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Functional specificity in the right human auditory cortex for perceiving pitch direction

Ingrid S. Johnsrude,[1] Virginia B. Penhune[2] and Robert J. Zatorre[2]

[1]*Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK,* [2]*Neuropsychology/Cognitive Neuroscience Unit, Montreal Neurological Institute, McGill University, Montreal, Canada*

Correspondence to: Ingrid S. Johnsrude, Wellcome Department of Cognitive Neurology, Institute of Neurology, 12 Queen Square, London WC1N 3BG, UK
E-mail: ingrid@fil.ion.ucl.ac.uk

Summary

Previous lesion and functional imaging studies in humans suggest a greater involvement of right rather than left auditory cortical areas in certain aspects of pitch processing. In the present study, adaptive psychophysical procedures were used to determine auditory perceptual thresholds in 14 neurologically normal subjects, and in 31 patients who had undergone surgical resection from either the right or left temporal lobe for the relief of intractable epilepsy. In a subset of the patients, the lesion encroached significantly upon the gyrus of Heschl or its underlying white matter as determined from MRI analysis. Subjects were asked to perform two different perceptual tasks on the same set of stimuli. In a pitch discrimination task, the subject had to decide whether two elements of a pure tone pair were the same or different. In a task requiring the judgement of direction of pitch change, subjects decided whether pitch rose or fell from the first tone to the second. Thresholds were determined by measuring the minimum pitch difference required for correct task performance. Mean thresholds in the pitch discrimination task did not differ between patient groups and control subjects. In contrast, patients with temporal lobe excisions that encroached upon the gyrus of Heschl in the right hemisphere (but not in the left) showed significantly elevated thresholds when judging the direction of pitch change. These findings support a specialization of function linked to right auditory cortical areas for the processing of pitch direction, and specifically suggest a dissociation between simple sensory discrimination and higher order perception.

Keywords: auditory cortex; hearing; hemispheric specialization; music; pitch

Abbreviations: HG = first transverse gyrus of Heschl; LTa/RTa = small removal from auditory regions from left or right hemisphere, respectively; LTA/RTA = large removal from auditory regions from left or right hemisphere, respectively

Introduction

A considerable amount of neuropsychological evidence and functional imaging data support the idea that structures within the human right hemisphere are specialized for at least some aspects of pitch processing (Milner, 1962; Divenyi and Robinson, 1989; Peretz, 1990; Zatorre and Samson, 1991; Zatorre *et al.*, 1992, 1994). In particular, studies requiring various types of spectral pattern analysis yield consistent evidence supporting a right hemisphere prepotency. For example, Zatorre found that patients with surgical excisions of the right, but not the left, auditory cortex are impaired at perceiving the pitch of complex tones with a missing fundamental (Zatorre, 1988). Similarly, patients with right but not left hemisphere vascular lesions were impaired on tasks requiring processing of complex spectral structure (Sidtis and Volpe, 1988; Robin *et al.*, 1990). Timbre discrimination tasks, in which discrimination must be based on harmonic structure, have also yielded similar evidence (Milner, 1962; Samson and Zatorre, 1994; Paquette and Peretz, 1997).

Discrimination of melodic pitch patterns is also generally more affected by damage to the right than to the left superior temporal area (Milner, 1962; Zatorre, 1985; Samson and Zatorre, 1988; Liégeois-Chauvel *et al.*, 1998), although much more severe deficits are observed after bilateral damage (Peretz *et al.*, 1994). Simple frequency discrimination, on the other hand, does not appear to involve right hemisphere cortical mechanisms preferentially. Unilateral excisions from primary and anterior secondary auditory cortex appear to affect such discrimination minimally or not at all (Milner, 1962; Berlin *et al.*, 1965; Zatorre, 1988; Zatorre and Samson, 1991), and this is consistent with studies showing that even large bilateral lesions of auditory cortex do not generally result in a permanent impairment on tests of simple frequency discrimination in humans (Peretz *et al.*, 1994) or other mammals (Meyer and Woolsey, 1952; Butler *et al.*, 1957; Wegener, 1964; Cranford *et al.*, 1976; Whitfield, 1980).

