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Right temporal cortex is critical for utilization of melodic contextual cues in a pitch constancy task

Catherine M. Warrier and Robert J. Zatorre

Montreal Neurological Institute, McGill University, Montreal, Canada

Correspondence to: Catherine M. Warrier, Communication Sciences and Disorders, Frances Searle Building, Northwestern University, Evanston, IL 60208, USA
E-mail: cwarrier@northwestern.edu

Summary

Pitch constancy, perceiving the same pitch from tones with differing spectral shapes, requires one to extract the fundamental frequency from two sets of harmonics and compare them. We previously showed this difficult task to be easier when tonal context is present, presumably because the context creates a tonal reference point from which to judge the test tone. The present study assessed the role of the right auditory cortex in using tonal context for pitch judgements. Thirty-six patients with focal brain excisions of the right or left anterior temporal lobe (RT, LT) and 12 matched control participants (NC) made pitch judgements on complex tones that could differ in fundamental frequency and/or spectral shape. This task was performed in isolation and within a melodic context. The RT group showed impairments both on trials in which extraction of pitch from differing spectral shapes was required (different-timbre trials) and when this was not required (same-timbre trials). All groups performed poorly in the isolated condition, but improved with melodic context. Degree of improvement varied in that the LT group performed normally, whereas the RT group was not able to obtain the same amount of facilitation from the melodic context. In particular, melodic context did not facilitate the RT group's performance on different-timbre trials. Excisions within Heschl's gyrus did not affect these results, suggesting that the impairments were due to the removal of the anterior temporal cortex. The results of this study therefore implicate right anterior auditory cortical areas in making pitch judgements relative to tones that were heard previously. We propose that auditory association areas located on the anterior portion of the superior temporal gyrus, an area with connections to frontal regions implicated in working memory, could be involved in holding and integrating tonal information.

Keywords: auditory cortex; context; pitch; spectral shape; association cortex

Abbreviations: ANOVA = analysis of variance; F0 = fundamental frequency; HG = Heschl's gyrus; LT = patients with left temporal lobe removal; NC = control participants; RT = patients with right temporal lobe removal; STG = superior temporal gyrus

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Introduction

One of our most important perceptual functions is the ability to recognize things as being the same under differing conditions, a concept known as perceptual constancy. It has been argued that detecting differences in stimuli is a relatively easy task for the nervous system to perform, but abstracting similarity from two differing objects is much more difficult (e.g. Whitfield, 1985). Pitch constancy, an auditory example of perceptual constancy, is the ability to judge two tones of differing spectral shape as having the same pitch, even though they do not sound exactly the same. For example, pitch constancy is necessary to hear that a flute and a piano are both playing middle C or that two vowels are spoken at the same pitch. To perform this task, it is necessary to extract the fundamental frequency (F0) from both sets of harmonics and compare them.

It is also important to be able to interpret the same event differently under different circumstances. The context in which a sound occurs can change its meaning or importance dramatically. Context can affect the way we hear and interpret tonal stimuli by affecting pitch perception (Deutsch, 1972*a*, *b*, 1982; Deutsch and Roll, 1974; Dewar *et al*., 1977; Krumhansl, 1979; Krumhansl and Castellano, 1983). Specifically, it appears that placing a tone within the context of a melody enhances the pitch perception of that tone by establishing a reference point from which to judge pitch. Most musical systems, including the Western tonal system, are based on the relationships between tones, particularly their frequency ratios to one another. A two-tone interval has a specific ratio between fundamental frequencies, which can be in tune or out of tune within that system. Hearing more notes creates more of a tonal reference point by which one can judge whether each tone is in or out of tune with the rest of the notes present (e.g. Deutsch, 1972*a*; Dewar *et al*., 1977; Krumhansl, 1979). Crowder (1993) states that 'even when there is no obvious melody, individual tones are not heard independently of a tonal context' (p. 137).

