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The role of auditory cortex in retention of rhythmic patterns as studied in patients with temporal lobe removals including Heschl's gyrus

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Abstract

This experiment examined the participation of the auditory cortex of the temporal lobe in the perception and retention of rhythmic patterns. Four patient groups were tested on a paradigm contrasting reproduction of auditory and visual rhythms: those with right or left anterior temporal lobe removals which included Heschl's gyrus (HG), the region of primary auditory cortex (RT-A and LT-A); and patients with right or left anterior temporal lobe removals which did not include HG (RT-a and LT-a). Estimation of lesion extent in HG using an MRI-based probabilistic map indicated that, in the majority of subjects, the lesion was confined to the anterior secondary auditory cortex located on the anterior-lateral extent of HG. On the rhythm reproduction task, RT-A patients were impaired in retention of auditory but not visual rhythms, particularly when accurate reproduction of stimulus durations was required. In contrast, LT-A patients as well as both RT-a and LT-a patients were relatively unimpaired on this task. None of the patient groups was impaired in the ability to make an adequate motor response. Further, they were unimpaired when using a dichotomous response mode, indicating that they were able to adequately differentiate the stimulus durations and, when given an alternative method of encoding, to retain them. Taken together, these results point to a specific role for the right anterior secondary auditory cortex in the retention of a precise analogue representation of auditory tonal patterns. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Rhythm is an integral component of music in every culture, but the way auditory temporal patterns are processed in the brain is little understood. The aim of this experiment was to examine the perception and retention of rhythmic patterns and to explore their neural substrates in the human brain. Previous neuropsychological studies of rhythm can generally be divided into those which examine basic parameters of temporal perception, such as perception of duration and temporal order (Efron, 1963; Robin et al., 1990; Swisher and Hirsh, 1972) and those which examine perception of musical rhythms (Peretz and Kolinsky, 1993; Peretz et al., 1994; Prior et al., 1990; Shapiro et al., 1981). The results of both types of study link these functions to the auditory cortex of the temporal lobes, but show no more specific localization within auditory cortex. In the present experiment, patients with varying amounts of removal in auditory cortex were tested on a rhythm perception and reproduction task, with the hypothesis that patients with larger removals would be more impaired. In designing the task, we attempted to strike a balance between the two types of study described above, using stimuli focussed on the perception of duration and temporal order, but which were similar to real musical rhythms. Further, the perception and retention of the auditory rhythms was contrasted with the perception and retention of visual rhythms to allow us to specify any observed deficit to the auditory domain. An important feature of this study was the use of post-operative MRI scans and a probabilistic map of the region of primary auditory cortex (Penhune et al., 1996), to identify and estimate the extent of surgical removal in these subjects.

Researchers interested in the function of the human brain have studied musical perception and production since the early 19th century when it was first observed

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that individuals with brain damage could be impaired specifically in musical functions, while other functions remained intact (Marin and Perry, in press). A few cases have been reported of patients with particular impairments in rhythm perception or production (Fries and Swihart 1990; Marin and Perry, in press; Mavlov, 1980), but these patients usually have substantial deficits in other areas of musical function and the location of their lesions is quite variable. The majority of neuropsychological investigations of rhythm perception have focussed on the study of groups of patients with brain lesions. As described above, these studies can generally be divided into two categories: (1) those that examine the basic parameters of temporal perception and (2) those that examine perception of musical rhythm. Studies of basic parameters have often made the link between the temporal perception thought to be required for human speech and the perception of musical rhythm. Researchers have tested patients using simple psychophysical paradigms, hypothesizing that patients with damage to the left, language-dominant, hemisphere would be impaired on these tasks. The hypothesis of left hemisphere dominance for auditory temporal perception has also been extended to studies of musical rhythm. The background and neuropsychological literature related to both types of study will be reviewed below.

The most frequently examined parameters in studies of basic temporal perception are: discrimination thresholds for the durations of sounds and silences (Allan, 1979), detection of gaps introduced into continuous sounds and identification of the temporal order of successive stimuli (Moore, 1989). Most of these experiments involve detecting very small differences between two stimuli (typically 2–50 ms), because they are geared toward understanding the temporal mechanisms underlying speech perception. Among the most important components of the auditory signal for perceiving speech are the very brief temporal changes which distinguish one phoneme from another (Blumstein and Stevens, 1979, 1980). In order to differentiate these phonemes, the auditory system must be able to resolve temporal changes in the 10–30 ms range (Phillips and Farmer, 1990). This time window is very different from that of typical musical rhythms, which usually occur over a period of seconds. However, it has often been assumed that the basic mechanisms for encoding temporal information should be similar in both cases.

A number of studies have documented deficits in perception of basic temporal parameters in patients with brain damage. Impairments in gap detection have been observed in patients with bilateral lesions to primary auditory cortex (PAC), who also show striking impairments in the ability to understand speech (Phillips and Farmer, 1990). Gap detection impairments have also been observed in patients with left and right anterior temporal lobe removals when stimuli are presented contralateral to the lesion (Efron et al., 1985). Robin et al. (1990) showed a dissociation between impairments in 'temporal' and 'pitch-based' aspects of auditory perception in patients with temporo-parietal damage: patients with left-hemisphere stroke were impaired on gap-detection and temporal pattern matching; and patients with right-hemisphere stroke were impaired in frequency-sweep discrimination and pitch-matching. Divenyi and Robinson (1989) made a similar attempt to classify temporal and pitch related functions, but they considered frequency-sweep discrimination to be a temporal task. They found left-hemisphere stroke patients to be impaired, but unfortunately, no localization information was available for these patients beyond their aphasic symptoms. Milner (1962) showed that patients with right anterior-temporal lobe removals were impaired in duration discrimination, but not in discrimination of musical rhythms. Impairments in temporal ordering have been shown for patients with left and right-temporal lobe removals when stimuli are presented contralateral to the lesion (Sherwin and Efron, 1980). Broca's speech area has also been implicated in temporal ordering (Efron, 1963; Swisher and Hirsh, 1972), but in both of these studies the only information regarding the location of the lesion are the patients' aphasic symptoms. Unfortunately, all studies of temporal order tested two sounds of different pitch, thus confounding pitch and order. Taken together, the data reviewed above link basic functions such as gap detection, duration discrimination and temporal ordering to the auditory cortex of the temporal lobe, but support no more precise localization within this region.

As noted above, the hypothesis that the left hemisphere might be dominant for the perception of auditory temporal information has also been extended to the perception of musical rhythm. In normal subjects, dichotic listening studies found a right-ear, left-hemisphere advantage for recognition of specifically rhythmic material (Gordon, 1978; Robinson and Solomon, 1974). Unfortunately, data from patient studies of musical rhythm are not so clear. As described above, Milner (1962) found no impairment in rhythm discrimination for patients with either left or right anterior-temporal lobe removals using the Seashore Test of Musical Talent (Saeveit et al., 1940). Using the same instrument, Kester et al. (1991) found that patients with right anterior-temporal lobe removals were impaired in discriminating changes in both rhythm and tempo. In a study requiring subjects to identify changes to familiar tunes, Shapiro et al. (1981) found that right-hemisphere damaged patients were impaired compared to controls and left-hemisphere damaged patients when making judgements where either pitch or rhythm was manipulated. However, in the experimental design, rhythm and pitch manipulations were made on different tunes, confounding the parameter of interest with the stimulus item. In addition, the patient groups were defined according to their neurological symptoms alone, with no direct information about the site of lesion. Prior et al. (1990) found left-hemisphere stroke patients to be poorer at discriminating rhythmic changes than right-hemisphere stroke patients and normal controls for both familiar and unfamiliar tunes. Using a rhythm discrimination task involving changes in the duration of single elements, Peretz (1990) found that both right and left-hemisphere stroke patients were impaired. Within these patient groups, she found two left-hemisphere patients who were impaired for rhythmic but not pitch based discrimination and two right-hemisphere patients who were impaired on pitch based, but not rhythm based discrimination. Following up this dissociation in two in-depth case-studies, it was found that patients with bilateral damage to the auditory cortex were impaired in their ability to discriminate melodic but not rhythmic changes (Peretz and Kolinsky, 1993; Peretz et al., 1994), providing evidence that rhythmic and melodic processing can be dissociated, but showing no clear lateralization to either hemisphere. In summary, review of the neuropsychological literature related to both basic temporal parameters and musical rhythm links these functions to the auditory cortices of the temporal lobe, but does not demonstrate a more precise localization within auditory cortex, nor any consistent lateralization to either the left or right hemisphere.