Thus, the current evidence suggests that the right auditory cortex is most important for specific types of pitch processing: either when the acoustic stimuli are complex (as in the missing fundamental task) or when the task itself is complex, or both (as in melodic discrimination tasks). If this generalization is correct, then certain specific cortical lesions might result in a dissociation between simple frequency discrimination and discrimination under more complex conditions, i.e. when the stimuli are acoustically simple, but the task requires some cognitive computation. The purpose of the present study was to test this prediction. In particular, we compared a simple frequency discrimination task with a task requiring the judgement of pitch direction, using an adaptive psychophysical procedure (Levitt, 1971) that should be optimally sensitive to impairment. Unlike simple frequency discrimination, pitch direction judgement requires sequential analysis and the perception of relative pitch, which we assume are higher order perceptual phenomena. An additional important goal of this study was to determine to what degree the primary auditory cortex or closely adjacent regions are implicated in the performance of these tasks. For this purpose, we tested patients with unilateral excisions extending into or sparing the lateral portion of the gyrus of Heschl, as determined from detailed quantitative lesion analysis using MRI (Penhune *et al.*, 1999).

Material and methods

Subjects

Each of the 31 patients who participated in this experiment had undergone surgical removal of brain tissue at the Montreal Neurological Hospital. These operations had been performed to relieve pharmacologically intractable seizures. In the majority of cases, the cause of the seizures was focal cerebral atrophy dating from birth or early life, although three cases of benign tumour (two developmental) were included. Patients with malignant tumours were excluded, as were those for whom there was evidence of cerebral damage other than the identified lesion. In addition, patients with language represented either wholly or partially in the right cerebral hemisphere, as determined by preoperative sodium amobarbital studies (Wada and Rasmussen, 1960; Branch *et al.*, 1964), were excluded from the experiment, as were those patients obtaining full scale IQ ratings below 75 on the WAIS-R (Wechsler Adult Intelligence Scale—Revised). The Ethics Committee of the Montreal Neurological Institute approved the experimental protocol, and written informed consent was obtained from all subjects before testing.

Lesion site and extent were examined on postoperative MRI scans, which were available for all but two patients (for whom surgical reports were used to judge the size and location of each excision). MRI scans were obtained on a Philips Gyroscan system with a 1.5 T superconducting magnet using a 3D FFE (fast field echo) acquisition sequence to collect 160 contiguous 1 mm T_1-weighted images in the sagittal plane [TR (repetition time) = 18 ms, TE (echo time) = 10 ms]. The lesion in all patients included the amygdala, uncus and temporal polar neocortex in one hemisphere. The extent of the resection along the hippocampus and parahippocampal gyrus varied from patient to patient, as did the extent of the lateral neocortical excision along the Sylvian fissure, the second temporal gyrus and the base of the temporal lobe. Patients were assigned to four different groups, based on the side of their excision (left, LT; right, RT) and the degree to which auditory cortices were included in the removal. The medial two-thirds of the first transverse temporal gyrus of Heschl was taken as the approximate location of the primary auditory cortex (Rademacher *et al.*, 1993; Penhune *et al.*, 1996), and secondary auditory regions were assumed to surround this location (Pandya and Sanides, 1973; Galaburda and Sanides, 1980; Rademacher *et al.*, 1996). If the first transverse gyrus of Heschl (HG) was encroached upon (either undercut or excised), the patient was classified as having a large removal from auditory regions (LTA or RTA). If the resection stopped anterior to the most lateral aspect of the HG, the patient was classified as having a small removal from auditory regions (LTa or RTa). Twelve patients were classified as LTa, six patients as RTa, five patients as LTA and eight as RTA. All patients were tested >3 months after their surgery. Fourteen neurologically normal control participants, matched to the patients with respect to age and level of education, were also tested (see Table 1 for demographic details of these five groups).

The extent of the lesions was quantified in the following manner. MR scans were linearly transformed into stereotaxic space (Talairach and Tournoux, 1988), and viewed using REGISTER, an interactive three-dimensional imaging software package (J. D. MacDonald, Brain Imaging Centre, Montreal Neurological Institute, Montreal) that allowed the individual scans to be viewed simultaneously in the coronal, horizontal and sagittal planes of section. The patients' scans were then co-registered with a probabilistic anatomical map of the gyrus of Heschl derived from MRI scans of normal subjects (Penhune *et al.*, 1996). Estimation of the extent of both excision and undercutting was made by finding the most anterior plane of section in each scan where the gyrus of Heschl had been removed or undercut, identifying these locations in stereotaxic space, and comparing these planes with the map. The probability maps (left and right) were scaled to show the region of 25–100% probability and were divided antero-posteriorly into 10 equal length segments, corresponding to a 0–10% resection, a 10–20% resection, etc. The posterior limit of resection and of undercutting was located within one of these intervals for each patient. Figure 1 outlines the method of classification using one RTA subject as an example, and Table 2 gives the extent of the lesion in the gyrus of Heschl in the LTA and RTA patients. For a more complete description of the lesion quantification procedure,

