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Contribution of different cortical areas in the temporal lobes to music processing

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Summary

Music processing ability was studied in 65 right-handed patients who had undergone unilateral temporal cortectomy for the relief of intractable epilepsy, and 24 matched normal controls. The ability to recognize changes in note intervals and to distinguish between different rhythms and metres was tested by presentation of sequences of simple musical phrases with variations in either pitch or temporal dimensions. The responses (right or wrong) enabled us to determine in which component of the music processing mechanism the patients had deficits and hence, knowing the positions of the surgical lesions, to identify their separate cerebral locations. The results showed that a right temporal cortectomy impaired the use of both contour and interval information in the discrimination of melodies and a left temporal cortectomy impaired only the use of interval information. Moreover, they underlined the importance of the superior temporal gyrus in melody processing. The excision of a part of the auditory areas (posterior part of the superior temporal gyrus) was found to be most detrimental for pitch and temporal variation processing. In the temporal dimension, we observed a dissociation between metre and rhythm and the critical involvement of the anterior part of the superior temporal gyrus in metric processing. This study highlights the relevance of dissociating musical abilities into their most significant cognitive components in order to identify their separate cerebral locations.

Keywords: pitch; music processing; epilepsy surgery; superior temporal gyrus; auditory cortex

Abbreviations: MQ = memory quotient; T1S = surgical excision of the middle and inferior temporal gyri on the lateral surface and the mesial limbic structures, in which the T1 area was spared; T1a = surgical excision of the anterior part of the superior temporal gyrus in addition to the structures described for T1S; T1p = surgery was either a lobectomy or a cortectomy including the posterior part of T1

Introduction

One of the most striking and probably distinctive anatomical correlates of the human species corresponds to the lateralization of linguistic functions in the left cerebral cortex. A widely held view attributes other auditory functions, such as those involving music and environmental sounds, to the right cerebral cortex. Close examination of the literature reveals, however, that music does not appear to depend critically on the integrity of the right hemisphere but rather to recruit processing components that are lateralized in both hemispheres (for reviews of research conducted with brain-damaged subjects see Zatorre, 1984; Basso and Capitani, 1985; Peretz, 1994). In fact, the observed bias in favour of the right hemisphere rests on an accumulation of data in a highly specific sector of music perception, i.e. the organization of pitch presented in isolation, in chords or in melodies. Few studies have focussed on dimension other than pitch organization, such as temporal aspect (duration), in musical processing. The study of Platel *et al*. (1997) showed the involvement of the left hemishere in temporal processing.

In fact, the notion of right hemispheric specialization for non-verbal auditory functions stemmed from the idea that the cerebral hemispheres are specialized for dealing with entire functions such as language or music. The possibility that components of these functions, rather than the entire function, might be lateralized differently was overlooked. Today, it is largely accepted that any attempt to explain hemispheric specialization in terms of whole functions or in terms of general-purpose principles, such as the 'analytical–

holistic' distinction (Bradshaw and Nettleton, 1981), cannot do justice to the complexity of the phenomenon. The current trend is to conceive of every mental function as relying on the involvement of a set of processing components, each of which has the potential to be lateralized differently in the brain (Allen, 1983).

In a previous study, Peretz (1990) designed a series of musical tests in order to assess the contribution of each hemisphere to various processing components that are known to be critically involved in music perception and memory. In that study, Peretz tested groups of stroke patients who had infarcts lateralized either to the left or to the right hemisphere. In accordance with the early literature, an overall right-hemisphere superiority was found for the processing of pitch, although a substantial contribution of the left hemisphere was documented as well. More importantly, she found evidence that music is not a monolytic entity that can be ascribed as a whole to one particular hemisphere, but rather a set of components that can be dissociated into different lateralization and patterns. For instance, processing pitch and temporal variations in the same musical sequences could be selectively disrupted by the cortical lesions. On the pitch dimension, a right-sided lesion was found to disturb the extraction of the melodic contour (i.e. the succession of pitch directions) whereas both a right-sided and a left-sided lesion was found to impair computation of pitch interval structure. On the temporal dimension, there was evidence for distinguishing two separate mechanisms, one for dealing with temporal grouping (referred to as 'rhythm') and one for attributing a metrical interpretation (referred to as 'metre'). However, neither of these two temporal processing components could be lateralized to one particular side of the cortex on the basis of the available data.

Although the results of Peretz (1990) confirm that both hemispheres are involved in music processing, the precise cortical regions within each hemisphere that contribute to the processing of the musical components under study could not be specified. The lesions were too coarse to make such anatomical inferences. The aim of the present study was to specify these neural regions, with special attention to the superior temporal gyrus or first temporal circonvolution (T1). Indeed, the auditory areas are localized in the posterior part of T1. According to Brodmann's classification, these T1 areas can be further divided into: area 41 or primary auditory cortex, lying in the posterodorsomedial part of Heschl's gyrus (Braak, 1980; Galaburda and Sanides, 1980); area 42, which is termed the secondary or associative area, occupying the lateral part of Heschl's gyrus and the planum temporale (Braak, 1978); and area 22, localized on the lateral surface of T1 (Fig. 1).

Our earlier investigations with evoked potentials recorded intracerebrally in humans have shown that these different morphological areas are functionally distinct (Liégeois-Chauvel *et al*., 1991, 1994). Auditory evoked potentials recorded in areas 41 and 42 of Heschl's gyrus clearly show anatomical segregation of the responses according to latency. The sources of different components of auditory evoked potentials lie in Heschl's gyrus along a mediolateral axis. Primary components (<30 ms latency) are generated from the most medial part of Heschl's gyrus; the sources of middle-latency components are distributed from the lateral part of area 41 to area 42 and the long-latency components are generated in area 42 (lateral part of Heschl's gyrus and the planum temporale). Moreover, a function for the superior temporal neurons in higher-order auditory processes is suggested by the observation of subjective auditory symptoms elicited by electrical stimulation of T1. Penfield and Perot (1963) and De Graaf *et al*. (1998) have noted a clear-cut difference in this auditory symptomatology between the primary and secondary areas. Most auditory hallucinations (elementary crude sensations such as buzzing) are elicited by electrical stimulation of the primary area, and auditory illusions (altered interpretation of heard sounds) by stimulation of secondary areas. Finally, recent PET studies investigating melodic perceptual processes in normal subjects have generally confirmed the critical contribution of T1 (Zatorre *et al*., 1994; Platel *et al*., 1997).

In order to delineate the different cortical areas of the temporal lobes that are involved in music processing, we tested patients who had undergone unilateral operation in one of the temporal lobes for relief of intractable epilepsy with the same musical tests as used by Peretz (1990). Stereoelectroencephalography was performed before surgery in most patients. This procedure consists of recording electrical activity from intracerebral electrodes stereotaxically implanted in various cortical regions of the brain, thereby allowing the investigation of epileptogenic zones in relation to anatomy (Bancaud, 1965, 1992). On the basis of this examination, the extent of the subsequent cortectomy was determined for each patient. Because this temporal lobe surgery was a tailored resection, it enabled us to classify the patients according to the side, the size and the location of the temporal areas that were resected. We will distinguish patients whose cortectomy spared T1 from those whose cortectomy included T1. In this latter group, we will differentiate cortectomy of the anterior part from that of the posterior part of T1.

The predictions were that a cortectomy involving T1 in the right temporal lobe should produce a double deficit, in the building of contour as well as in the anchorage of interval information on the melodic dimension. A similar cortectomy on the left side should only disturb the process of interval abstraction, according to the results of Peretz (1990). With respect to temporal information, and in line with the recent PET data collected by Platel *et al*. (1997), a general bias towards the left T1 structures (which would interrupt connections with the left insula) for recognition of elements of music might be expected.