The present study explores the neural mechanisms that underlie pitch constancy, as well as how context can affect this perception. We investigated the problem by testing patients with unilateral excisions in the temporal lobe in order to assess the involvement of this area of cortex in these processes, basing our paradigm on a previous study in which we tested neurologically normal listeners (Warrier and Zatorre, 2002). In that study, we found that in addition to the establishment of a tonal reference point from which to judge subsequent pitches, tonal context can affect pitch constancy, or the extraction of pitch from differing spectral shapes. The results indicated that a difficult pitch constancy task was made easier by placing the stimuli in a melodic context. Although comparing the pitches of two tones differing in timbre proved to be very difficult in isolation, performance increased dramatically when the same tones were presented within the context of a familiar melody. This result implied that listeners were able to use contextual information to their advantage when performing the pitch extraction necessary for the task.

Some aspects of pitch perception appear to involve the right auditory cortex, as patients with lesions in this region have exhibited difficulty on certain tasks involving pitch. Simple frequency discrimination tasks can be performed at normal levels by patients with either right or left temporal lobe lesions (e.g. Milner, 1962; Zatorre, 1988; Johnsrude *et al*., 2000). Even bilateral lesions of the auditory cortex do not necessarily cause permanent impairments on such tasks (Peretz *et al*., 1994; for review see Whitfield, 1985), although fine-grained pitch discrimination may depend on the integrity of both auditory cortices (Tramo *et al*., 2002). However, patients with right temporal lobe lesions show impairments on other pitch processing tasks. For example, a study by Zatorre and Samson (1991) showed that although patients with right or left temporal lobe lesions performed as well as controls on a simple pitch discrimination task, right-sided lesions caused impairments when interfering tones were inserted between the standard and comparison tones. In addition, lesions in either temporal lobe affect discrimination of melodic pitch patterns, a more complex task, but right-sided lesions seem to cause more severe impairments (Milner, 1962; Liégeois-Chauvel *et al*., 1998; Samson and Zatorre, 1988; Peretz, 1990). Functional neuroimaging studies conducted on normal listeners support the lesion data in that a variety of tasks involving pitch processing elicit right temporal and frontal activations (Zatorre *et al*., 1992, 1994; Holcomb *et al*., 1998; Perry *et al*., 1999; Patterson *et al*., 2002). Although frontal lobe regions are not typically associated with auditory processing *per se*, they generally become active when the task investigated involves a working memory component.

Other studies have specifically implicated the cortex in the lateral aspect of the right Heschl's gyrus (HG), an area adjacent to the primary auditory cortex (Morosan *et al*., 2001) in pitch-related processing. Johnsrude and colleagues (2000) found that patients with right or left temporal lobe lesions were unimpaired on a frequency discrimination threshold test. However, when asked to determine the direction of the pitch change in the same stimuli, only patients whose right temporal lobe lesions extended into HG were impaired. In another lesion study (Zatorre, 1988), no difficulties were observed on a simple pitch discrimination task using complex tones, but when the fundamental frequency component was removed from each tone, patients with right temporal lobe lesions that included HG were impaired. This study thus specifically implicated the right HG in extracting pitch from tones differing widely in spectral shape.

The present study investigates the neural correlates of pitch constancy and context effects by testing patients who have had unilateral temporal lobe excisions. The goals of the study were two-fold. First, we wanted to investigate the role of the right auditory cortex in the spectral processing of tones. For this we tested patients with temporal lobe excisions and a normal control group on a pitch constancy task. Based on previous studies showing that patients with right temporal lobe lesions are impaired on many pitch-related tasks (see above), we predicted that they would also have difficulty with the pitch constancy task. More specifically, given Zatorre's (1988) findings using tones with missing fundamentals, we predicted that patients whose right-sided lesions encroached on HG would be impaired when the task required extraction of pitch from tones of differing spectral shape, but not when a direct comparison was available and this process was unnecessary.

Secondly, we were interested in examining whether patients with right temporal lobe lesions would be able to utilize tonal information contained in contextual tones to facilitate the task. Therefore, we used the paradigm of Warrier and Zatorre (2002), which showed melodic context to facilitate pitch extraction from tones differing in spectral shape in neurologically normal listeners. We predicted that the contextual information would not aid patients with right temporal lobe lesions on this task to the same extent as control participants.