Table 1 *Demographic information about participants*

Group		No.	Handedness		Sex		Age (years)		Education (years)	
			R	L	M	F	Mean	Range	Mean	Range
Normal control	NC	14	12	2	6	8	29.2	20–52	14.1	10–17
Left temporal	LTa	12	11	1	9	3	36.7	26–48	13.8	11–18
Left HG resection	LTA	5	5	0	4	1	35.6	28–47	13.0	12–15
Right temporal	RTa	6	6	0	4	2	33.7	22–49	11.0	6–14
Right HG resection	RTA	8	8	0	3	5	41.5	33–53	12.4	9–18

HG = first transverse gyrus of Heschl; R = right; L = left.

see Penhune *et al.* (Penhune *et al.,* 1999). None of the patients had a complete removal of the gyrus of Heschl, and the lesion was limited to undercutting in some patients. Furthermore, as a result of surgeons' concern for language function, the extent of the resection along the sylvian fissure tended to be smaller in the left hemisphere than in the right; this was also true for the patients in whom the gyrus of Heschl was spared (LTa and RTa).

Stimuli

Stimuli were 201 pure tones of 100 ms at all integer frequencies between 1000 and 1200 Hz inclusive, synthesized using the MITSYN system (Henke, 1976) running on an IBM-compatible computer. The test routines were all programmed using MAPLE software and were administered via computer in a sound-attenuated room, through a TASCAM (www.tascam.com) M-06 amplifier and Telephonics (www.telephonics.com) TDH-39 earphones. All stimuli were equalized for intensity according to their root-mean-square amplitude, and presented at a comfortable intensity of 73–77 dB sound pressure level (A), as measured at the headphone via a sound pressure meter.

Procedure

There were two tasks, simple discrimination and pitch direction judgement, performed in that order. Difference thresholds were determined by using a two-alternative forced choice within an adaptive 'staircase' psychophysical paradigm (Levitt, 1971; Divenyi and Robinson, 1989). In both tests, two tones were presented successively in each trial and the subject was required to make a binary decision about them. In simple discrimination, participants had to decide whether the two elements were at the same pitch or were different, whereas in pitch direction judgement, participants were asked to decide whether the first tone was higher or lower in frequency than the second one (Fig. 2). Participants indicated their choice by pressing one of two keys on a computer keyboard with their right hand. In both tasks, both responses had an equal probability of being correct on every trial. This was done to reduce demand artefact. The pairs of sounds were presented with an interstimulus interval of 850 ms and an intertrial interval of 1 s (measured from the subject's response to the onset of the next stimulus pair).