Method

Subjects

Sixty-five patients with unilateral temporal cortectomy and 24 normal controls served as subjects. The patients had

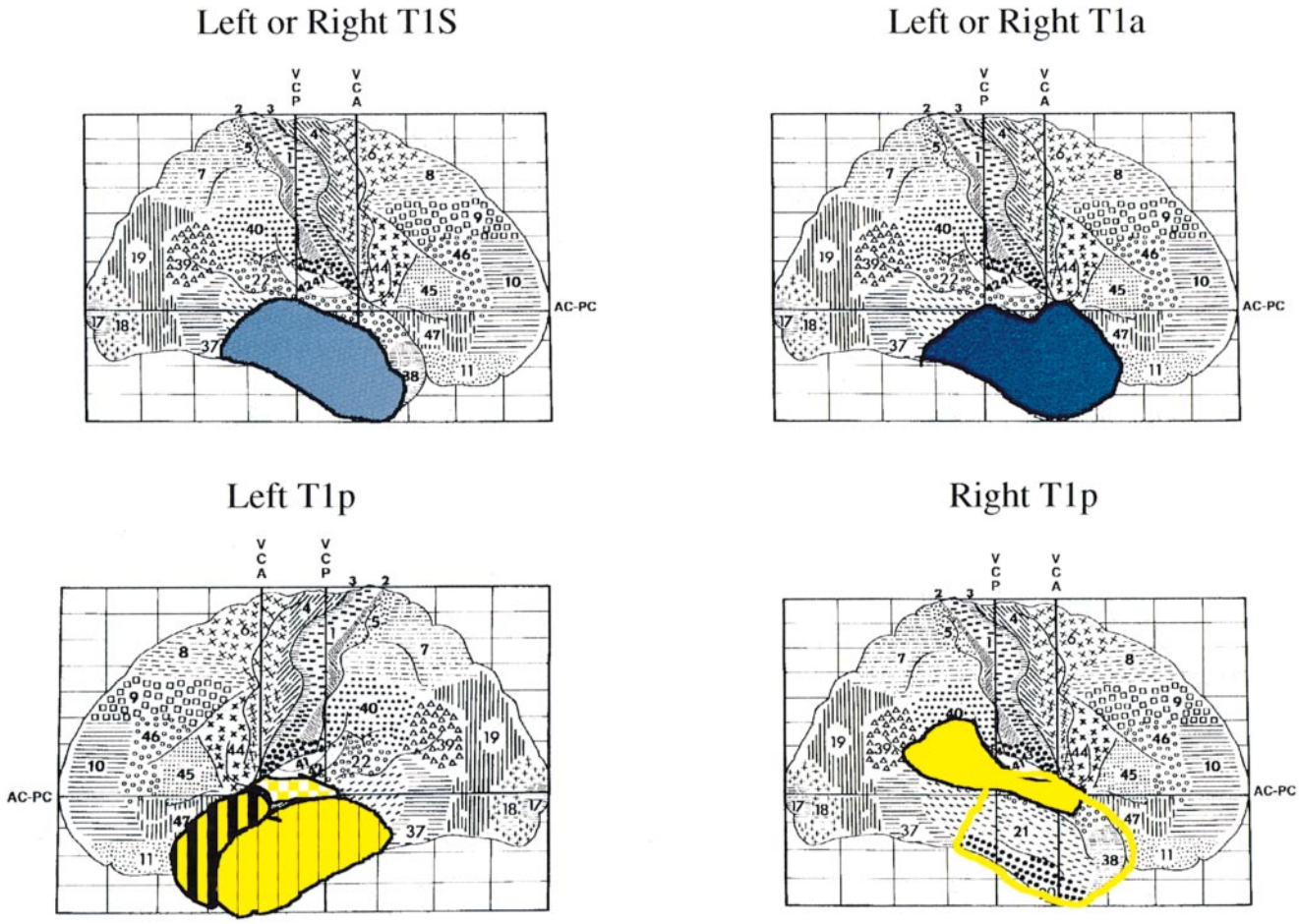

Fig. 1 Schematic diagrams of left and right temporal cortectomies represented on the lateral surface in Talairach's basic referential system. The three dimensions are AC–PC line (anterior–posterior commissures), VCA and VCP (vertical lines traversing the posterior margin of the anterior and posterior commissure, respectively). Brodmann areas are located in this referential system. *Top left*: sky blue area shows the boundaries of a left or right cortectomy sparing the first temporal circonvolution (T1). *Top right*: dark blue area shows the boundaries of a left or right cortectomy including the anterior part of T1. Area 38 and the anterior part of area 22 are removed. *Bottom left*: schematic diagram of a left temporal cortectomy and/or lobectomy (hatched yellow area) including the posterior part of T1 encroaching on the lateral part of Heschl's gyrus (yellow squared area). *Bottom right*: diagram of a right lobectomy (area encompassed by yellow line) and temporoparietal cortectomy (full yellow area encompassed by black line). This surgery removes the planum temporale (area 42) and a part of the angular (area 39) and supramarginal (area 40) gyri. This was performed only on the right side. These two types of surgery included the lateral part of Heschl's gyrus (see general comments in the text).

undergone a cortectomy either in the left temporal lobe (n = 22) or in the right temporal lobe (n = 43; in three of them the cortectomy extended into the parietal lobe). In most patients (85%), epilepsy had begun in childhood. After surgery, all the patients selected for this study were seizure-free at the time of examination. Patients came from three centres: Hôpital Pontchaillou, Rennes (51 patients); Hôpital Ste Anne, Paris (six patients); and the Montreal Neurological Institute, Montreal (eight patients). Patients with atypical language representation and with a full IQ below 80 on the Wechsler Adult Intelligence Scale—revised were excluded from the present study.

Figure 1 depicts the neuroanatomical classification of the patients into three groups according to the site of the cortectomy performed in each temporal lobe. The 'T1-spared' surgery (T1S) included the middle (T2) and inferior temporal (T3) gyri on the lateral surface and the mesial limbic structures (LS); in five patients the T1S surgery also included the temporal pole. The 'T1a-damaged' surgery (T1a) involved the anterior part of the superior temporal gyrus (T1) in addition to the structures described above. Since surgery was a tailored resection, the size of the neocortical removal along the sylvian fissure and along the base of the temporal lobe varied from one patient to another. However, the posterior limits of the cortectomy always lay between vertical lines transecting the posterior margin of the anterior and posterior commissures according to Talairach's referential system (Fig. 1) (Talairach *et al*., 1974, 1988). The 'T1p-damaged' surgery (T1p) was either a lobectomy or a cortectomy including the posterior part of T1. This temporoparietal cortectomy is performed only on the right side and never on the left, so as to leave language functions in Wernicke's area