Methods

Participants

All thirty-six patients tested had undergone focal unilateral cerebral excision at the Montreal Neurological Hospital for relief of

Table 1 *Participant characteristics*

	n (M/F)	Age (years)	Education (years)	Music experience (years)	Full-Scale IQ (WAIS-R)
NC	12 (3/9)	36.8 (22–52)	13.2 (9–17)	1.2 (0–5)	–
LT	18 (14/4)	35.4 (22–49)	13.5 (10–18)	4.5 (0–15)	106.4 (89–135)
RT	18 (7/11)	36.9 (24–53)	12.8 (8–19)	1.9 (0–15)	101.6 (82–120)

Numbers in parentheses are ranges except in first column, where they indicate gender.

pharmacologically intractable epilepsy, with 18 temporal lobe excisions on the left (LT) and 18 on the right (RT). Patients were excluded from the study if they presented atypical speech representation, known damage outside the region of surgical excision, EEG abnormality contralateral to the side of the lesion, a malignant tumour, a Full-Scale WAIS-R IQ (Wechsler Adult Intelligence Scale—Revised) <75, or evidence of hearing loss or impairment. Twelve neurologically normal control participants (NC), matched to the patients with respect to age and level of education, were also tested. Musical experience was generally limited in each group, 79% of all participants having ≤2 years of training and/or experience. Table 1 outlines participant characteristics. The ethics committee of the Montreal Neurological Institute approved the experimental protocol, and written informed consent was obtained from all participants before testing, in accordance with the Declaration of Helsinki.

All resections included the amygdala, uncus and anterior temporal lobe in one hemisphere. The extent of resection along the hippocampus and parahippocampal gyrus varied from patient to patient, as did the extent of the lateral neocortical excision along the sylvian fissure, the second temporal gyrus and the base of the temporal lobe. Patients were divided according to side and whether the lesion extended posteriorly into HG, the medial portion of which contains the primary auditory cortex (Liégeois-Chauvel *et al*., 1991; Rademacher *et al*., 2001).

Lesion classification was performed according to a method described by Penhune and colleagues (Penhune *et al*., 1999). First, each patient's postoperative MRI scan was transformed into standardized stereotaxic space (Talairach and Tournoux, 1988). These scans were then co-registered with a probabilistic map of HG developed by Penhune and colleagues (Penhune *et al*., 1996), which allows identification and estimation of removal in this area. Of the 18 patients in the RT group, seven had lesions encroaching upon HG. The remaining 11 patients' lesions stopped anterior to this area. Of the 18 patients in the LT group, three had lesions encroaching upon HG and the remaining 15 had lesions that stopped anterior to this area (Fig. 1).

Stimuli

The stimuli were synthesized digitally using MITSYN software (Henke, 1981). All test tones were 500 ms duration, with rise and fall times of 10 ms. Contextual tones used in the melodic condition varied in length according to the necessary tone durations. Three timbres were created by varying the relative intensities of 11 harmonics. One emphasized the lower harmonics (Low), another emphasized the middle harmonics (Middle) and sounded brighter than Low, and the last emphasized the higher harmonics (High) and sounded brighter than Middle (Fig. 2). Individual tones ranged in fundamental frequency from 164.81 to 1108.70 Hz (E3 to C6), with test tones always presented between 261.63 Hz (C4) and 480.35 Hz [A4 + 52 ¢ (cents: logarithmically equal steps in frequency; equal cent differences are perceived as roughly equal pitch differences in any frequency range)]. Stimuli were presented with MAPLE (McGill Auditory Perception and Linguistic Experiments) software (Achim *et al*., 1992). Sounds were presented binaurally at 75 dB SPL (sound pressure level) through Sennheiser HD424 headphones. Sample stimuli can be heard at www.zlab.mcgill.ca

Procedure

The testing session was broken down into three sections: (i) explanatory phase; (ii) isolated condition; and (iii) melodic condition, in that order. A block of 12 practice trials was presented before each test condition. Participants responded by pressing a key on the computer keyboard. The entire session, conducted in a sound-attenuated room, took between 60 and 75 min.

Explanatory phase

To ensure that everyone understood the concepts relevant for the task, an explanatory phase was conducted with a keyboard before testing. Pitch was demonstrated by hearing different notes played on the keyboard. An informal quiz was then performed in which the participant indicated whether two notes had the same pitch, with interval size varying from large (7th) to small (2nd). Timbre was then explained as 'instrument sound' by playing two notes of the same frequency with different instrument sounds available on the keyboard. After presenting a variety of exemplars, a second quiz was given in which two tones of different instrument sounds were played, and the participant determined whether the pitch stayed the same, disregarding the change in instrument. Interval size was again varied from large to small. This informal testing was continued until the experimenter was confident that the participant understood the concepts of pitch and timbre.