Simple discrimination

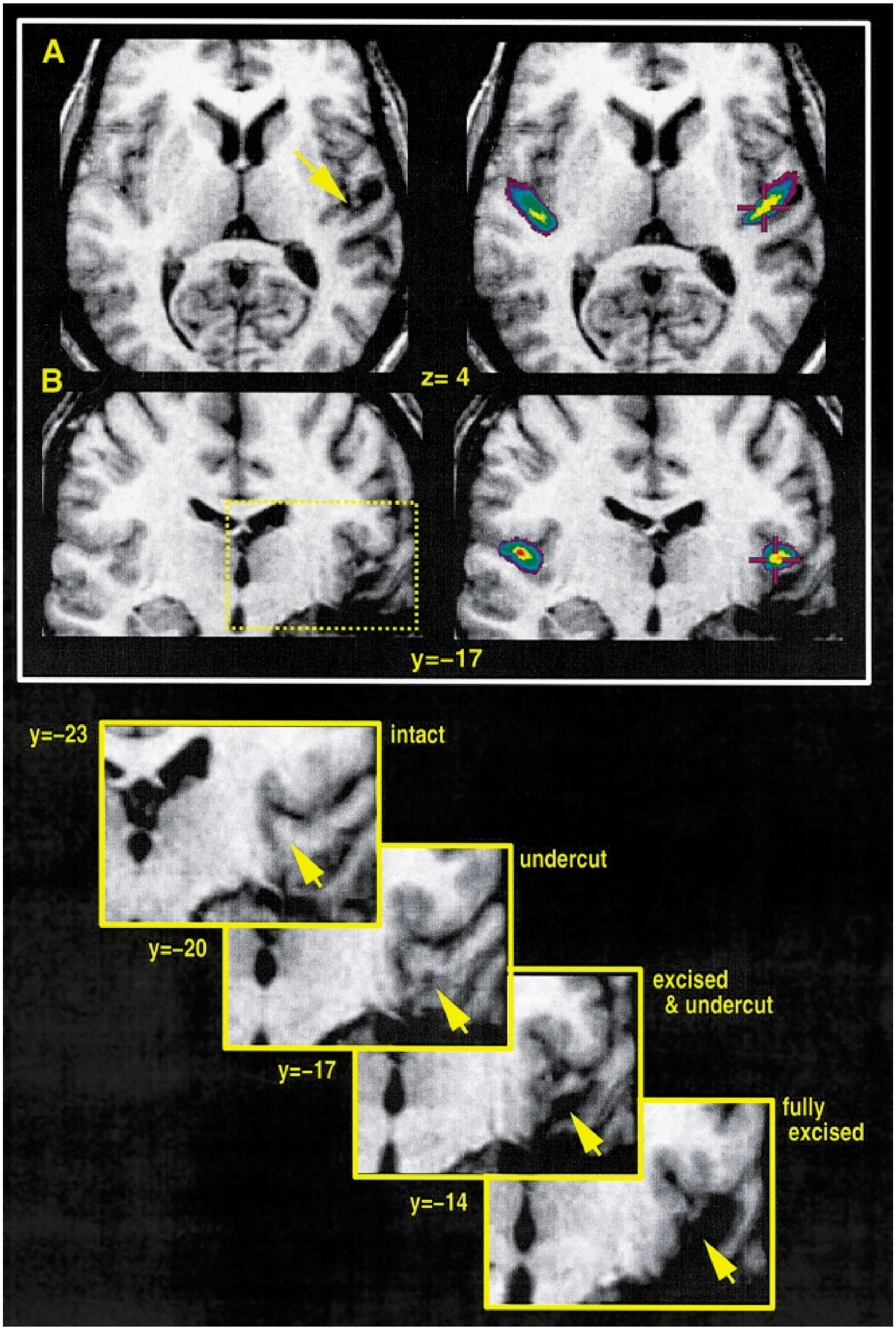
On half of the trials (randomly selected), both elements were at 1000 Hz, and thus there was no pitch difference. These trials did not count in the psychophysical procedure. On the other half of the trials, the first element of the pair was 1000 Hz (the comparison tone) and the second element was higher. The starting pitch difference between the two tones of the stimulus pair was 200 Hz, which is large enough to elicit a correct response in the large majority of listeners. The rule of the adaptive procedure was to decrease the difference in pitch between the two tones of a trial after two correct responses on successive non-zero pitch difference trials (referred to as descending trials) and increase it after one (ascending trials). The initial step size was 20%, increasing to 50% after the first error. The test was terminated after six reversals between descending and ascending trials. The series of trials between successive reversals is called a 'run'. Thresholds were calculated by averaging the midpoints of either the last two ascending runs or the last two descending runs for each subject on each task.

Pitch direction judgement

The procedure in this task was identical to that just described, except that the two tones of all stimulus pairs were always at different frequencies, and the 1000 Hz 'comparison' tone was presented first on half of the trials (randomly selected) and second on the other half. As in simple discrimination, the starting pitch difference between the two tones was 200 Hz, and this pitch difference changed on subsequent trials according to the performance of the subject. Pitch difference thresholds for this task were calculated in the same way as for simple discrimination.

Results

Threshold means and standard errors across groups are shown in Fig. 3. A two-way repeated measures ANOVA (analysis of variance) including the factors condition (simple or directional task) and group (one control and four patient groups) revealed a significant interaction between the two factors, $F(4, 40) = 8.21$, $P < 0.0001$. There was no difference among the groups on thresholds obtained in the pitch discrimination task, $F(4, 40) = 0.27$, $P > 0.10$, but there was a highly significant difference among groups on thresholds obtained in the pitch direction task, $F(4, 40) = 18.86$, $P < 0.00001$. *Post hoc*



Newman–Keuls tests showed that thresholds in the RTA group were higher than in all other groups: LTA, $Q(10, 40) = 11.6$, $P < 0.01$; LTa, $Q(4, 40) = 9.08$, $P < 0.01$; normal control, $Q(3, 40) = 8.61$, $P < 0.01$; RTa, $Q(2, 40) = 6.72$, $P < 0.01$. Although LTAs appeared to have somewhat lower thresholds than normal control subjects, this effect was not significant.