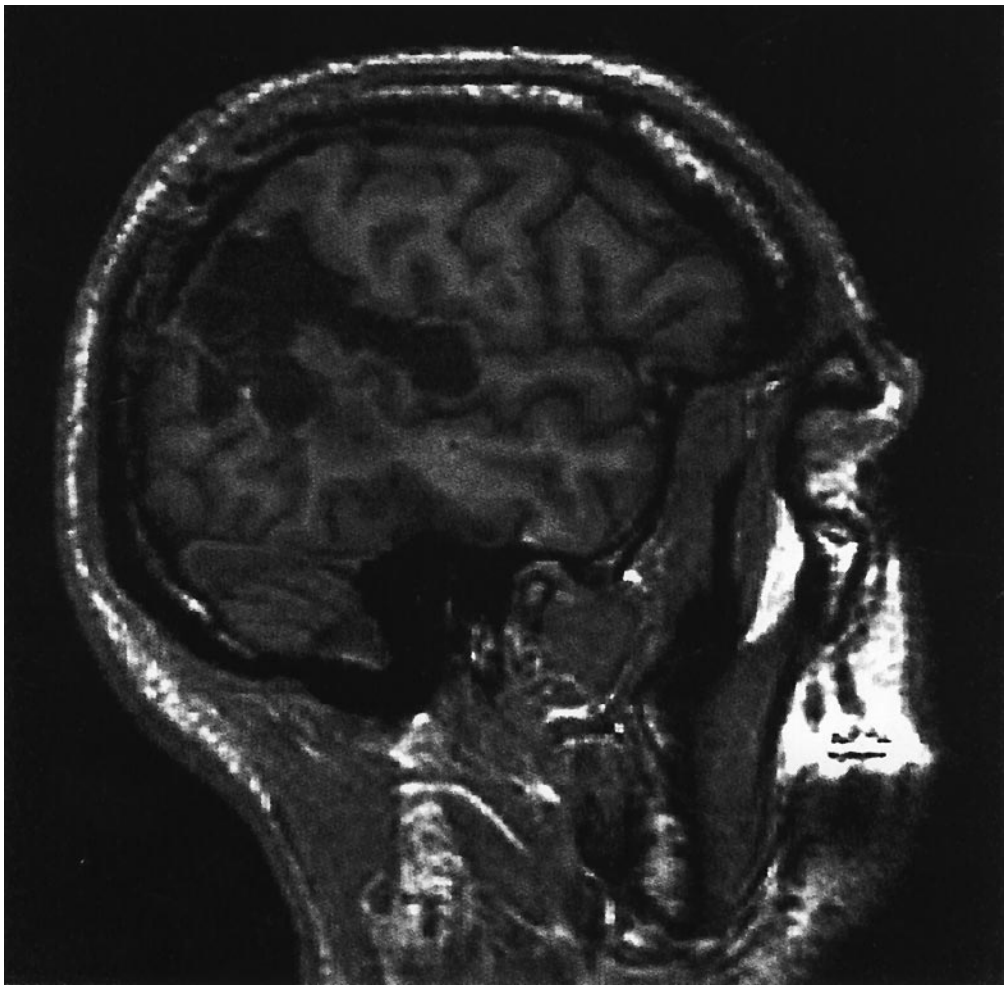

Fig. 2 Sagittal view of the MRI of the temporoparietal cortectomy performed in Case 55. Removal of part of areas 22, 42, 39 and 40.

unaffected. The site and size of the surgery was verified by MRI 6 months after the surgical intervention. As can be seen in Fig. 2, the postoperative MRI of Case 55 confirmed excision of the lateral part of the Heschl's gyrus, the planum temporale and part of the parietal lobe. This patient belonged to the T1p group.

Thirty-three patients had a right ($n = 19$) or left ($n = 14$) T1S temporal cortectomy. Thirteen patients had a right ($n = 8$) or left ($n = 5$) temporal cortectomy that included the anterior part of T1 (T1a-damaged). Five patients had a right temporal lobectomy or temporoparietal cortectomy including the posterior part of T1, and three patients had a left temporal lobectomy including the posterior part of T1 up to the transverse gyri of Heschl. These eight patients were classified in the third group of T1p-damaged cases. In the latter group, two patients had a partial removal of Heschl's gyrus. Since their performance did not differ from that of the other subjects in the group, the patients were not notably different from other T1p patients.

At the time of assessment, most patients were under antiepileptic medication. Postoperatively, the doses were significantly lower compared with the preoperative period. Most patients were under monotherapy with carbamazepine or valproate. The doses decreased as a function of post-operative time, explaining why some of the patients (delay >2 years) were free of medication. The inclusion of the patients tested in this study depended on the success of surgery, i.e. all patients had to be seizure-free. We thereby avoided eventual confusion between the respective roles of surgery and epileptogenic processes in data analysis

Patients were tested, on average, 12 months postoperatively except the Canadian patients, who were tested 7 years postoperatively on average. The neuropsychological follow-up (at 6, 12 and 24 months) showed the stability of their performance 6 months postoperatively. We did not observe any difference in the scores obtained in the different melodic tests between subjects tested 1 year and 7 years post-operatively, indicating that comparison between such patients is valid. An additional group of 11 patients was tested twice, once before and once after surgery, to compare the effects of epilepsy itself and of surgery on performance in musical tests. These patients were treated as a distinct group. Ten of them underwent a T1S type of surgery and the remaining patient a T1p surgery.

Table 1 *Characteristics of the different groups of subjects*

Classification of patients according to anatomical site of cortectomy	Sex		Age (years)	Education (years)	IQ	MQ
	M	F				
Right T1 spared (T1S)	12	7	33	12	96.6	101
Left T1 spared (T1S)	7	7	31	10	92	88
Right T1a damaged (T1a)	5	3	30	10	91	89
Left T1a damaged (T1a)	3	2	39	12	101	90
Right T1p damaged (T1p)	1	4	32	11	88+	97
Left T1p damaged (T1p)	3		38	10	94.3	96
Pre-post RT1 spared	4	6	32	10	96	103
Pre-post RT1p damaged	1		36	15	105	105
Normal controls	13	11	32	12		

*IQ = 91; visuospatial IQ = 85.

The normal control subjects were selected to match the cortectomized patients as closely as possible in terms of age, sex, education and musical background (Table 1). A small number of controls compared with the number of patients was selected. They exhibited high homogeneity in scores across ages and education levels. In Table 1 the sex distribution, average age and years of education are summarized for each group, as well as the full IQ and memory quotient (MQ) on the Wechsler Memory Scale—revised, for the groups of patients. The right and left brain-damaged patients and normal control subjects did not differ in age ($F < 1$) or in years of education [$F(2,72) = 1.15$]. The patient groups were not found to differ in IQ [$F(3,52) = 1.84$] but were found to differ in MQ [$F(3,52) = 3.24$, $P < 0.02$]. The left temporal cortectomy patients were impaired in memory (with a mean MQ of 88.4) compared with the right temporal cortectomy patients (mean MQ, 97.3). The T1p-damaged group was found to have a lower IQ, due to a visuospatial deficit. However, their verbal performance was normal. All subjects were right-handed as assessed by a handedness questionnaire (Oldfield, 1971). No musician, either amateur or professional, participated in this study: 10% of the subjects in each group could be considered as having had some musical experience in their childhood when they learned to read music, i.e. between 5 and 8 years of formal musical training, but they no longer practised. None of them had perfect pitch

Material and procedure

The material was an updated version of the musical test battery used by Peretz (1990). Of the seven subtests, described hereafter as 'musical structure manipulation', three were modified. The changes concerned (i) the transposed condition, which was discarded and replaced by the 'key-violation' condition, and (ii) the 'rhythm' test, which incorporated pitch variations. Finally, all subtests included an equal number of positive and negative trials and were produced by a computer-controlled synthesizer. The stimuli were generated on an IBM-AT compatible microcomputer controlling a Yamaha TX-81Z synthesizer. The chosen tempo was fixed at 120 crochets per minute and the voice was approximately that of a piano. The analogue output was recorded on a Sony digital (DAT) recorder, which was also used to play melodies to the subjects.

Except for the first test, which used familiar musical excerpts, all the others were constructed from the same pool of 30 novel musical sequences. These sequences were tonally structured and made up of two phrases following Schoenberg's (1940) principles. Half were written in double time and half in triple time. The two-phrase sequences were used in the metric condition. For all the other conditions, only the second phrase of each sequence served as the stimulus. These second phrases were four bars long, were of ~4 s duration and contained from 8 to 19 notes (mean = 10.7). Restriction to the second phrase was motivated by the need to reduce the length of the testing session as much as possible. This was not possible for the metric task, which required presentation of longer sequences in order to allow subjects to build a stable metrical interpretation.