Overall, interpretation of many of these studies is made difficult by the use of patient groups with large or poorly described lesions. Further, drawing parallels between the results of the two types of experiments is problematic because of incompatibilities in the stimuli used. In the basic studies, parameters such as duration and temporal order which are typically conjoined in musical rhythm are examined separately. In addition, the time-frame over which these parameters are evaluated is brief, usually 2–50 ms, much shorter than the time-frame relevant for a typical musical rhythm. Further, most of these stimuli involve only two elements, many fewer than a typical musical rhythm. Finally, the most commonly used paradigm, gap detection, has no clear parallel in the perception of musical rhythm. Conversely, while experiments with musical stimuli have the advantage of being musically relevant, they often confound rhythm and pitch judgements, or require other cognitive processes, such as naming, which are not specific to rhythm processing per se. Most importantly, perceptual judgements of longer musical stimuli require the involvement of working memory, which is often not considered in the interpretation of the results.

1.1. Experimental design

For the present experiment a task was developed that taps both duration and temporal order, within auditory temporal patterns similar to real musical rhythms. The paradigm was based on a series of studies in which normal subjects reproduced auditory and visual rhythmic patterns (Glenberg and Jona, 1991; Glenberg et al., 1989). These patterns were composed of short and long elements with a constant inter-tone-interval (ITI). Subjects' responses were scored for each element in the rhythm, producing a percentage correct score for each position in the sequence. Across several experimental conditions, Glenberg showed a robust effect of modality: auditory rhythms were more accurately reproduced than visual rhythms. In one experiment (Glenberg et al., 1989), subjects reproduced the rhythms in two different ways: a dichotomous response mode (DICH) in which 'short' and 'long' keys were pressed for short and long elements and a continuous response mode (CONT), in which subjects pressed a single key, using the key-press and key-release durations to imitate the rhythm. These results showed similar levels of performance for the two response modes. For the present experiment, auditory and visual rhythmic patterns similar to those used by Glenberg were developed and both the DICH and CONT response modes were used. This paradigm presents several advantages: First, by using the two types of stimuli, the effect of auditory cortex lesions on performance of auditory rhythms can be compared to that for visual rhythms. Second, the two response modes require subjects to encode the rhythmic patterns differently in working memory: the CONT condition promotes explicitly temporal encoding, while the DICH promotes verbal, categorical mediation. This allows comparison of the effect of auditory cortex lesions under two different encoding/working memory conditions.

1.2. Hypotheses

The subject groups tested in this experiment were patients with unilateral anterior temporal-lobe removals that included Heschl's gyrus (HG) and patients with unilateral anterior temporal-lobe removals that did not include this region. The region of primary auditory cortex is located on the posterior-medial two-thirds of HG (Rademacher et al., 1993). The rest of the gyrus contains secondary auditory cortex which continues onto the surface of the temporal lobe both anterior and lateral to HG (Galaburda and Sanides, 1980). Therefore, patients with standard anterior temporal lobe excisions would have some removal of anterior secondary auditory cortex. Those with excisions which included HG would have larger secondary cortex removals, as well as possible primary auditory cortex removals. Based on the neuropsychological literature described above and the different task manipulations, four specific hypotheses were made about the performance of these groups. First, if auditory rhythm processing is specifically dependent on temporal lobe auditory cortex, performance for auditory, but not visual rhythms should be impaired. Second, if rhythm processing is lateralized, as are certain other aspects of auditory perception, then whether a deficit is observed should depend on the side of excision. Third, if the observed deficit is the result of a disturbance in basic auditory function (e.g. duration perception), the degree of deficit might depend on whether the removal extends into PAC-r. Finally, it was predicted that if PAC-r was important for the encoding or retention of the specifically temporal dimension of the stimuli, then a deficit might be observed for the CONT, but not the DICH response mode.

2. Methods

2.1. Subjects

Four groups of patients with surgical excisions for the relief of intractable epilepsy were tested in this experiment. These were: nine patients with right and seven patients with left anterior temporal-lobe removals that were reported at surgery to extend into HG (RT-A and LT-A, respectively); and 15 patients with right and 18 with left anterior temporal-lobe removals that included only secondary auditory cortex anterior to HG (RT-a and LT-a, respectively). In the RT-A and LT-A patients, hippocampal removals were confined to the pes (approximately the anterior 0.5 cm of the hippocampus); whereas in the RT-a and LT-a patients, hippocampal removals varied from 1.5–3.0 cm in extent. Thus, the RT-A and LT-A groups have large auditory cortex removals and small hippocampal removals, whereas the RT-a and LT-a groups have large hippocampal removals and small auditory cortex removals. The contrasting lesion types in these groups allow comparison of the effects of auditory cortex and hippocampal removals on perception and retention of the rhythm sequences. Thirteen normal control subjects (NL) were also tested.

Patient subjects had extensive neuropsychological and seizure evaluations as part of their pre- and post-operative testing. Primary inclusion criteria for this study were: WAIS-R Full-Scale IQ score >75; relatively focal, static or atrophic lesion (including tumors of grades 1 and 2 and some arteriovenous malformations); no significant EEG abnormality contralateral to the side of lesion; no evidence of diffuse impairment not specific to the lesion site and no evidence of hearing loss or impairment. Subjects with HG removals returned to the hospital specifically for research testing and received follow-up neuropsychological testing, including memory and language tests at this time. Relevant data are reported in the Results section and in Table 3. NL subjects were matched for age, handedness, years of education and extent of musical training. Subjects were right-handed and were tested in their preferred language, either French or English. All subjects gave written informed consent and the experimental protocol was approved by the Ethics Committee of the Montreal Neurological Institute (MNI).

2.2. MRI scan acquisition

Patient scans were performed on a Philips Gyroscan system with a 1.5 T superconducting magnet using a 3-D FFE acquisition sequence to collect 160 contiguous 1 mm, T1-weighted images in the sagittal plane ($TR = 18$ ms, $TE = 10$ ms). These data were transformed into standardized stereotaxic space (Talairach and Tournoux, 1988) using an automatic registration program developed at the McConnell Brain Imaging Center at the MNI. This registration procedure uses a multiscale 3-D cross-correlation procedure to match each individual MRI volume to the average ($n = 305$) MR brain volume previously aligned with stereotaxic space (Collins et al. 1994). This resampling results in a volume of 160 1 mm slices with an in-plane matrix of 256×256. Once patient scans were transformed into the standardized space, they were coregistered with the probabilistic map of PAC-r, allowing identification and estimation of the removal in that region, as will be described in detail below. This and the other data analysis programs were run on SGI workstations.