Given that the sample sizes were relatively small, we conducted non-parametric Kruskal–Wallis tests to verify that there was no effect of group on simple pitch discrimination thresholds, $\chi^2(4) = 4.49$, $P > 0.1$, and that there was an effect of group on pitch direction thresholds, $\chi^2(4) = 12.42$, $P = 0.014$. This latter effect was analysed further using Mann–Whitney *U* tests, which yielded a pattern of significance essentially identical to that observed in the Newman–Keuls tests.

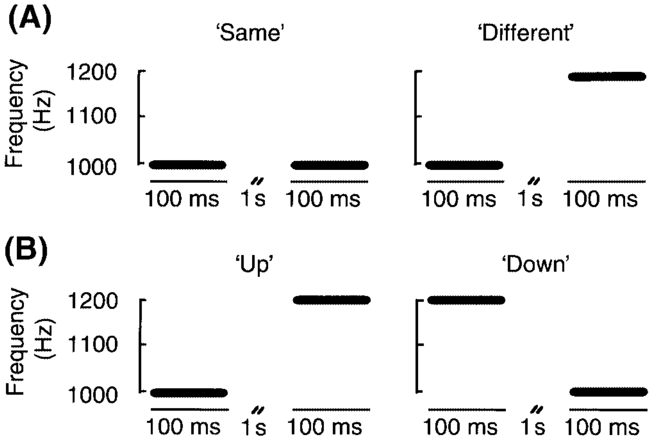


Fig. 2 (**A**) The two possible starting trials for the simple discrimination task are illustrated. Correct performance on two consecutive 'Different' trials (identifying the two tones as different in pitch) resulted in a decrease in the frequency difference between the two tones on the next 'Different' trial, whereas a single error on such trials resulted in an increase in the frequency difference on the next 'Different' trial, according to the adaptive rule described in the text. (**B**) The two possible starting trials for the pitch direction task. In this task, correct performance on two consecutive trials (correctly identifying the direction of the pitch change) resulted in a decrease in the frequency difference between the two tones of a stimulus pair on the next trial, whereas an error resulted in an increased frequency difference between these two items, according to the adaptive rule described in the text.

Although pitch direction thresholds appeared to be slightly higher than same–different thresholds in normal control, LTa and RTa groups, these differences were not statistically significant. When we compared thresholds on the two tasks within groups, only the RTA group showed a significant difference in threshold between the two tasks, $Q(6, 40) = 9.29$, $P < 0.01$). The same pattern of results was obtained using a non-parametric (Wilcoxon matched-pair signed-rank) test. This is evident in the individual data, shown in Fig. 4. Whereas five of the eight subjects in the RTA group obtained a difference between the two thresholds which was >75 Hz, none of the subjects in any of the other groups did. Figure 5 presents the psychophysical curves obtained on the two tasks by the eight subjects in the RTA group. As may be seen in this figure, all RTA patients demonstrated normal convergence towards the threshold frequency on the simple task, whereas all but one demonstrated abnormally high thresholds on the directional task; note, however, that only one subject was unable to perform the directional task at the highest threshold (200 Hz), whereas all the others did converge on a lower final value.

We attempted to correlate the psychophysical threshold on the pitch direction judgement task with the magnitude of damage to the auditory cortex in the RTA group, but found

Table 2 *Details of the extent of undercutting and excision observed in the first transverse gyrus of Heschl (HG) in the left and right hemispheres in LTA and RTA patients*

Patient	% HG excised	% HG undercut
Left hemisphere		
LT 1	0	10–20
LT 2	0	10–20
LT 3	0	40–50
LT 4	20–30	30–40
LT 5	40–50	50–60
Right hemisphere		
RT 1	0	40–50
RT 2	0	20–30
RT 3	50–60	60–70
RT 4	30–40	60–70
RT 5	20–30	40–50
RT 6	20–30	40–50
RT 7	40–50	50–60
RT 8	80–90	90–100

