) 389–398.

[108] P. Tallal, R. Ross, S. Curtiss, Familial aggregation in specific language impairment, J. Speech Hear. Disord. 54 (1989) 167–173.

[109] M. Tervaniemi, A. Kujala, K. Alho, J. Virtanen, R.J. Ilmoniemi, R. Näätänen, Functional specialization of the human auditory cortex in processing phonetic and musical sounds: a magnetoencephalographic (MEG) study, NeuroImage 9 (1999) 330–336.

[110] M. Tervaniemi, S.V. Medvedev, K. Alho, S.V. Pakhomov, M.S. Roudas, T.L. van Zuijen, R. Näätänen, Lateralized automatic auditory processing of phonetic versus musical information: a PET study, Hum. Brain Mapp. 10 (2000) 74–79.

[111] J. Tiihonen, H. Katila, E. Pekkonen, I.P. Jääskeläinen, M. Huotilainen, H.J. Aronen, R.J. Ilmoniemi, P. Räsänen, J. Virtanen, E. Salli, J. Karhu, Reversal of cerebral asymmetry in schizophrenia measured with magnetoencephalography, Schizophr. Res. 30 (1998) 209–219.

[112] H. Tiitinen, P. May, K. Reinikainen, R. Näätänen, Attentive novelty detection in humans is governed by pre-attentive sensory memory, Nature 372 (1994) 90–92.

[113] A.W. Toga, P.M. Thompson, Mapping brain asymmetry, Nat. Neurosci. Rev. 4 (2003) 37–48.

[114] L.G. Ungerleider, M. Mishkin, Two cortical visual systems, in: D.J. Ingle, M.A. Goodale, R.J.W. Mansfield (Eds.), Analysis of Visual Behavior, MIT Press, Cambridge, MA, 1982.

[115] C. von Economo, L. Horn, Über Windungsrelief, Masse und Rindenarchitektonoik der Supratemporalfläche, ihre individuellen und ihren Seitnunterschiede, Z. Neurol. Psychiatrie 130 (1930) 678–757.

[116] J. Wada, T. Rasmussen, Intracarotid injections of sodium amytal for the lateralization of cerebral speech dominance, J. Neurosurg. 17 (1960) 266–282.

[117] J.D. Warren, B.A. Zielinski, G.G.R. Green, J.P. Rauschecker, T.D. Griffiths, Perception of sound-source motion by the human brain, Neuron 34 (2002) 139–148.

[118] C. Wernicke, Der aphasische symptomencomplex: eine psychologische studie auf anatomischer basis, in: G.H. Eggert (Ed.), English Translation in Wernicke's Works on Aphasia, A Sourcebook and Review, Mouton Publishers, The Hague, 1874, 1977.

[119] C.F. Westbury, R.J. Zatorre, A.C. Evans, Quantifying variability in the planum temporale: a probability map, Cereb. Cortex 9 (1999) 392–405.

[120] R.J. Zatorre, Neural specializations for tonal processing, Ann. N.Y. Acad. Sci. 930 (2001) 193–210.

[121] R.J. Zatorre, P. Belin, Spectral and temporal processing in human auditory cortex, Cereb. Cortex 11 (2001) 946–953.

[122] R.J. Zatorre, A.C. Evans, E. Meyer, A. Gjedde, Lateralization of phonetic and pitch discrimination in speech processing, Science 256 (1992) 846–849.

[123] R.J. Zatorre, D.W. Perry, C.A. Beckett, C.F. Westbury, A.C. Evans, Functional anatomy of musical processing in listeners with absolute pitch and relative pitch, Proc. Natl. Acad. Sci. U. S. A. 95 (1998) 3172–3177.

[124] R.J. Zatorre, P. Belin, V. Penhune, Structure and function of auditory cortex: music and speech, Trends Cogn. Sci. 6 (2002) 37–46.

[125] R.J. Zatorre, M. Bouffard, P. Ahad, P. Belin, Where is ‘where’ in the human auditory cortex, Nat. Neurosci. 5 (2002) 905–909.