2.3. Stimuli and task conditions

The stimuli used in this experiment were 6-element auditory and visual rhythmic patterns, composed of short (250 ms) and long (750 ms) elements separated by a constant (250 ms) ITI. These durations were selected to produce a simple 2:1 ratio (duration + ITI). In the auditory conditions, the elements were 3000 Hz tones with 5 ms rise and fall times delivered binaurally over headphones. Volume was adjusted to a comfortable level for each subject. In the visual conditions, the elements were 2.5 cm white squares which appeared sequentially at the same location in the center of a computer monitor, positioned approximately 45 cm from the subject's eyes. In both conditions, each sequence was followed by a pause during which the subjects were instructed to imitate the sequence using one of the two response modes. Subjects were given graded practice for each response mode by modality combination before performing the test sequences. Figure 1 illustrates the practice and test sequences, as well as the modes of response. Practice stimuli (see panel A) were made up of sets of simple 3-element sequences, followed by simple 6-element sequences and finally four 6-element sequences that were similar in difficulty to the test sequences. The simple practice sequences were designed to require an equal number of short and long responses. Test stimuli (see panel B) were 16 different randomly-presented sequences which were the same for all conditions. These sequences were constructed to be of equal difficulty, such that each one had no more than three repeated elements and contained at least three transitions from short to long or long to short. These rules produce syncopated rhythmic

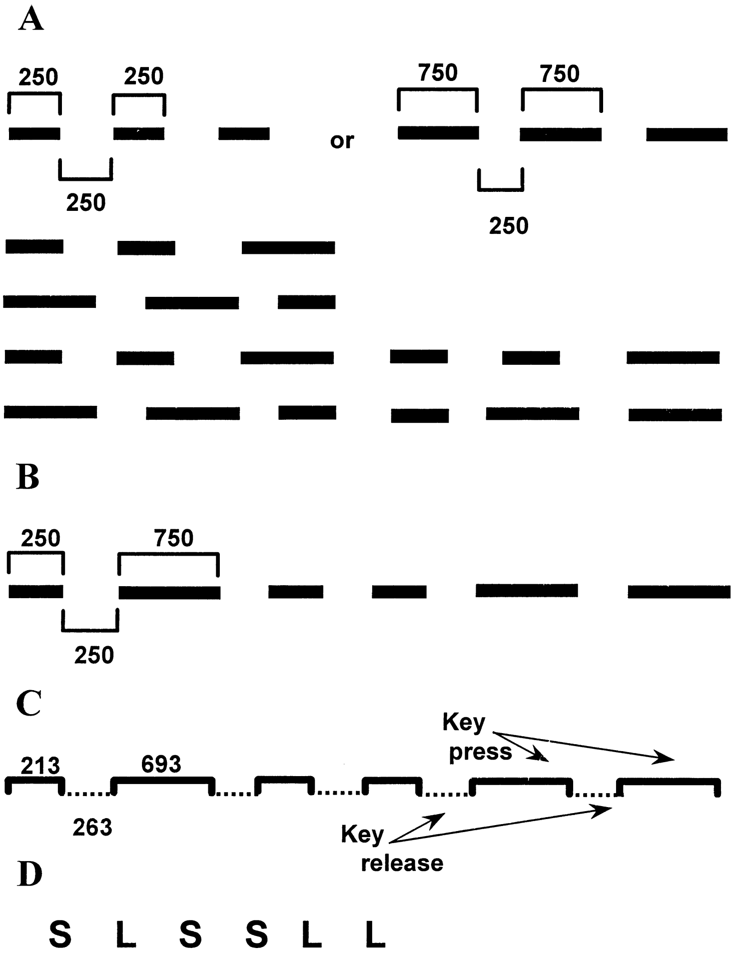

Fig. 1. Practice and test sequences and response modes for the rhythm task. The same sequences were used for both the auditory and visual modalities. **Panel A** illustrates the simple 3-element and 6-element practice sequences. **Panel B** gives an example of one of the 16 test sequences. **Panels C and D** illustrate the continuous and dichotomous response modes and the data recorded by the computer.

patterns, i.e. rhythms which are temporally regular, but do not conform to a simple musical beat pattern. Stimulus delivery and response collection were controlled by MAPLE software (Bregman et al., 1992) running on a 486/50 IBM compatible computer.

All subjects used both response modes to imitate the sequences in separate blocks. In the CONT condition (Fig. 1, panel C), subjects were instructed to imitate the sequences by tapping on a single key of the computer keyboard; holding it down for the duration of each element and lifting it for the silence in between. In the DICH condition (see panel D), subjects were instructed to imitate the duration and order of the elements by pressing the ‘short’ key for each short sound and the ‘long’ key for each long sound. In the DICH condition subjects were specifically instructed that the duration of the key-press was irrelevant and that key-presses could be as long or as short as was comfortable. Subjects had unlimited time to respond, but were instructed to avoid pausing within the sequence, once they had begun their response. No auditory or visual feedback accompanied the subjects’ responses.

2.4. Procedure

The two modalities, auditory and visual, and the two response modes, CONT and DICH, produced a total of four conditions. The order of presentation of the four conditions was counterbalanced for response type and modality across subjects within each group. In each testing session, subjects were first given the practice trials and then the test sequences for each condition. If a subject had difficulty with the practice trials, they were repeated. Any subject who was unable to perform the simple practice trials was excluded. Four subjects, 2 LT-a and 2 RT-a were excluded for this reason. The experimenter gave verbal feedback on performance of the practice trials to be certain that subjects correctly implemented the two response modes. In particular, in the CONT mode, feedback was given to ensure that subjects used the key-press to imitate the durations and that short and long key-presses were readily distinguishable. During the test sequences, occasional verbal feedback was given to ensure that subjects maintained attention. Sequences could be repeated if the subject requested. There were no differences among the groups for the number of repeated sequences for either the auditory or the visual modality. All responses were recorded by the computer. In the CONT condition (Fig 1, panel C), the key-press and key-release durations were recorded, in the DICH condition, a binary code was recorded. During the debriefing following the testing, subjects were questioned as to their musical training and experience. This information was used to derive a global Index of Musical Training and Experience which is described below.

2.5. *Data analysis*

Responses were scored as correct or incorrect for each element in the sequence and averaged across sequences to determine the overall percentage correct for each of the six elements. For the DICH condition, scoring was straightforward: subjects' 'short' and 'long' responses were matched to each element of the test sequences. Scoring for the CONT condition was more complex and a number of different methods were implemented. The first method was similar to that used by Glenberg et al. (1989). Here, the cut-point between the two responses which resulted in the greatest overall percentage correct across all sequences was derived using an iterative scoring process with 10 ms increments between 150 and 550 ms. Two additional methods were implemented, designed to look more specifically at the subjects' ability to reproduce the correct stimulus durations. These analyses used individual subjects' responses on the eighteen simple practice sequences to define the duration of short and long responses which would be considered correct for the test sequences. The advantage of these scoring methods is that they take into account the variability of each subjects' response and do not penalize subjects who might perform either more slowly or more quickly overall. In the first method, the median split, median short and long responses were determined from the practice trials and the mid-way point between the difference was used as the upper and lower bounds for a correct short or long response, respectively, on the test sequences. In the second method, the average and SD of the short and long response durations for the practice sequences were determined, excluding obvious outliers. A correct short response for the test sequences was then defined as $< \mathrm{Avg}_{\mathrm{short}} + 1.5$ SD and a correct long response was defined as $> \mathrm{Avg}_{\mathrm{long}} - 1.5$ SD. This scoring method is stricter than the median split, requiring the subject to maintain a stable response for each duration and scoring as incorrect ambiguous responses which fall between the upper and lower bounds for short and long.

An important issue for interpreting the data from this experiment is being able to distinguish subjects' ability to make the motor responses required to reproduce the sequences from their ability to encode or retain them. It is possible that subjects could correctly perceive the durations, but would be unable to make the appropriate motor response to reproduce them correctly. The DICH response condition provides one control for this problem, because precise motor control is not required to make an accurate response. In order to examine these issues more closely in the CONT response condition, the averages and SDs for the short and long responses in both the practice sequences and the test sequences were compared across groups as a measure of response variability. In addition, percentage difference scores were computed comparing the total produced and expected durations of each sequence [(produced − expected)/expected]. These measures were intended to examine global changes in tempo of response—speeding up or slowing down—in the patient groups. Finally, average time to first response was examined, again as an index of possible slowing.

Another important issue for the interpretation of these data is the degree to which musical training or experience might affect performance. Individuals with more musical training might approach the task differently and indeed might perceive and reproduce the sequences differently. A recent study of brain morphology in musically trained individuals found differences in the size of the corpus callosum in subjects who began their musical training before the age of seven (Schlaug et al., 1995). For this reason, a global Index of Musical Training and Experience, ranging from 0–8, was derived for each subject. This index took three specific factors into account: years of musical training or experience, whether training began before or after age seven and whether or not the subject currently engaged in any musical practice. The criteria for each index score are detailed in Table 1.