Familiarity test

This test consisted of 10 familiar musical excerpts mixed with 10 unfamiliar excerpts. The 10 familiar excerpts were taken from pre-existing vocal and instrumental pieces in equal number and were all judged to be highly familiar, with a mean rating of 4.9 (range, 4.8–5.0) on a five-point scale, where 1 means very unfamiliar and 5 very familiar (Peretz *et al*., 1995). The 10 unfamiliar musical fragments were the reverse in pitch and time of 10 other familiar excerpts. The reversed versions approximated familiar stimuli structures while failing to evoke a sense of familiarity (Hébert *et al*., 1995). Familiar and unfamiliar fragments were matched in length (mean duration, 9.9 and 10.0 s, respectively). The task was to judge whether or not an excerpt was familiar. Since no patient ever failed to do well at this task (Peretz, 1990; the same applied to the present study; but see Peretz *et al*., 1994, for specific failures after bilateral lesions to the auditory cortex) and they all enjoyed doing it, this test was always first presented to the subject as a 'warm up' test and as a means of adjusting the sound level, if necessary.

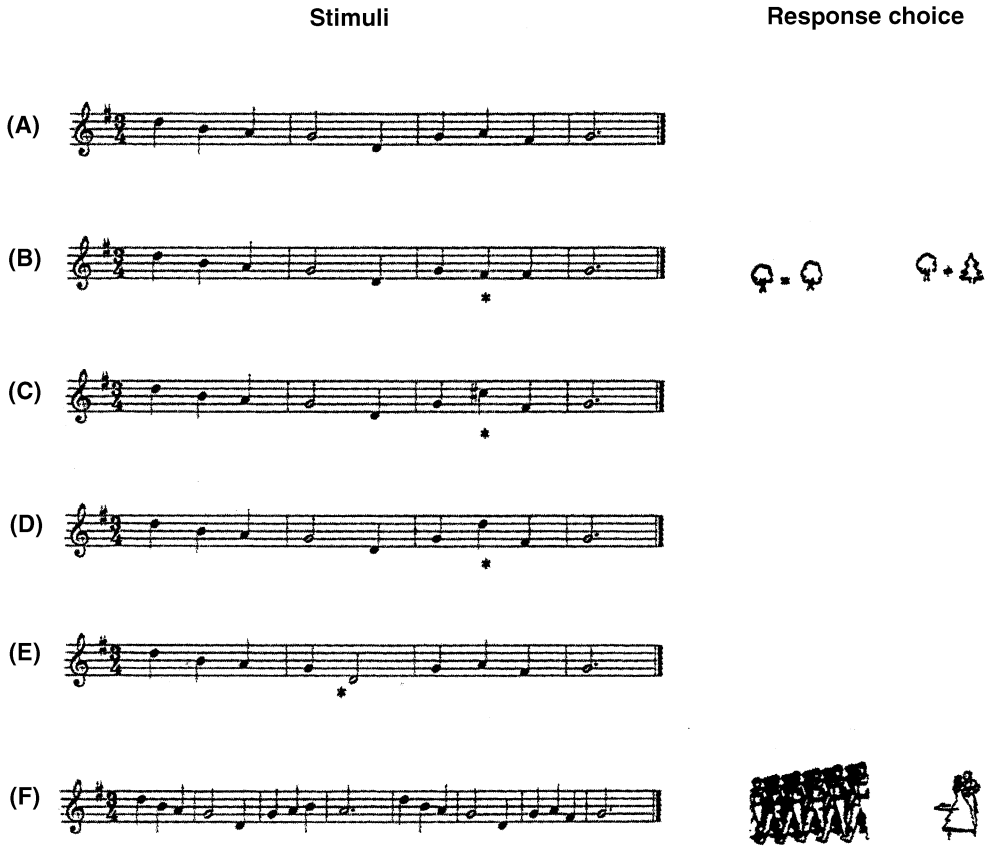

Fig. 3 Example of an initial melody (**A**), its contour-violated (**B**), its key-violated (**C**), its contour-preserved (but interval-violated) (**D**) and its rhythmic (**E**) transformation. **F** represents the entire two-phrase sequence (of which the second phrase corresponds to **A**) used in the metric task. Symbols for response choice are also shown. *Critical note.

Pitch organization conditions

Three types of manipulation were applied to the second phrase of 15 original sequences.

One manipulation consisted of creating a contour-violated alternative melody by modifying the pitch of one note so that the pitch direction of the adjacent intervals was changed [see Fig. 3B compared with 3A for an example of a contour change: the interval directions adjacent to the changed note (which has been identified with an asterisk) have been modified from a lower-pitch note on its left and a lower-pitch note on its right (basic melody A) to a higher-pitch note on its left and the same note on its right (melody B), while keeping to the original key]. The position of the note with modified pitch was varied across melodies; half fell in the beginning of the melody and half at the end, avoiding the first and last note positions.

The second manipulation consisted of creating a key-violated alternative melody by modifying the same note so that it was out of key (to the same extent in terms of semitone distance across stimuli), in keeping with the original contour (see melody C in Fig. 3). This change is particularly salient because the changed note sounds out of tune.

The third manipulation consisted of creating a contour-preserved or interval-violated alternative melody of these contour-violated and key-violated melodies by modifying the same note (to the same extent, in terms of semitone distance, across stimuli), but in keeping with the original contour and key (see melody D in Fig. 3).

Average interval changes were made so that they were equivalent across the three conditions, with a mean of 4.3, 4.3 and 4.2 semitones apart from the original note in the contour-violated, key-violated and interval-violated conditions, respectively. The minimal interval change was set to three semitones and the maximal interval change was set to seven semitones. The changes generally fell into the frequency range of the melody.

Three sets, each consisting of two practice trials and 30 experimental trials, were constructed with these melodies. Each trial consisted of a warning signal and a target melody followed, after a 2 s silent interval, by a comparison melody. Duration of the intertrial interval was 5 s. A first set, prepared for the contour-violated condition, was constructed so that 15 trials were made of identical melodies and 15 trials of different melodies, consisting of the contour-violated pairs (e.g. melodies A and B in Fig. 3). The second and third sets, prepared for the key-violated and the interval-violated conditions, respectively, were similar to the contour-violated condition set in that they kept the same target melodies; the

only modification was that each different comparison melody was replaced by its key-violated alternative (e.g. A and C in Fig. 3) or by its preserved-contour alternative (e.g. A and D in Fig. 3). Melody pairs were, however, presented in each set in a random order. These three conditions will be referred to as the contour, key and interval conditions.

Temporal organization tasks

As mentioned previously, the 30 entire two-phrase sequences served as stimuli for the metric task. The sequences (see e.g. Fig. 3F) in double (march) or triple (waltz) time were recorded for presentation to the patient in random order with an intertrial interval of 5 s. These experimental trials were preceded by four practice trials.

For the rhythm task, the stimuli were derived from the second phrase of the 30 sequences used in the metric task, in order to correspond to the target melodies used in the pitch organization conditions. One manipulation was applied to these isolated phrases to create different comparison patterns. Two-thirds of the stimuli that were modified in the pitch organization conditions served here as alternatives as well. These temporal alternatives involved a temporal grouping change by interchanging the time values of two adjacent notes. This particular change was such that the size of each temporal group defined by temporal proximity (Lerdhal and Jackendoff, 1983) was changed, while keeping the metre and the total number of sounds identical (compare E with A in Fig. 3). The serial positions of these changes varied across patterns. Thus, the only cue available for discrimination was the temporal grouping of the notes (i.e. the rhythm). A set of two practice and 30 experimental trials was constructed with these temporal patterns in the same way as the pitch organization conditions.

Recognition test

From the initial set of 30 second-phrase melodies, 15 were selected for the recognition part of this study. Each of them had been presented at least five times in the same format (including the one embedded in the two-phrase sequences). Note, however, that the presentation rate was far higher when the various transformations of these melodies (such as the contour-violated alternative or the rhythmic version) were perceived by the subjects as examples of a central tendency corresponding to the original melody (Welker, 1982). In addition to these 'old' melodies, a set of 15 recognition 'foils' was prepared. These new melodies were constructed along the same principles, but differed from the old ones in their exact temporal and pitch pattern. These 30 sequences were then recorded in random order with a 5 s silent interval between them.