Fig. 1 The upper panel illustrates the MRI scan of a patient with a large removal from the right auditory region: the excision includes the anterolateral 50–60% and the undercutting extends to 60–70%. The scan is presented in the horizontal (**A**, $z = 4$) and coronal (**B**, $y = -17$) planes of section. The images on the left show the patient's scan alone with an arrow indicating the region of excision/undercutting. The images on the right show the patient's scan co-registered with a probabilistic map of the HG, which has been scaled to show the voxels that have a 25% or greater probability of being in gyrus of Heschl (Penhune *et al.*, 1996). The cursor indicates the same position in standardized space as the arrow. The yellow box on the coronal section indicates the region of the removal pictured in close-up in the lower panel. The lower panel shows four close-up views of the same scan, illustrating the transition from intact, to undercut, to fully excised tissue (coronal sections taken at 3 mm intervals). Arrows indicate the location of gyrus of Heschl. In the section labelled 'undercut', note the very thin band of white matter connecting the remaining portion of HG to the rest of the brain. In the section labelled 'excised and undercut', note the unexcised strip of presumed grey matter tissue.

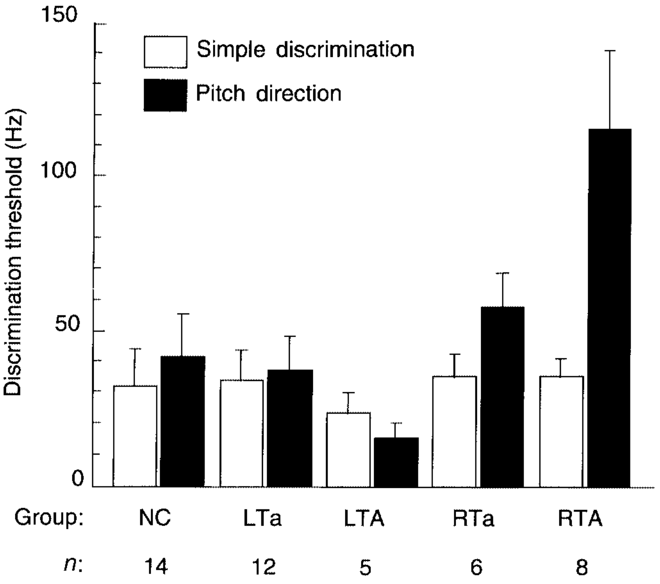


Fig. 3 Mean frequency difference discrimination thresholds (+ standard error) observed in the five groups. The simple discrimination thresholds were not different across the groups. Thresholds in the pitch direction task were significantly higher in the RTA group than in any of the other groups. NC = normal control.

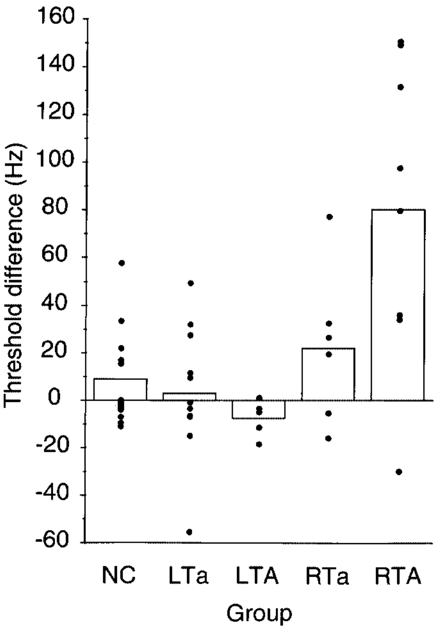


Fig. 4 Difference between pitch direction threshold and simple discrimination thresholds (pitch direction minus simple discrimination). The bars give the average threshold difference for each group, and individual data are superimposed upon these. NC = normal control.

no significant association. Although the patient with the largest removal also had the highest threshold, the patients with the next highest thresholds were among those with smaller excisions.

Discussion

Patients with right temporal lobe excisions that encroached upon HG demonstrated higher thresholds for determining the direction of pitch change than did controls, or patients with left temporal lobe removals. In sharp contrast, their thresholds for simple discrimination were similar to those obtained by normal control subjects. This dissociation is particularly striking since the stimuli and mnemonic demands were precisely the same in both tasks. Thus, for patients in the RTA group, there exists a region of frequency difference within which they are able to say that two tones are different, but are unable to determine which of the two is lower or higher in pitch. It is important to note that this deficit depends on the magnitude of the pitch difference between the two tones, since all but one of the RTA patients were able to perform the task at higher threshold values.