Table 1
Index of musical training and experience

Score	Criteria
0	No training or experience
1	1–3 years training or experience, no current practice
2	1–3 years training or experience before age 7, no current practice
3	3+ years training or experience, no current practice
4	3+ years training or experience before age 7, no current practice
5	1–3 years training or experience, current practice
6	1–3 years training or experience before age 7, current practice
7	3+ years training or experience, current practice
8	3+ years training or experience before age 7, current practice

3. Results

3.1. Estimation of PAC-r removals

Estimates of lesion extent for the LT-A and RT-A patients were made from post-operative MRI scans which had been transformed into the standardized stereotaxic space of Talairach and Tournoux (1988). The identification and estimation of lesion extent were made using REGISTER, an interactive 3-D imaging software package. Individual scans were coregistered with a map of the region of primary auditory cortex (PAC-r) developed in a previous study (Penhune et al., 1996). The scans were viewed simultaneously in the coronal, horizontal and sagittal planes of section. The most important result of the lesion estimation was the finding that in the majority of patients with HG removals the excision extended only to the anterior one-half to two-thirds of the gyrus. Given that primary auditory cortex usually covers only the posterior two-thirds of the gyrus (Rademacher et al., 1993), the removals in these patients generally included only the anterior secondary auditory regions, with very limited removal in primary auditory cortex itself. Results of the lesion estimation for each patient are presented in Table 2.

The estimation was complicated by the fact that in many of the cases, in addition to the cortical-r removal, some extent of the white matter underlying the region was removed because the resections tended to angle back under the superior temporal gyrus. This angling back frequently undercut the remaining tissue creating what could be a further functional lesion. The white matter tracts leading from the medial geniculate nucleus of the thalamus to PAC-r course through the medial portion of the temporal lobe and then fan out along the gyrus (Pfeifer, 1920). In a number of cases, there was no removal of PAC-r at all, but varying degrees of undercutting were present. Figure 2 (top panel) shows an example of a patient with an RT-A removal in which the anterior-lateral 50–60% PAC-r was excised and was undercut to the 60–70% level. Figure 2 (bottom panel) illustrates the appearance of the excised and undercut regions in close-up views.

Table 2
Lesion extent

Subject	Side	HG Removal % Excised	% Undercut	Rank	Hippocampal removal
LT-A2	L	20–30	30–40	4	h
LT-A2	L	40–50	50–60	3	h
LT-A3	L	0	0	0	h
LT-A4	L	0	10–20	9	h
LT-A5	L	0	0	0	h
LT-A6	L	0	40–50	6	h
LT-A7	L	0	10–20	9	h
RT-A1	R	0	40–50	6	H
RT-A2	R	0	30–40	7	h
RT-A3*	R	50–60	60–70	2	h
RT-A4	R	30–40	60–70	4	h
RT-A5	R	20–30	40–50	5	h
RT-A6	R	20–30	40–50	5	h
RT-A7	R	40–50	50–60	3	h
RT-A8	R	0	20–30	8	h
RT-A9	R	80–90	90–100	1	H

* Indicates the subject pictured in Fig. 2.
h $<$ 1.5 cm hippocampal removal; H $>$ 1.5 cm hippocampal removal.

Estimation of the extent of both excision and undercutting was made by finding the most anterior plane of section in each scan where PAC-r had been removed and/or undercut, identifying these locations in stereotaxic space and comparing these planes with the map. The map was scaled to show the region of 25–100 % probability and was divided anterio-posteriorly into 10 equal-length segments on each side, representing 0–10% resection, 10–20% resection, etc. Because the average extent of PAC-r is greater on the left, the segments were relatively larger on the left. The anterior limit of the resection and/or undercutting was located within one of these intervals for each patient. All of the RT-A patients had some excision or undercutting of PAC-r, but two of the putative LT-A patients had no removal at all. For the majority of the patients described in the surgeon's report as having a removal in HG, the extent of the excision tended to be overestimated. Thus ten patients were described as having complete removals, whereas none of the patients had a complete removal in the region. Even the patient whose undercutting was estimated at 90–100% from the map could be seen to have remaining tissue on close inspection of the scan. This is consistent with the findings of previous studies quantifying surgical removals (Awad et al., 1989; Corkin et al., 1997; Jones-Gotman et al., 1997) which indicate that the extent of removal is often overestimated at the time of surgery. It must, of course, be remembered that these excisions were performed with the goal of eliminating seizure activity as recorded at the time of surgery, not with the goal of making a full removal of HG. These findings do, however, illustrate the difficulty of identifying HG given the limited field of view available in a standard surgical procedure, and demonstrate the potential importance of such probabilistic maps to both surgeons and researchers.

All patients in this study had some degree of removal in the hippocampus. In accordance with previous studies (Samson and Zatorre, 1988; Zatorre and Samson, 1991) removals <1.5 cm were designated 'h' and removals >1.5 cm were designated 'H'. In the LT-A and RT-A groups, hippocampal removals were confined to the pes, with the exception of two RT-A subjects who had larger removals (Table 2). In the LT-a and RT-a groups, the removals varied, with the majority having removals greater than 1.5 cm (LT = 13/18; RT = 13/15).