Mode of responses to tests

Each subject performed in a single session with as many pauses between conditions as requested by the subject. They listened to the prerecorded tapes via a speaker placed on a table in front of them. The intensity level was adjusted for each subject. The session began with the familiarity decision test. Then either the pitch organization conditions or the temporal tasks were presented. The order of presentation for these two main subtest categories was counterbalanced within each group. In each subtest category, the order of presentation of the tests was determined using a Latin square. The session ended with the recognition test.

For all three pitch organization conditions and the rhythm test, subjects were required to perform a 'same–different' classification task. They had to judge, on each trial, whether the target sequence and the comparison sequence were the same. Prior to each condition, two practice trials were presented and a symbol (Fig. 3) was used on the top of the response sheet to help in choosing the right answer. The practice trials were repeated until the subject indicated that he or she understood what was required from him or her. Then the subjects were presented with the 30 experimental trials corresponding to the practice trials. No feedback on the accuracy of the responses was provided. Subjects responded orally.

For the metric task, subjects were informed that they would be hearing waltzes and marches, between which they had to discriminate. They had to mark a cross below the symbol corresponding to the time (Fig. 3). Subjects were encouraged to tap along with what they perceived to be the underlying beat of each sequence. Feedback on the response was provided only on the four practice trials. For the recognition test, subjects were instructed that they would be hearing some of the tunes that they had been listening to during the session and that these tunes would be mixed with new tunes. Their task was to respond 'yes' if they recognized the tune and 'no' otherwise. This last test came as an incidental memory test, since subjects were not informed in advance that their memorization of the tunes would be tested later.

The patients and control subjects gave informed consent to all tests administered. This project was approved by the Comité Consultatif de Protection des Personnes dans la Recherche Biomedicale (Rennes, France), Ethics Commission, March 5, 1993.

Results

The results were first analysed according to the side (left or right) of the cortectomy as well as the involvement of T1 (T1 damaged versus spared) in order to assess the specific contribution of T1 to music processing. In order to specify more accurately the cortical regions within T1 that may be more specifically involved in music processing, the T1-damaged group was further fractionated according to the site (anterior versus posterior) of the resection in the T1 region. Finally, the results obtained pre- and postoperatively are presented.

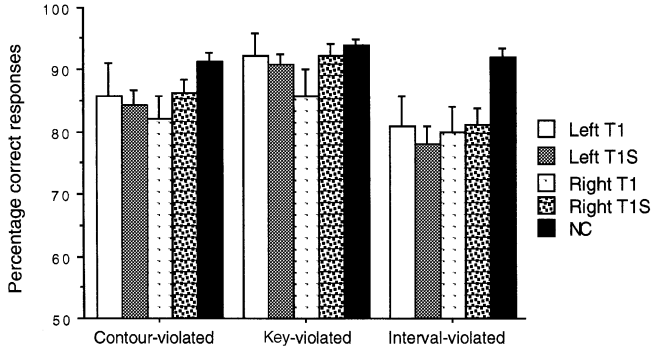

Fig. 4 Mean percentage of correct responses and SD obtained for each pitch organization condition in each group (see comments in the text). NC = normal control.

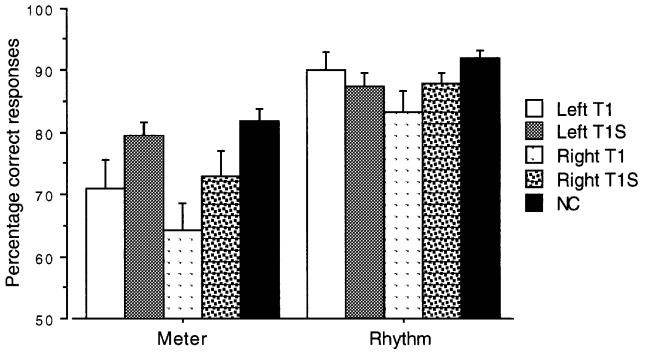

Fig. 5 Mean percentage of correct responses and SD obtained for each temporal condition in each group (see comments in the text). NC = normal control.

Effect of T1 resection: left and right comparison

Pitch organization conditions

The mean percentages of correct responses of each group according to the melodic conditions are presented in Fig. 4. The raw scores were submitted to analysis of variance, including the three conditions as the within-subjects factor and the five groups as the between-subjects factor. The analysis revealed a significant interaction between Group and Condition [$F(6,138) = 2.42$, $P < 0.01$]. Before considering further the origin of the observed interaction, we performed a Levene test to verify the variance homogeneity of the results in each condition. This test revealed variability only for the interval condition ($P < 0.02$). Therefore, in that particular condition non-parametric tests were used instead of variance analyses.

In the key condition, patients were not found to perform differently from the control subjects. There was no Group effect [$F(4,74) = 1.7$]. In the contour condition, the analysis revealed a Group effect [$F(4,74) = 2.37$, $P < 0.05$], the right T1 group showing the only significant impairment compared with normal controls (Newman–Keuls, $P < 0.05$). In the interval condition, the Kruskal–Wallis one-way analysis also yielded a significant Group effect [$H(4) = 16.5$, $P < 0.002$]. Multiple comparisons between groups were performed using the Mann–Whitney test. All patient groups were found to perform significantly below the control group ($U = 111$, 46, 91 and 37 for the right T1S, right T1, left T1S and left T1, respectively; all $P < 0.02$). The four patient groups did not differ from one another ($P > 0.6$)

Temporal organization tasks

The mean percentages of correct responses obtained for each group of brain-damaged patients and their matched controls in the two tasks involving temporal judgements are shown in Fig. 5. Performance on the two tasks was analysed separately because task parameters were different, the metre task requiring a 'waltz–march' judgement on each musical stimulus and the rhythm task requiring a 'same–different' classification for two successive sequences.

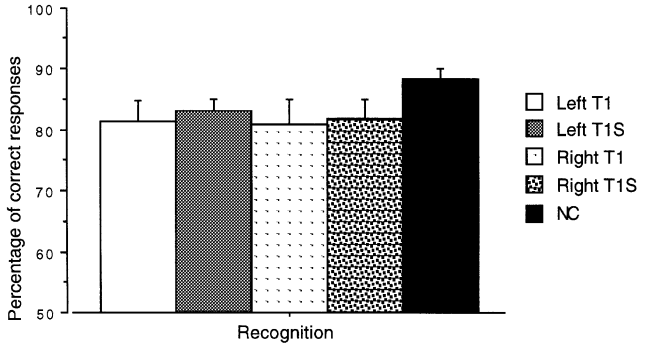

Fig. 6 Mean percentage of correct responses and SD obtained for recognition condition in each group (see comments in the text).

Because the scores were not homogeneously distributed in these two conditions (Levene test, $P < 0.007$), non-parametric tests were performed on the data. In the rhythm test, patients were not found to differ from the normal controls [$H(4) = 6$, n.s.]. In contrast, in the metre task a reliable Group effect emerged [$H(4) = 13.9$, $P < 0.01$]. Subsequent comparisons using the Mann–Whitney test indicated that only the right and left T1 groups were impaired compared with normal controls ($U = 27$ and 37, respectively, $P < 0.02$). These two patient groups (left T1 and right T1) did not differ from each other ($U = 35$, $P < 0.3$). Thus, the T1 structure on each side seems to be critically involved in distinguishing metre.

Recognition task

The mean percentage of correct responses is shown in Fig. 6. All left brain-damaged patients obtained a score of >73% correct responses on this incidental memory task. The scores of the right brain-damaged groups were, however, more variable (range, 14–30 out of 30 correct). None of the statistical comparisons was significant: patients' scores did not differ from those of the normal controls, nor did the patients differ from one another [$H(4) = 5.4$, *n*.s.]. It is worth mentioning that the scores obtained on this musical memory test did not correlate significantly with the MQ obtained on the Wechsler memory scale [$r(50) = 0.16$].

Effects of site: comparison between anterior and posterior portion of T1

Given that most excisions of the posterior part of T1 were performed on the right side for obvious clinical reasons, as mentioned previously, the side of surgery will not be taken into consideration in the following analyses. Only the site of excision within the T1 region, with respect to its anterior versus posterior portion, will be considered.