A variety of cytoarchitectonic studies support the conclusion that the human primary auditory cortex (koniocortex) occupies the medial portion of HG in both hemispheres (Galaburda and Sanides, 1980; Rademacher *et al.*, 1993, 1996; Morosan *et al.*, 1996). The primary cortices are largely co-extensive with the primary auditory region as defined physiologically in several species including humans (Woolsey and Walzl, 1942; Merzenich and Brugge, 1973; Celesia, 1976; Hendry *et al.*, 1990; Liégeois-Chauvel *et al.*, 1991; Morel *et al.*, 1993). This primary region is surrounded by a number of interconnected cortical fields (Galaburda and Sanides, 1980; Kaas and Hackett, 1998; Pandya and Sanides, 1972; Pandya and Seltzer, 1982; Seldon, 1985; Rademacher *et al.*, 1996), that are also tonotopically organized (Merzenich and Brugge, 1973; Morel *et al.*, 1993; Rauschecker *et al.*, 1995; Talavage *et al.*, 1997; Rauschecker, 1998). The temporal lobe excisions of all the patients in the current study would have encroached upon some of the more anterior auditory fields in the superior temporal gyrus, irrespective of the encroachment upon HG, which is perhaps why patients in the RTa group also tended to have slightly higher thresholds than normal on the pitch direction task. Additionally, the resections in most of the RTA patients were restricted primarily to the anterolateral portion of HG, and so probably did not encroach much upon the primary cortical area corresponding to AI in the monkey. Nonetheless, it was only when the lateral edge of HG was excised or undercut that significant impairments were observed. The expression of the deficit in pitch direction judgement would thus appear to depend upon damage to secondary auditory cortices near the lateral edge of the right HG, perhaps corresponding to field R in the macaque (Morel *et al.*, 1993; Rauschecker *et al.*, 1997), and not necessarily upon damage to AI. Given that previous studies have demonstrated tonotopicity in the gyrus of Heschl, with low tones represented laterally and high tones medially (see, for example, Talavage *et al.*, 1997), it is possible that these subjects would have exhibited lower thresholds on the pitch direction judgement task if they had been tested on higher frequencies.

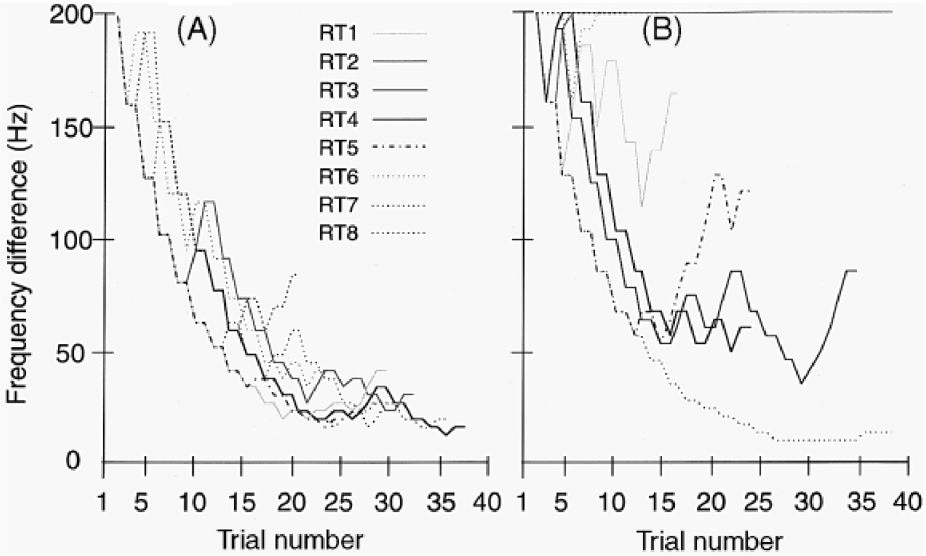


Fig. 5 Psychophysical curves observed in the eight patients with right temporal lobe lesions encroaching upon gyrus of Heschl (RTA group). (**A**) Simple discrimination. (**B**) Pitch direction judgement. Thresholds on the pitch direction task were significantly higher than thresholds on the simple discrimination task in this group only.

Although damage to auditory cortical areas was, in general, less extensive in the left hemisphere than in the right in our population, this fact by itself is not sufficient to explain why the left temporal lobe groups were not impaired. Resections in three of the LTa patients extended to a point just anterior to HG, and, in at least three of the LTA patients, probably encroached upon the primary auditory cortex. Yet no impairment was evident in any individual within these groups. The effect thus appears to represent a clear demonstration of functional hemispheric specialization.