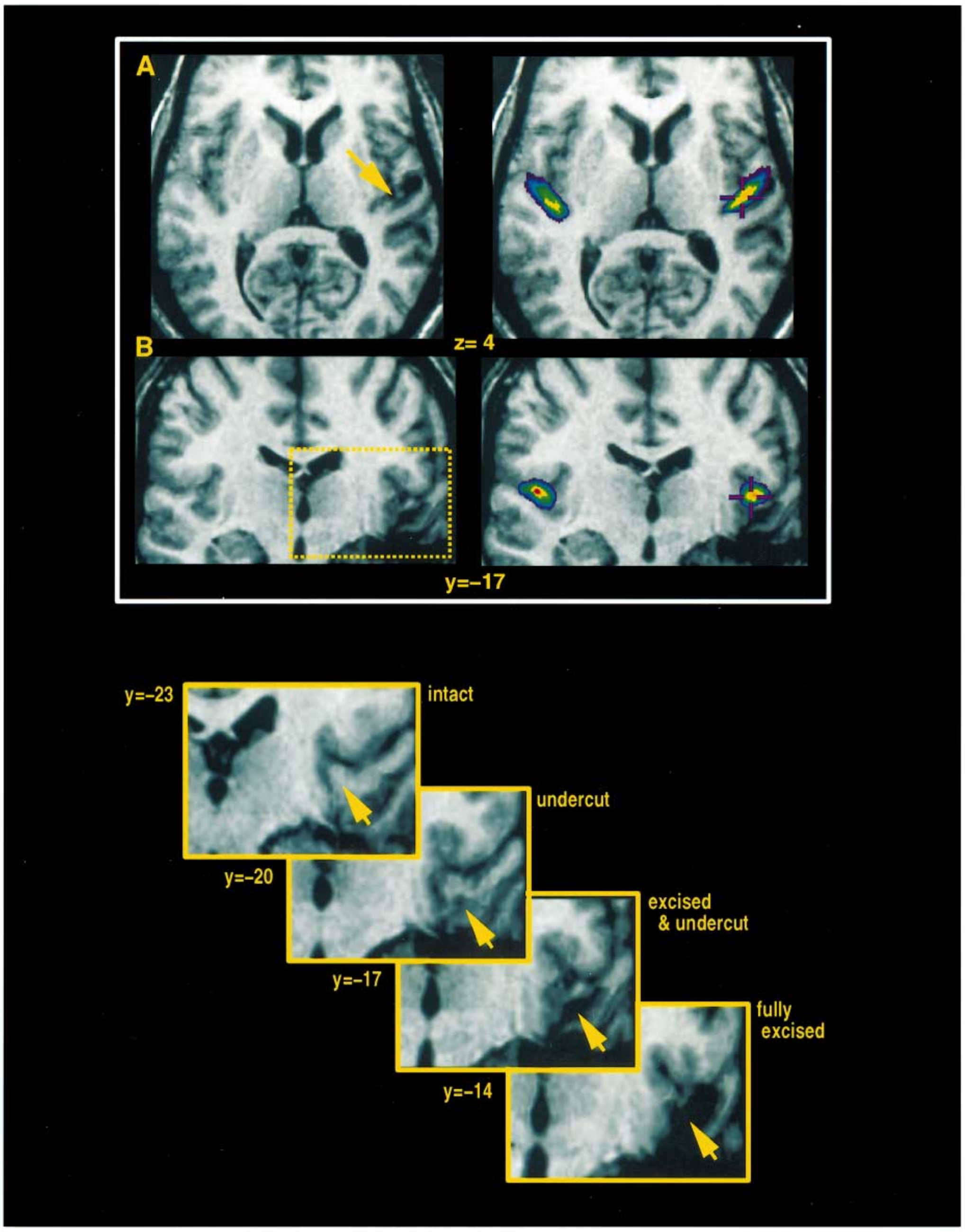

Fig. 2. The upper panel illustrates the MRI scan of a patient with a right PAC-r removal where the excision includes the anterior-lateral 50–60% and the undercutting extends to 60–70%. The scan is presented in the horizontal (A: $z = 4$) and coronal (B: $y = -17$) planes of section. The images on the 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 coregistered with the probabilistic map (scaled from 25–100% probability). The cursor indicates the same position in standardized space as the arrow. The box in the lower left corner 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 PAC-r. In the section labeled 'undercut' note the very thin band of white matter connecting the remaining portion of PAC-r to the rest of the brain. In the section labeled 'excised & undercut' note the unexcised strip of presumed grey matter tissue.

3.2. Neuropsychological and demographic data

The neuropsychological and demographic data as well as the number of subjects in each group are listed in Table 3. Of the 7 LT-A patients, two were excluded entirely from analysis because their surgical removals did not extend into PAC-r, leaving five patients in this group. One RT-A subject was unable to complete the visual CONT condition due to time constraints, leaving eight patients for that condition. Of the other patient groups, one of the RT-a and two of the LT-a subjects completed only the CONT condition due to fatigue or other limi-

Table 3
Neuropsychological and demographic data

Group	*n*	Age	SD	ED	SD	FSIQ	SD	Music	SD
NLs	13	39.0	11.6	13.5	2.2	**	**	1.9	2.0
RT-A	9(8)	41.6	8.4	12.8	3.5	107.3	11.9	2.0	2.3
LT-A	5	35.4	8.4	12.8	1.1	105.8	11.9	2.0	3.1
RT-a	15(14)	33.0	10.3	11.9	3.1	98.5	14.2	2.1	2.6
LT-a	18(16)	35.9	7.1	13.6	2.9	104.8	16.4	1.7	1.3

tations on testing time. Thus the Ns for the CONT response mode were RT-a = 15 and LT-a = 18 and for the DICH response mode were RT-a = 14 and LT-a = 16.

Table 3 also gives the average ages, years of education and musical training index for all subjects, as well as the Full-Scale IQ scores for the patient groups. No significant differences were observed among the patient groups and the normal controls for age ($F(4,55) = 1.45$, $P < 0.23$), years of education ($F(4,55) = 0.87$, $P < 0.49$) or musical training index ($F(4,51) = 0.09$, $P < 0.99$ (NB: data were not available for four subjects on this measure)). None of the patient subjects or normal controls were former or current professional musicians. Finally, no difference in Full-Scale IQ score was observed among the four patient groups ($F(3,42) = 0.85$, $P < 0.48$ (NB: FSIQ was not available for one RT-A patient who did not complete the full assessment at the time of surgery)).

3.3. *Behavioral data*

Results on the rhythm reproduction task for the different response modes and scoring methods are reported separately (Figs 3 and 4) and will be described in detail below. In all cases, percentage correct scores were determined for each position in the 6-element sequences by collapsing across the 16 test trials in each modality. Auditory and visual sequences were analysed separately using ANOVA with Position as the repeated measure and Group as the between subjects factor. Across modalities and for all scoring methods, there was a significant effect of Position, such that percentage correct declined across the six positions. For all scoring methods, the visual condition showed a significant Position × Group interaction, but no main effect of Group. In the auditory condition, there was no Position × Group interaction, but a significant effect of Group. Because differences between groups across the six positions were of greatest interest, and in order to make further analyses compatible across the two modalities, post-hoc tests of simple main effects were conducted across groups at each position. When tests of simple main effects were significant, differences between each patient group and the NLs were assessed using Tukey's HSD with the harmonic N to compensate for differences in group size. Results of the post-hoc tests were considered significant when $P < 0.05$.

Overall, the pattern of results in the CONT condition was quite similar for all of the scoring methods. When performance was collapsed across positions, the RT-A group showed overall poorer performance for the auditory but not the visual rhythms. This decrement was most evident when scoring emphasized accurate reproduction of the individual stimulus durations. When performance was examined at each position, the RT-A group performed poorly early in the sequences, at positions 2 and 3, while performance for the other patient groups dropped only at the final position. None of the patient groups showed an overall impairment for the visual rhythms, but all groups performed more poorly at the final position. Measures of response variability indicated that none of the patient groups were impaired in their ability to use the key-press response to reproduce the sequences. Results from the DICH condition showed no group differences in performance for the auditory condition, even at the final position. In the visual modality, only the LT-A group performed more poorly at the final position.

3.4. *Response variability*

In order to interpret the RT-A patients deficit in the CONT condition, it is necessary to establish that the impairment is not a result of a disturbance in the subjects' ability to make the required motor response. For this reason, a number of measures of response variability were examined. Possible differences between groups for each measure were assessed using one-way ANOVA followed by Tukey's HSD tests with a harmonic N when required. Table 4 presents the averages and SDs of long and short responses for both the practice and test sequences. For the test sequences, only correct responses were used. No significant group differences in average response durations were found. Significant differences in SD were found only between the LT-A group and NLs for the auditory short practice response ($F(4,55) = 2.6$, $P < 0.05$) and between the RT-A group and the NLs for the visual short practice response ($F(4,54) = 3.15$, $P < 0.02$), with both patient groups having larger SDs than NLs. The observed difference in variability for the visual response would not appear to account for RT-A group's poorer performance for the auditory sequences alone. Further, such differences in SD would not necessarily lead to lower scores for the test sequences: in the iterative and median-split scoring methods, the SD is irrelevant to the score and the SD method by definition accounts for individual differences in variance. Table 5 presents the average time to first response and the average percentage difference scores for the total duration of each sequence. No significant group differences were found on any of these measures for either modality. Taken together, these results indicate no consistent impairment in