Pitch organization conditions

The percentage of correct responses obtained for each group in the three conditions involving pitch organization judgements are shown in Fig. 7A. As can be seen, the T1p group scored lower than the T1a group across conditions. This observation was confirmed statistically (contour: $U = 13$, $P < 0.001$; key: $U = 18$, $P < 0.005$; interval: $U = 20$, $P < 0.008$; Mann–Whitney test).

The comparison of performance between the T1a and normal control groups showed surprising results. The scores of the T1a group did not differ significantly from those of the normal control group across the three melodic tasks [mean scores for the two groups, respectively, were as follows: contour: 27.2 (T1a) versus 27.4 (normal controls) ($U = 142$, $P < 0.9$); key: 28.9 (T1a) versus 28.1 (normal controls) ($U = 113$, $P < 0.2$); interval: 26 (T1a) versus 27 (normal controls) ($U = 111$, $P < 0.2$)]

These data demonstrate the specific involvement of the posterior part of T1 in sequential pitch organization. The individual scores of the T1p patients are presented in Table 2. When considering the mean performance of normal controls minus 2 SDs as the cut-off point below which the scores obtained by patients can be regarded as indicating a genuine deficit, the pattern underlying the results described above emerges even more clearly. In both the contour and the key condition, five of the eight patients were found to exhibit a deficit. In the interval condition, seven patients could be so classified. Note, however, that a deficit in one condition does not accompany a deficit in another condition, pointing to the existence of separable mechanisms, with one important exception: a deficit in the contour condition always accompanies a deficit in the interval condition, as observed by Peretz (1990).

It may be the case that some of these patients did poorly on the melodic tests because of a deficiency in short-term memory. To assess this possibility, we measured whether or not patients exhibited a distance effect in melody comparisons, following the same procedure as in Peretz (1990). Since the melodies were of varying length and incorporated a single note change in different serial positions, we divided the stimuli into long melodies with a late note change (mean distance of 19 notes from the beginning of the sequence) and short melodies with an early change (mean distance of 11 notes). Normal controls gave 94 and 93% correct responses in discriminating short melodies with an early change and long melodies with a late change, respectively. Thus, normal controls exhibited little sensitivity to this factor, although their high level of performance may have created a ceiling effect. Similarly, the T1a group was 90% correct for both the short and the long melodies. In contrast, the T1p group performed at a much lower level, with 64 and 60% correct for the short and long melodies, respectively. Nevertheless, there was little evidence for the presence of a distance effect in this particular group either.

Temporal organization tasks

The results are shown in Fig. 7B. In the rhythmic condition, the T1p group gave performances significantly lower than the T1a group ($U = 27$, $P < 0.03$). In the metric task, the T1p group scored slightly better than the T1a group, but the difference did not reach significance ($U = 46$, $P < 0.4$)

On the contrary, the T1a group scored significantly lower than the normal control group ($U = 54$, $P < 0.002$), which was the reverse of their performance on the melodic tasks.

Two patients (Cases 44 and 42) who were typical of the group that underwent an excision including the anterior part of T1 (T1a) and of the group that underwent removal of the posterior part of T1, respectively, were retested 6 months later in order to evaluate the stability of their deficit. As can be seen in Table 2, patient 44, with a T1p surgery, maintained her impaired performance on the melodic tests while performing in the low normal range on the temporal tests. Similarly, patient 42, with a T1a surgery, maintained an excellent performance on the melodic tests and a marked deficit for the metre task, on which he obtained 11 and 8 correct responses (out of 30) on the two testing sessions, respectively. These results suggest that the observed deficits are remarkably stable.

Recognition memory

The mean percentages of correct responses obtained on the incidental memory recognition test were 84 and 76 for the T1a and T1p groups, respectively (Fig. 7C). These scores did not differ significantly ($U = 46$, $P < 0.2$). When divided into hits (corresponding to a 'yes' response to a melody that was indeed presented in the previous tests) and 'false' responses (corresponding to 'yes' responses to novel melodies), we found that the two groups did not differ in hit rates (92 and 91% for the T1a and T1p groups, respectively) but differed slightly in terms of false responses, the T1p group making more false responses than the T1a group (38 and 20% false responses, respectively).

Pre- and postsurgery comparison

Ten patients with a right temporal lobe epilepsy were tested before T1S surgery and 6 months afterwards; one further patient was tested before and after T1p surgery. Overall, the T1S group tended to perform better after surgery than

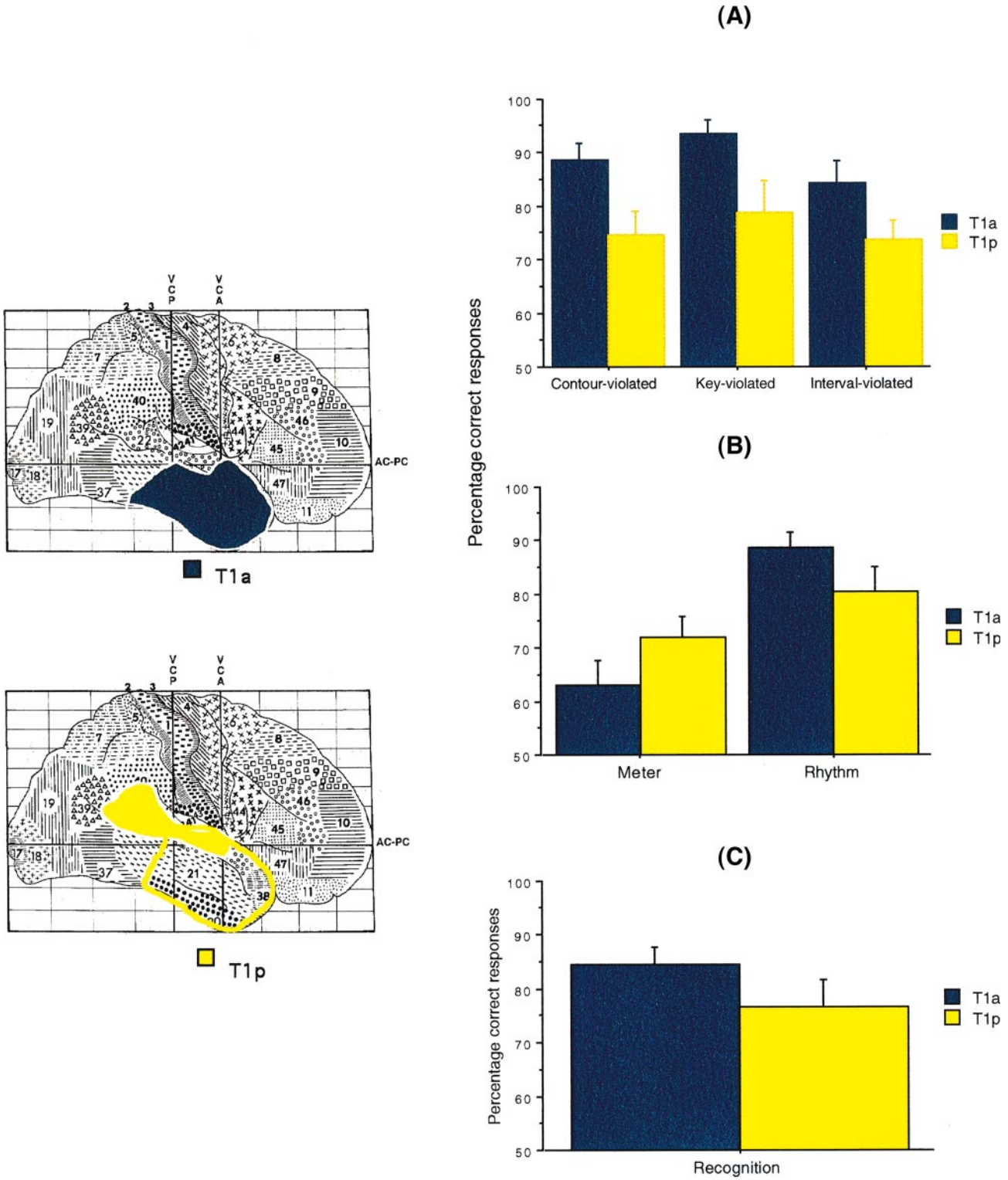

Fig. 7 Comparison of mean percentage of correct responses and SD obtained for each pitch organization, temporal and recognition condition between patients whose surgery included the anterior part of T1 (T1a) and the posterior part of T1 (T1p), independent of the side of cortectomy. *Left*: schematic diagram of the two types of surgery (see comments in legend of Fig. 1) independent of the side of cortectomy (for clarity only the right view is shown). *Right*: each colour histogram corresponds to a different surgical excision (see comments in the text).