Several prior lesion studies (Milner, 1962; Samson and Zatorre, 1988; Zatorre, 1985; Liégeois-Chauvel *et al.*, 1998) have shown that patients with right superior temporal resections are impaired at using pitch contour information to discriminate between two short melodies. Pitch contour extraction requires the accurate encoding and sequencing of a succession of changes in the direction of pitch. The pitch direction task that we employed in the current study is therefore the simplest case of a contour perception task. Most of the previous studies on melodic discrimination have reported greater deficits for patients whose excisions extend more posteriorly along the right superior temporal gyrus, perhaps because melodic perception depends critically on computations of pitch direction such as were assessed here. Most of these studies, however, also report significant deficits even for anterior lesions, unlike our findings in the RTa group. This discrepancy could reflect the greater cognitive demands involved in assembling multiple pitch changes into an abstract representation of melodic contour, which may require additional processing from cortical fields in the anterior portion of the right superior temporal region. The latter conclusion is also consistent with functional imaging studies, which have reported that regions in the right superior temporal gyrus outside of the primary auditory cortex are active when subjects perceive melodic stimuli (Binder *et al.*, 1997; Zatorre *et al.*, 1994).

The finding of normal thresholds for simple pitch discrimination in all patient groups is consistent with previous work on patients with unilateral temporal lobe resections (Milner, 1962; Berlin *et al.*, 1965), and with studies showing that even large bilateral lesions of the auditory cortex do not necessarily result in a permanent impairment on tests of simple frequency discrimination in humans or other mammals (Meyer and Woolsey, 1952; Butler *et al.*, 1957; Wegener, 1964; Cranford *et al.*, 1976; Whitfield, 1980; Peretz *et al.*, 1994). Although such lesions in animals can destroy learned discriminations of simple tones, discriminative ability is restored by retraining (Butler *et al.*, 1957; Whitfield, 1980). Since most of the patients were tested several years after their surgery, any transient disruption in simple frequency discrimination would have had ample time to clear.

We were unable to document any relationship between lesion extent and performance in the affected (RTA) group. Large intersubject variability, in addition to a small sample size, probably contribute to masking any existing relationship between the magnitude of the deficit and the extent of the lesion. Furthermore, the procedure we used for estimating the degrees of excision and undercutting is limited to determining lesion extent and cannot take into account individual variability in the functional importance of the cortex and white matter tracts affected by each patient's lesion.

The principal finding in the present study, the dissociation between simple pitch discrimination and pitch direction judgements, has several important implications. First, in accord with the hypothesis that functional differences exist between cortical regions, it suggests that certain rather subtle aspects of pitch processing depend differentially on the integrity of specific subregions within the auditory cortex.

These findings indicate the necessity of carefully defining the cognitive processes required for the performance of any given task, as well as the importance of obtaining objective estimates of the precise areas damaged.

Secondly, the results are in accord with the postulated generalization that areas of secondary cortex surrounding primary regions may be responsible for more complex aspects of perceptual processing. Specifically, the region of the right auditory cortex in the lateral portion of HG would appear to be involved in assigning a spectral order to pitch information, which itself may be extracted at a prior stage. It is this aspect of the cognitive representation of pitch that specifically appears to be disturbed in the RTA patients. We speculate that the tonotopically organized fields that are known to exist in this area may play a role in representing pitch by assigning direction across successive elements of a melody based on the frequency of these elements within an organized scheme. This conclusion is consistent with single unit data recorded from AI and AII in the cat (McKenna *et al.*, 1989), and lateral belt areas in the monkey (Rauschecker, 1998), indicating differential responses to direction of pitch change.

Thirdly, and also in accord with considerable prior lesion and imaging data, the data from the present study indicate that important differences exist in the functional specialization of the right and left auditory cortical regions. The processing of pitch information appears to depend preferentially on right hemisphere mechanisms, which may be complementary to left hemisphere mechanisms for the processing of speech sounds. However, this functional specialization seems to be relative, not absolute, since all but one RTA patient succeeded in performing the pitch direction task, albeit at a much higher threshold than normal. This phenomenon could arise if pitch representation were coarser in left auditory cortical areas compared with equivalent areas on the right. According to this conjecture, patients with RTA lesions could use their intact left auditory cortex to accomplish the task, but the less fine-grained representation of pitch in the left hemisphere would lead to a much higher threshold.

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