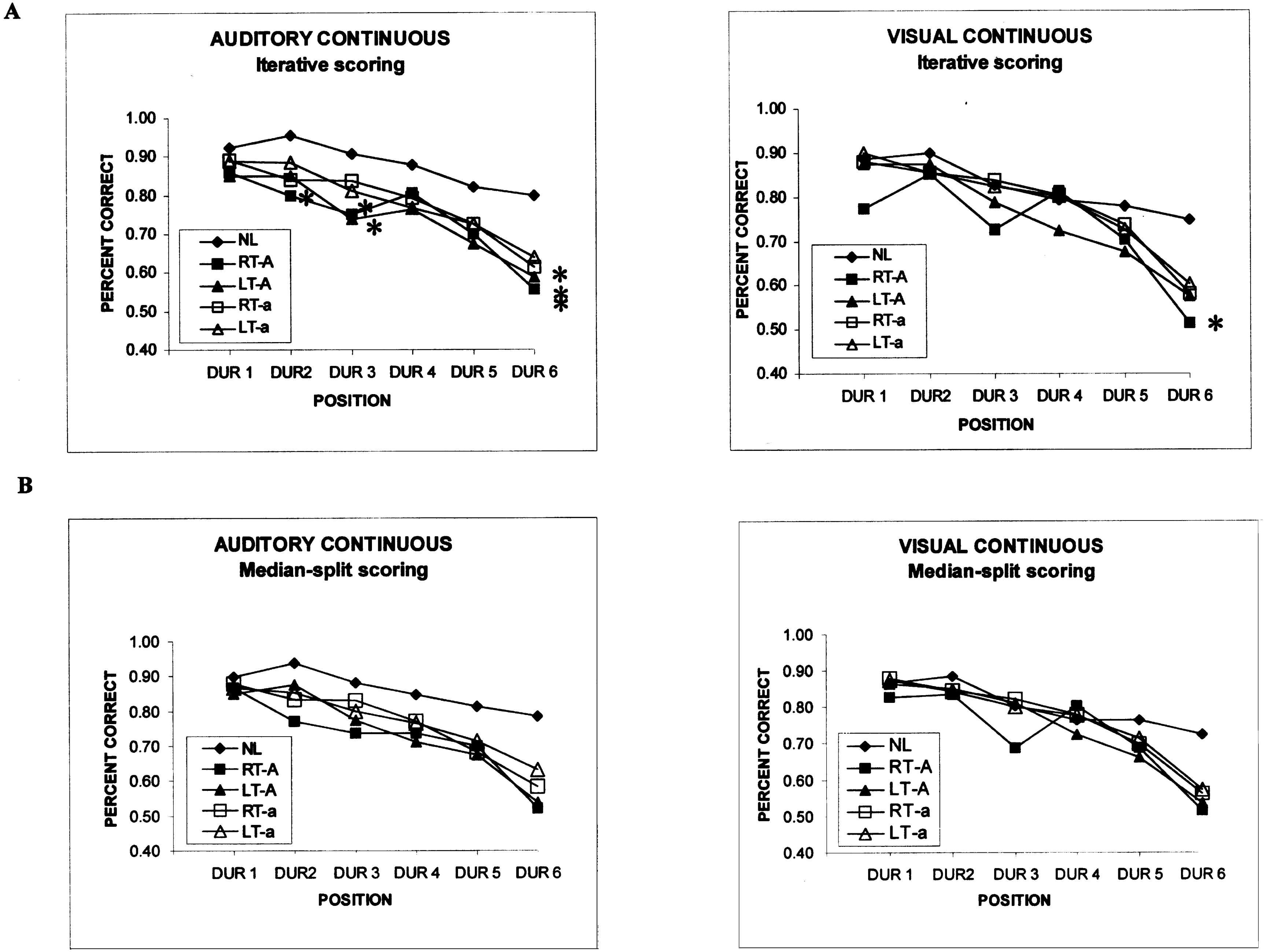

Fig. 3. Performance of patients and normals on the auditory (left column) and visual (right column) rhythms for the CONT response mode. The graphs in the upper panel illustrate performance scored with the iterative method and the graphs in the lower panel illustrate performance as scored with the median split method. An asterisk indicates a significant difference obtained between the patient group and normals.

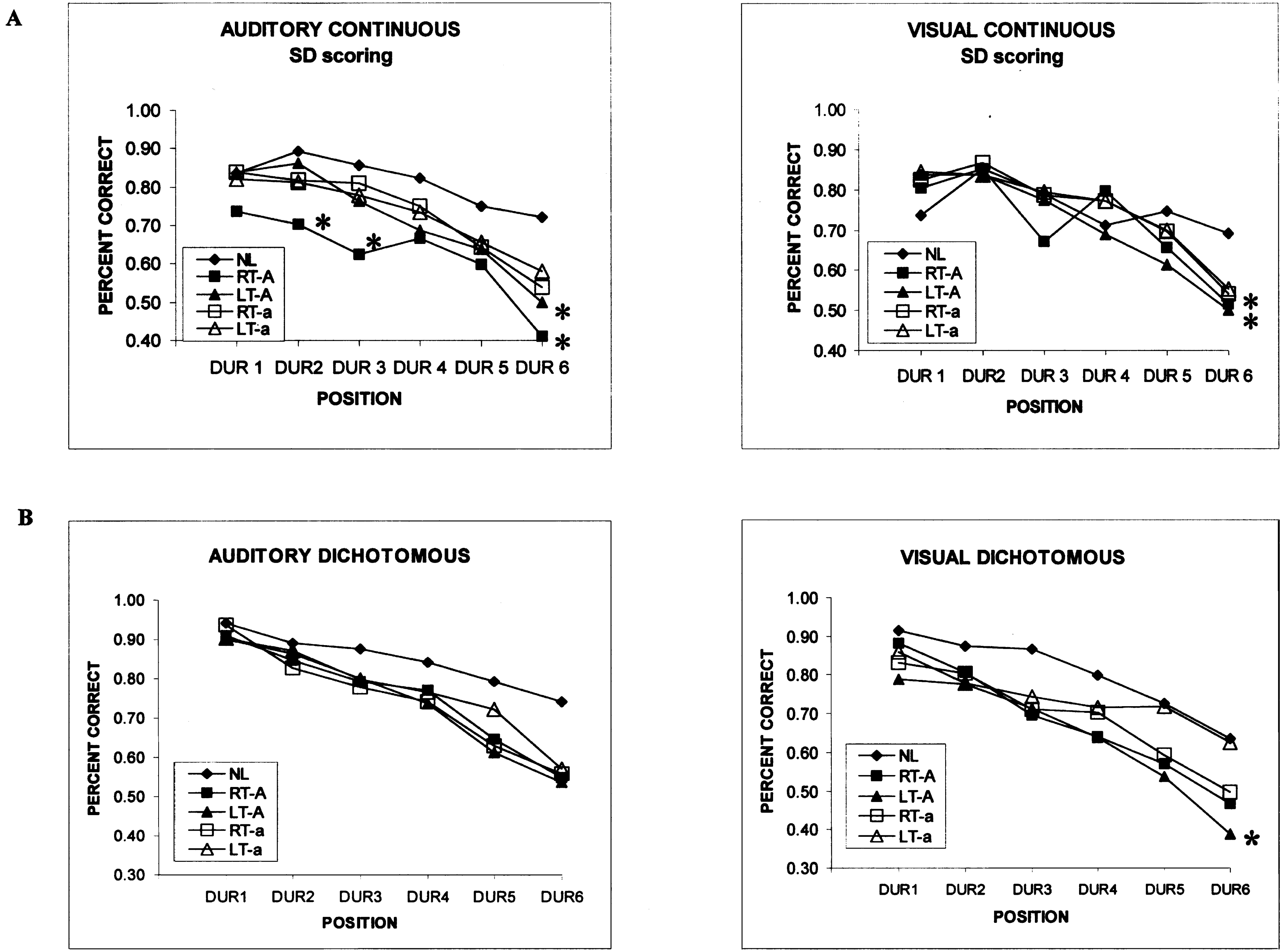

Fig. 4. Performance of patients and normals on the auditory (left column) and visual (right column) rhythms. The graphs in the upper panel illustrate performance for the CONT response mode scored with the SD method. The graphs in the lower panel illustrate performance for the DICH response mode as scored with the median split method. An asterisk indicates a significant difference obtained between the patient group and normals.

Table 4
Averages and SDs of short and long responses for practice and test trial data

	Auditory				Visual			
	Practice data		Test data		Practice data		Test data	
Group	Short	Long	Short	Long	Short	Long	Short	Long
NL	212±41	627±127	214±50	690±131	219±45	602±136	220±49	691±14
RT-A	198±55	672±171	218±58	751±166	260±119*	659±209	209±55	781±159
LT-A	221±89*	695±172	215±60	767±128	264±109	595±199	227±53	737±151
RT-a	201±55	693±154	188±53	777±165	223±78	615±173	207±42	771±191
LT-a	216±59	629±142	204±50	683±122	222±72	576±156	202±46	690±125

*Indicates a significant difference for the SD only.

Table 5
Latency to first response and average percentage differences for response and total sequence durations

Group	Auditory Latency to first response	Visual	Auditory Duration	Visual Duration
NL	909±419	1496±704	−0.12	−0.11
RT-A	1342±1071	1624±588	−0.13	−0.08
LT-A	1674±1194	1822±901	−0.06	−0.06
RT-a	1346±735	1696±498	−0.10	−0.08
LT-a	1312±586	1759±479	−0.14	−0.15

No significant differences obtained.

subjects' ability to reproduce the required motor response.