Table 2 *Individual scores of the T1p group in each condition*

Case/condition	Contour memory	Scale	Interval	Metre	Rhythm	Incidental
LT1pD (Case 19)	19*	22*	22*	17*	24	24
LT1pD (Case 16)	22*	27	21*	23	25	21*
LT1pD (Case 17)	28	27	21*	22	30	21*
RT1pD (Case 44)	16* (15)	15* (15)	19*	27 (29)	20* (23)	20*
RT1pD (Case 50)	18*	20*	16*	15*	20*	19*
RT1pD (Case 47)	25	30	24	22	26	28
RT1pD (Case 46)	22*	19*	19*	18*	20*	28
RT1pD (Case 54)	25	21*	21*	20	20*	17*
RT1pD (Case 55)						
Postsurgery	22 (20)	27	23 (19)	24	28	29
Presurgery	21	30	25	21	28	–
Cut-off point	22.9	25.5	22.8	20	24	22

The maximal possible score is 30. Case 55 was tested before surgery and twice (1 year apart) after surgery. The postsurgery retest results are given in parentheses. *Scores that are below the cut-off point. Case 44 was tested twice 6 months apart, after surgery.

before; this improvement did not, however, reach significance (contour: $U = 46$; key: $U = 33$; interval: $U = 46$; metre: $U = 42$; rhythm: $U = 30$; all $P > 0.10$)

The patient who underwent surgery that included the posterior part of T1 scored slightly lower on the pitch organization tests after surgery than before. His scores obtained after surgery are presented in Table 2 together with those of patients who underwent similar surgery. His postsurgery scores were very similar to those of the patients who had had T1p surgery without prior testing.

General discussion

Overall, the results obtained with patients who underwent unilateral cortectomy in the temporal lobe for the relief of intractable epilepsy replicate and extend the results obtained by Peretz (1990) with patients who had sustained a unilateral vascular accident. In particular, the present study highlights the determining role of the posterior part of the superior temporal gyrus (T1p) in music processing.

The present data were obtained after epilepsy surgery, hence the role of epilepsy itself must be discussed first. Indeed, the cortical localization of surgery appeared to be the only factor that determined the occurrence of a deficit in musical perception. Neither a possible neural circuit reorganization caused by epilepsy nor an effect of antiepileptic medication could be held responsible for the present results. Cerebral abnormalities extending beyond the epileptogenic zone excised by surgery could theoretically be present in patients with long-term intractable epilepsy. However, this remains highly speculative in the types of epilepsy included in the present study. In addition, the material analysed here dealt with a deficit and not with the recovery of functions after surgery. However, the possibility of cortical network reorganization remote from the epileptogenic zone could be considered in the following conditions: (i) early cerebral damage leading to partial or subtotal hemispheric atrophy (Patterson *et al*., 1989, 1991; Vargha-Khadem *et al*., 1991); (ii) mesial temporal atrophy with hippocampal atrophy, and the sprouting of mossy fibres, building up excitatory microcircuits (Sutula *et al*., 1989). In the latter condition, especially several months after surgery, no reason has been established to suggest impairment of auditory cognition. Our patient population did not meet the usual required characteristics of the former condition. In fact the duration of epilepsy was variable (mean, 17 years). MRI was normal in 38% of the patients; a small and circumscribed lesion existed in 30% and hippocampal sclerosis in 13%. There were four cases with moderate temporal atrophy and only one case with moderate hemiatrophy of late occurrence (see Appendix). This reinforces the evidence that even if long-term intractable epilepsy could lead to abnormalities in cerebral organization they were not observable in the auditory perception of our patients. This is confirmed by the comparison of data obtained before and after T1S surgery, which did not lead to a deficit. Concerning a possible influence of antiepileptic medication, the scores did not differ significantly according to drug regimen, indicating that their medication did not interfere with the performance of our patients.

In agreement with Peretz's (1990) results, a right-sided cortectomy was found here to be detrimental to the processing of both contour and interval information in the discrimination of melodies and a left-sided cortectomy was found to compromise abstraction of interval but not contour information. Also, no isolated deficit could be observed in the contour condition, which was systematically associated with deficits in the interval condition, whereas isolated deficits in the interval condition were found. Altogether, these results are highly consistent with the hierarchical principle of co-operation between the hemispheres put forward by Peretz (1990). According to this principle, a right hemisphere lesion, by disrupting the processing subsystem required for representing the melody contour, deprives the intact left hemispheric structures of the anchorage points necessary for encoding interval information. Thus, unilateral brain damage in either hemisphere can affect the extraction of interval information. In the case of damage to the left hemisphere

structures, the neural circuitry necessary for dealing with the interval features would be disrupted while leaving intact that involved in building the global melody representation in the right superior temporal gyrus. That the right superior temporal gyrus (T1) contributes to the provision of this contour representation, on which the left hemisphere processes can operate, is attested by the fact that right-sided cortectomies that involved T1, compared with cortectomies that spared T1, were found to impair performance in the contour condition. Thus, beyond replication of Peretz's results, the present results show that it is not the whole right hemisphere nor the whole right temporal lobe but the superior temporal gyrus that is critical in melody processing.

The present study suggests that the posterior and not the anterior part of T1 is critically involved in melody processing. Patients whose cortectomy involved the posterior portion of T1 (including the posterior part of area 22, the planum temporale and, in two cases, the lateral part of Heschl's gyri) showed clear evidence of a deficit, particularly in the processing of sequential pitch variations. In contrast, patients whose cortectomy involved the anterior part of T1 obtained scores that fell within normal variation except in the metric task. This fact will be discussed further. These results suggest first that unilateral partial resection of the secondary auditory areas (lateral part of Heschl's gyrus and the planum temporale) that spare the primary auditory cortex (area 41; dorsoposteromedial part of Heschl's gyrus), which is never removed in such surgery because of its anatomical situation, is sufficient to impair melody discrimination. Secondly, these findings bring important knowledge of the functional organization of the anterior part of T1 (area 22), which has often been considered to be an associative auditory region. The fact that the T1a group was not impaired compared with normal controls allows us to hypothesize that the anterior part of this area is not involved in pitch perception. The latter group could be also considered as an intra-patient control group compared with normal subjects.

Similar results have been reported in the literature of animal experiments. Dewson *et al*. (1970) showed that a relatively small unilateral cortical lesion in the posterior temporal gyrus of monkeys produces a defect in auditory sequence discrimination performance. No deficit was found with a unilateral ablation of the inferotemporal cortex. To our knowledge, human subjects with similar lesions have never been compared with normal subjects for auditory deficits. The excisions performed at the Montreal Neurological Institute were such that the anterior portion of T1 was systematically removed (Rasmussen, 1983; Olivier *et al*., 1988; So *et al*., 1989). Yet Zatorre (1985, 1988) and Samson and Zatorre (1988) noted that when the excision extended more posteriorly into Heschl's gyrus an additive deficit was observed in pitch-related tasks. It may be the case that it is not the involvement of Heschl's gyrus *per se* that is critical for pitch-related tasks but the posterior regions of T1, since this type of excision (encroaching into Heschl's gyrus) also extends further into these regions. According to the present results, it is this posterior extension of the lobectomy that would be most detrimental for the processing of pitch variation.