3.5. *Iterative scoring*

Analysis of the iterative scoring method (Fig. 3) showed a significant effect of Position for both modalities (Aud: $F(5,275) = 44.47$, $P < 0.001$; Vis: $F(5,270) = 42.00$, $P < 0.001$) and a significant Position × Group interaction for the visual condition only (Aud: $F(20,275) = 1.14$, $P < 0.30$; Vis: $F(20,270) = 1.69$, $P < 0.03$). A significant effect of Group was present for the auditory condition (Aud: $F(4,55) = 2.98$, $P < 0.03$; Vis: $F(4,54) = 0.99$, $P < 0.42$) and post-hoc tests showed that both the RT-A and LT-A groups performed more poorly overall than the NLs. Tests of simple main effects were significant at positions 2,3 and 6 (2: $F(4,55) = 3.34$, $P < 0.02$; 3: $F(4,55) = 2.51$, $P < 0.05$ and 6: $F(4,55) = 4.49$, $P < 0.01$), with RT-A subjects impaired at position 2; RT-A and LT-A subjects impaired at position 3 and RT-A, LT-A and RT-a subjects impaired at position 6. In the visual condition, tests of simple main effects were significant only at position 6 ($F(4,54) = 3.88$, $P < 0.01$) with RT-A subjects impaired.

3.6. *Median split scoring*

Analysis of the median-split scoring method revealed a similar pattern of results to that seen for the iterative scoring method (Fig. 3). There was a significant effect of Position for both modalities (Aud: $F(5,275) = 51.54$, $P < 0.001$; Vis: $F(5,270) = 48.83$, $P < 0.001$) and a significant Group by Position interaction for the visual condition only (Aud: $F(20,275) = 1.53$, $P < 0.07$; Vis: $F(20,270) = 1.61$, $P < 0.05$). In the auditory condition, there was a marginally significant effect of Group (Aud: $F(4,55) = 2.47$, $P < 0.06$; Vis: $F(4,54) = 0.61$, $P < 0.65$) and post-hoc tests on group means showed that the RT-A group performed more poorly overall than the NLs. Tests of simple main effects were significant at positions 2 and 6 (2: $F(4,55) = 3.35$, $P < 0.02$ and 6: $F(4,55) = 4.96$, $P < 0.01$), with RT-A subjects alone impaired at position 2 and RT-A, LT-A and RT-a subjects impaired at position 6. In the visual condition, post-hoc tests of simple main effects were significant at only position 6 ($F(4,54) = 3.59$, $P < 0.01$), with both RT-A and LT-A subjects impaired.

3.7. *SD scoring*

Using the SD scoring method (Fig. 4), there was a significant effect of Position for both modalities (Aud: $F(5,275) = 51.45$, $P < 0.001$; Vis: $F(5,270) = 48.78$, $P < 0.001$) and a significant Group by Position interaction for the visual condition (Aud: $F(20,275) = 1.4$, $P < 0.12$; Vis: $F(20,270) = 2.55$, $P < 0.01$). There was a significant effect of Group for the auditory condition (Aud: $F(4,55) = 3.32$, $P < 0.02$; Vis: $F(4,54) = 0.34$, $P < 0.85$) and post-hoc tests showed that the RT-A group performed more poorly overall than NLs. Tests of simple main effects were significant at positions 2, 3 and 6 (2: $F(4,55) = 3.46$, $P < 0.01$; 3: $F(4,55) = 3.92$, $P < 0.01$ and 6: $F(4,55) = 5.76$, $P < 0.01$), with RT-A subjects alone impaired at positions 2 and 3 and LT-A and RT-a subjects impaired at position 6. In the visual condition, post-hoc testing revealed a significant simple main effect only at position 6 ($F(4,54) = 3.28$, $P < 0.02$), with RT-A and LT-A subjects impaired.

3.8. Dichotomous response

Results of analyses for the DICH (Fig. 4) condition were quite different than those obtained for the CONT condition. While the main effect of Position was preserved (Aud: $F(5,255) = 68.47$, $P < 0.001$; Vis: $F(5,255) = 58.09$, $P < 0.001$), there was no Position × Group interaction or main effect of Group for either modality. In order to compare these results with those of the CONT condition, a test of simple main effects was performed at position 6 only. The ANOVA was significant in both conditions (Aud: $F(4,51) = 2.53$, $P < 0.05$; Vis: $F(4,51) = 3.16$, $P < 0.02$), but in the auditory condition, no one group was impaired relative to controls ($P < 0.05$), while in the visual condition, only the LT-A group was significantly impaired.

4. Discussion

The results of this experiment showed that patients with right temporal-lobe removals which included PAC-r showed overall poorer performance for auditory but not visual rhythms. This decrement was observed only in the CONT condition and was most evident with the SD scoring method which emphasized accurate reproduction of the individual stimulus durations. The RT-A group performed poorly across the sequences, while performance for the other patient groups dropped only at the final position. These subjects were not impaired in their ability to make an adequate motor response, as demonstrated by measures of response variability. RT-A patients were also not impaired in the auditory DICH condition, even at the final position, indicating that they were able to adequately differentiate the stimulus durations, and given an alternative method of encoding, were able to retain the sequences. Thus, the observed deficit appears to be the result of an impairment in the ability to retain an accurate representation of the temporal dimension of the auditory stimuli. All patient groups were impaired at the final position for all conditions, possibly indicating a general decrement in memory span across the groups.

Because of the importance of the SD scoring method to the interpretation of these results, a brief discussion of all the scoring methods is warranted. The iterative method is the least specific, with its primary advantage being that it optimizes percentage correct. Thus it is surprising that it was the only condition in which LT-A subjects showed overall poorer performance for the auditory sequences. The disadvantages of this method are that the data to be scored are themselves used to generate the scoring criterion. Secondly, setting the cut-point between short and long responses according to overall percentage correct is relatively insensitive to subjects' ability to reproduce the true stimulus durations accurately. The median-split method solves the first of these problems by using the practice data to generate the scoring criteria for the test data. However, like the iterative method, all responses are categorized as either short or long, which gives only a rough estimate of the subjects' ability to reproduce the stimulus durations accurately. Unlike the both the median-split and iterative methods, where all responses are categorized, in the SD method, responses which fall between the 1.5 SD below and 1.5 SD above, are considered to be ambiguous and are scored as incorrect. Therefore, the RT-A patients' poorer performance when scored with this method indicates the production of a greater number of ambiguous responses. This is in spite of the fact that subjects with larger SDs would have a correspondingly larger range of acceptably correct response. Interpreting this result could be problematic if these subjects were impaired in their ability to make a stable motor response. However, RT-A subjects did not differ significantly from NLs in the variability of either practice or test responses for the auditory sequences, demonstrating that the greater number of ambiguous responses is not the result of an impairment in motor production per se.

Examination of the results of the CONT condition alone would leave open two possible mechanisms underlying the RT-A patients' deficit: an impairment in perception or an impairment in retention. Comparing these results with those in the DICH condition allowed clarification of this issue. None of the patient groups was impaired compared to NLs in the auditory DICH condition, even at the final position. This indicates that the RT-A subjects were able to distinguish the two durations adequately and that when given an alternative method of encoding them, were able to retain them. The DICH response mode directly encourages the subject to encode the durations with the verbal labels 'short' and 'long', thus making a specifically analogue representation of the stimuli in working memory unnecessary. Thus, the deficit observed for the RT-A subjects could be described as a deficit in the retention of a precise analogue representation of the auditory stimulus. Conversely, reliance on verbal labels in the DICH condition may underlie the LT-A subjects' relatively poorer performance for the visual sequences with this response mode.

As described above, the hallmark of the RT-A subjects poorer performance was the production of a greater number of ambiguous responses. There are at least two possible reasons for this: the first is an impaired ability to retain the precise durations of the individual elements in the sequences and the second is an impaired ability to retain the sequence of the elements. Performance of RT-A patients on the simple practice trials indicates that they are able to retain the stimulus durations, but in the context of the complex sequences, this retention is impaired. This could result from interference across the sequence which inhibits the retention of the individual elements, or problems in sequencing which result in the production of ambiguous responses. Performance of RT-A patients in the DICH condition indicates that they can retain the sequence of elements adequately when given an alternate means of encoding the durations in working memory. Therefore, a possible explanation for these patients poorer performance in retaining the auditory durations is a greater effect of interference. This is consistent with the findings of Zatorre and Samson (1991) who showed that patients with RT-A and RT-a lesions were impaired in retaining a pitch over a time interval filled with interfering pitches.