The critical involvement of T1p in sequential pitch organization is consistent with most studies in which PET has been used in normal subjects. In particular, the present results agree well with the results reported by Mazziotta *et al*. (1982). In their pioneering study, these authors report increased cerebral glucose metabolism in the posterior temporal regions, particularly in the right posterior–superior temporal region, for the discrimination of melodic sequences differing by a single note (i.e. the Seashore tonal memory test). The results are also consistent with the PET findings of Zatorre *et al*. (1994), who showed increased activation in the right frontal and right superior temporal gyrus when subjects had to discriminate pitch changes inserted at the beginning and the end of a melodic sequence. These results do not, however, show a focal increase in the posterior portion of T1, as our results and those of Mazziotta *et al*. (1982) would predict, but an overall activation of the T1 area. One piece of data that is difficult to reconcile with this set of concordant evidence for the determinant role played by T1 in sequential pitch discrimination can be found in Platel *et al*. (1997). These authors recently reported significant PET activation in unexpected areas of the brain—the left cuneus/precuneus (corresponding to Brodmann areas 18/19)—for monitoring pitch changes. However, the design of this latter study was very complex in its assessment of several musical processing components at once. Hence, further examination of the tasks used by Platel *et al*. in systematic and isolable conditions should be the goal of future studies.

Several questions remain as to the functional significance of the effects of auditory area excision in the posterior part of T1 on music processing. One possibility is that the deficits are due to a global impairment of hearing. However, examination of data for individual subjects (Table 2) reveals that the observed deficits do not apply to every condition for the large majority of patients. Global impairment of hearing would entail depressed performance in all conditions. Spared areas of discrimination suggest rather that the deficits do not have a common low-level auditory origin. Moreover, the audiograms and the recordings of surface auditory evoked potentials in the majority of patients (i.e. in the 57 French patients) were normal for both ears. The patients did not display or complain about any specific auditory problem in everyday life. Thus, the observed deficits in the musical tasks are not likely to have arisen from a sensory loss. The other possibility is that the patients with posterior T1 excisions suffered from a short-term memory deficit. Indeed, most tests used here were quite demanding in this respect, by requiring the subjects to retain in their memory a long sequence and to compare it with a following sequence in order to achieve the 'same–different' discrimination tasks. Again, examination of individual patterns of performance is not consistent with a short-term memory deficit in the group

of patients. Several patients exhibited a deficit in pitch organization conditions but not in the rhythm condition, although all conditions required a 'same–different' classification of sequences of the same length. Moreover, the patients did not show sensitivity to the number of notes intervening between the notes to be differentiated. Thus, the functional contribution of the posterior areas of T1 cannot easily be determined by a single test. Rather it seems that this region is involved in several, potentially separable, mechanisms that contribute to the build-up of a musical representation.

Up to now, we have focused our discussion on the conditions that involved discrimination of pitch variations without considering those concerned with temporal variations in great detail. There are several reasons for considering temporal variations separately. First, there is increasing evidence that pitch and temporal variations are processed by distinct mechanisms (Peretz, 1990; Peretz and Kolinsky, 1993; Thompson, 1994). Secondly, the present study provides new suggestions as to how and where these temporal mechanisms are organized in the temporal lobes. More specifically, the rhythm condition was found to be generally spared by the various excisions considered here. In contrast, the metre task was found to be differentially affected depending on the type of excision. Involvement of T1, this time its anterior portion, seems to be critical for metric derivation. We did not find evidence for a laterality effect.

This outcome is different from that observed previously by Peretz (1990) in an interesting way. Peretz (1990) found that metre judgements were spared in the presence of disrupted rhythmic discrimination. We observed the opposite here, as did Polk and Kertesz (1993) in a single case study. Altogether the results illustrate a double dissociation between metre and rhythm. They further support the notion that metric organization of a sequence is not dependent upon rhythmic organization, as posited in Lerdhal and Jackendoff's (1983) model of the mental representation of music. These authors view the interpretation of metre as a separate level of analysis that is not determined by the organization of the relative durations of notes; the latter is governed by a distinct set of rules. Therefore, the present data can be viewed as fitting their model.

The finding that the anterior part of T1 is most critically involved in metric interpretation is novel. To our knowledge, the neural basis of metric organization has not been studied before. Consequently, the present results are isolated and require confirmation using different methods and techniques. They highlight the relevance of dissociating musical abilities into their most significant cognitive components in order that their cerebral location can be pinpointed.

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Appendix

Patient	Sex	Age (years)	MRI	Duration of epilepsy (years)
Left temporal cortectomy, T1 spared (LT1S)				
Case 1	M	58	Cavernus angioma	14
Case 2	M	14	Tumour	4
Case 3	M	16	Tumour	4
Case 4	F	19	Normal	15
Case 5	F	53	Normal	20
Case 6	F	19	Tumour	8
Case 7	F	32	Left temporal asymmetry	27
Case 8	M	30	Tumour	21
Case 9	F	32	Tumour	23
Case 10	M	25	Hippocampal atrophy	17
Case 11	M	42	Normal	31
Case 12	F	24	Cavernus angioma	4
Case 13	M	37	Hippocampal atrophy	30
Case 14	M	18	Hippocampal atrophy	14

Right temporal cortectomy, T1 spared (RT1S)				
Case 23	M	24	Normal	17
Case 24	M	37	Normal	31
Case 25	M	41	Normal	5
Case 26	F	32	Cavernus angioma	20
Case 27	F	42	Tumour	7
Case 28	M	25	Normal	24
Case 29	F	25	Normal	12
Case 30	F	21	Hippocampal atrophy	19
Case 31	M	39	Normal	32
Case 32	M	37	DNT	4
Case 33	F	24	Cavernus angioma	5
Case 34	F	38	Vascular malformation	10
Case 35	M	32	Normal	23
Case 36	M	43	Normal	20
Case 37	M	46	Tumour	2
Case 38	M	18	Tumour	1
Case 39	M	25	Normal	20
Case 40	F	40	Normal	25
Case 41	M	35	Normal	33
Left temporal cortectomy, anterior and/or posterior T1 damaged (LT1a and LT1p)				
Case 15	M	37	Tumour	9
Case 16	M	45	Head trauma	19
Case 17	M	52	Head trauma	36
Case 18	F	42	Tumour	14
Case 19	F	25	Hippocampal atrophy	18
Case 20	M	44	Normal	36
Case 21	M	35	DNT	14
Case 22	M	36	Normal	32
Right T1S and T1p temporal cortectomy in patients who had been tested before and after surgery				
Case 55	M	36	Cavernus angioma	20
Case 56	F	26	Normal	24
Case 57	M	31		
Case 58	M	25	Hippocampal atrophy	11
Case 59	F	30	Normal	27
Case 60	F	33	Normal	16
Case 61	M	42	Cavernus angioma	24
Case 62	F	20	Normal	15
Case 63	M	20	Normal	10
Case 64	F	32	Calcification	25
Case 65	F	36	Normal	30
Right temporal cortectomy, anterior and/or posterior T1 damaged (RT1a and RT1p)				
Case 42	M	28	Normal	26
Case 43	M	22	Hippocampal sclerosis	10
Case 44	F	29	Hemiatrophy	24
Case 45	M	23	Cavernoma	4
Case 46	F	40	Right temporal lobe atrophy	35
Case 47	F	42	Right temporal lobe atrophy	35
Case 48	M	44	Hippocampal atrophy	4
Case 49	M	37	Hippocampal atrophy	33
Case 50	F	29	Right temporal lobe atrophy	8
Case 51	F	33	Right temporal lobe atrophy	28
Case 52	M	27	Normal	12
Case 53	M	31	Normal	12
Case 54	M	20	Tumour	1