The finding that RT-A patients are impaired in the retention of auditory durations is partially consistent with the finding of Milner (1962) who showed that a mixed group of RT-A and RT-a patients were impaired in the discrimination of durations in the 20–350 ms range. It is also consistent with a number of findings suggesting involvement of the right-temporal lobe in memory and imagery for other types of musical stimuli. In the study described above, Milner (1962) also found that the same group of RT-A and RT-a patients were impaired in the retention and discrimination of short tonal sequences. This work was extended by Zatorre and colleagues in a series of experiments examining melodic discrimination (Samson and Zatorre, 1988; Zatorre, 1985). They found all right temporal patients to be impaired, but that in addition, both RT-A and LT-A removals showed incrementally greater impairments. Similarly, in the pitch retention study described above, Zatorre and Samson (1991) found both RT-A and RT-a patients to be impaired. Taken together, these results confirm the importance of the right temporal lobe and particularly right PAC-r for tonal memory and discrimination. However, they also indicate that disruption of left PAC-r can affect performance on certain tasks as well. This was also evident in the present experiment, where LT-A subjects showed some degree of impairment on the auditory task, particularly when scored with the iterative method. If the results of the present study are considered in this context, it seems possible that the observed impairment is not specific to retention of auditory duration but to tonal retention in general. It may be that the representation of a tonal sequence in temporal auditory cortex combines both pitch and duration information and that disruption of function in this region results in poor encoding and/or retention of both parameters. An experiment specifically contrasting retention of pitch and duration information would allow us to see if these parameters are encoded separately or together.

Further evidence for the involvement of the right temporal lobe in tonal memory comes from a PET study in which retention and discrimination of tones within a melody was compared to passive listening (Zatorre et al., 1994). This subtraction showed activation of the right middle temporal gyrus, a region of multimodal cortex which projects to the hippocampal memory system (Suzuki and Amaral, 1994). Extending this line of work to the study of musical imagery, Zatorre and Halpern (1993) found that patients with RT-a excisions were impaired in their ability to generate an auditory image of a familiar song. In a related PET experiment, they found that posterior and anterior auditory association areas of both temporal lobes were active when subjects imagined hearing a familiar tune (Zatorre et al., 1996). When considered in this context, the RT-A patients' impairment could be seen as a deficit in the generation or retention of an accurate auditory image of the temporal sequences. As discussed above, this degraded auditory image could be specific to auditory duration, but might also include pitch.

These results are not consistent with some previous studies suggesting left-hemisphere specialization for auditory temporal and/or rhythmic processing (Efron, 1963; Gordon, 1978; Platel et al., 1997; Prior et al., 1990; Robin et al., 1990; Robinson and Solomon, 1974; Swisher and Hirsh, 1972). Given the number of parameters which contribute to the rhythmic precept—the durations of sounds and silences, temporal order, grouping and accent—this does not seem surprising. While it may be the case that certain aspects of rhythm are preferentially processed by either the right or left hemisphere, the notion of a clear-cut lateralization of all aspects of rhythmic processing is probably too simple. These results are also not consistent with the hypothesis linking perception of rhythmic stimuli to putative left-hemisphere specialization for temporal processing of verbal stimuli. This discrepancy probably results from the large difference in temporal grain between the two types of stimuli. As has been clearly argued by Phillips (1993), the critical timeframe for perception of verbal stimuli is in the 10–50 ms range and it is in this timeframe that patients with left-hemisphere auditory cortex lesions show deficits. A recent PET study comparing the response of left and right auditory cortex to rapid (40 ms) and extended (200 ms) frequency transitions found a left-sided asymmetry in activation for the rapid, but not the extended stimuli (Belin et al., 1998). Additionally, in a study examining discrimination of brief temporal sequences Ehrlé et al. (1997) showed that patients with left temporal lobe atrophy showed impairments only at the fastest presentation rate (80 ms ISI). The timeframe of most musical stimuli, including those in this experiment, is much larger than those which elicited these left-hemisphere deficits. Therefore, the present results do not contradict the potential role of the left auditory cortex in processing of temporal information relevant to speech perception, nor do they necessarily show a general right hemisphere specialization for processing of temporal duration. Rather, the deficit observed for the RT-A patients may be better described as resulting from the role of the right auditory cortex in the retention of a precise representation of tonal patterns.

An important factor in interpreting these results is understanding the relative location of these patients' lesions within the auditory cortex of the temporal lobe. The primary auditory cortex (PAC) in man generally covers approximately the medial half to two-thirds of HG (Galaburda and Sanides, 1980; Rademacher et al., 1993). As judged in relation to the probabilistic map of PAC-r, the majority of excisions in these patients did not extend beyond this point and thus presumably resulted in relatively limited excisions to PAC itself. These excisions would, however, have included anterior auditory regions which cover the lateral portion of HG and extend onto the superior temporal plane. These regions are comprised of secondary auditory fields and multimodal association areas (Galaburda and Sanides, 1980). While primary regions are most likely involved in the initial processing of incoming auditory stimuli, secondary regions are more likely to be involved in more complex processes such as retention. Columbo (1990) showed that lesions of secondary auditory areas in monkeys resulted in impaired performance for an auditory short-term memory task.

It is also important to consider the fact that it is the secondary auditory regions which send connections to the frontal cortex (Cipolloni and Pandya, 1989; Pandya and Yeterian, 1990; Petrides and Pandya, 1988) and hippocampus (Insausti et al., 1987; Suzuki and Amaral, 1994). The majority of frontal connections from anterior secondary auditory regions project ipsilaterally to the ventral portion of the dorsolateral prefrontal cortex (Pandya and Yeterian, 1990). In studies with both humans and primates, this region has been implicated in active retrieval from working memory (Owen et al., 1996; Petrides, 1994). In the PET studies of tonal memory and image generation described above (Zatorre et al., 1994), activation of right-frontal regions was observed in the same conditions showing right temporal activation, linking temporal-lobe retention mechanisms to frontal-lobe working memory mechanisms. For this reason, it would be predicted that both secondary auditory areas and ventrolateral prefrontal cortex would be active in a PET activation study using a similar task.

It might be argued that the observed deficit could be related to damage to the hippocampal region, given the role of this structure in memory processing. However, the majority of the RT-a and LT-a patients had hippocampal removals which were larger than all but two of the RT-A patients, but did not show similar deficit in retention of the auditory sequences. It is, however, the case that the RT-A lesions tended to be more extensive than the LT-A lesions, perhaps contributing to their overall poorer performance.

5. Conclusion

In conclusion, the results of this experiment showed that patients with right temporal-lobe removals which included PAC-r were impaired in the retention of auditory but not visual rhythms. This decrement was most pronounced when accurate reproduction of the individual stimulus durations was emphasized. The subjects were not impaired in their ability to make an adequate motor response, as demonstrated by measures of response variability. Subjects were also not impaired in the auditory DICH condition, indicating that they were able to adequately differentiate the stimulus durations and, given an alternative method of encoding, were able to retain the sequences. Localization and estimation of lesion extent in PAC-r using a probabilistic map of the region indicated that, in the majority of subjects, the lesion was confined to the anterior secondary auditory cortex, with little encroachment on PAC. Taken together, these results were interpreted as demonstrating a specific role for the right anterior secondary auditory cortex in the retention of a precise analogue representation of the temporal dimension of the auditory stimuli. In contrast, patients with left PAC-r removals and patients with right or left temporal-lobe removals which did not include PAC-r but who had larger hippocampal removals were not impaired on this task. These data are consistent with the role of the right temporal lobe in memory and imagery for non-verbal auditory patterns. In contrast, they do not support the hypothesized link between putative left-hemisphere timing mechanisms required for the perception of speech and timing mechanisms required for processing musical rhythm.

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