Isolated context

In the isolated context condition, each trial consisted of two tones presented with an interstimulus interval (ISI) of 100 ms. The first tone was randomly presented at one of six frequencies corresponding to whole-tone steps starting at C4 (261.63 Hz) and continuing to A4 (466.16 Hz). The second tone was 0 (same) or 35 or 52 ¢ higher than the first tone. These values were chosen on the basis of data from the earlier behavioural study. Each semitone of the musical scale is 100 ¢, and therefore 50 ¢ corresponds to a quarter-tone. Each pair of test tones could be presented in one of three timbre pairings: (i) same (Low–Low, High–High); (ii) small difference (Low–Middle, High–

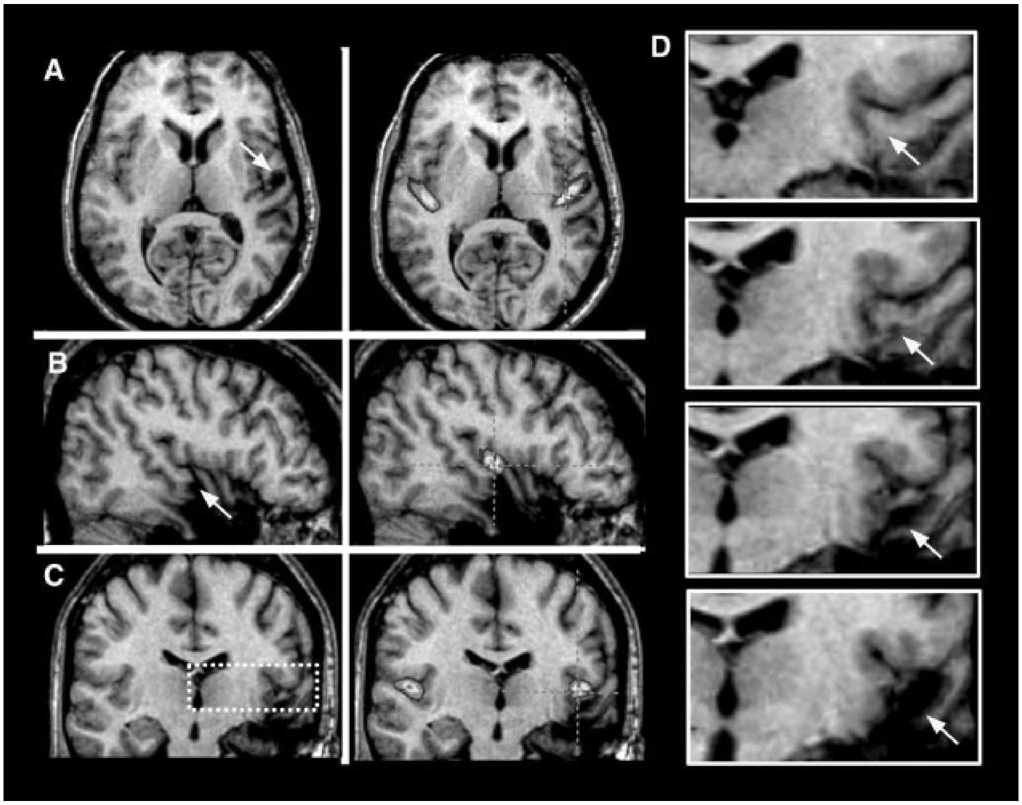

Fig. 1 MRI scan of a patient with a removal in the right temporal lobe in whom the excision includes the anterior–lateral 50–60% of Heschl's gyrus (HG), and the undercutting extends to 60–70%. The MRI scan is transformed into standardized stereotaxic space; illustrated are planes of section oriented horizontally (**A**, $z = 4$), sagittally (**B**, $x = 46$) and coronally (**C**, $y = -17$). In panels **A**, **B** and **C** the left side shows the patient's scan alone, with an arrow indicating the region of excision/undercutting. The images on the right side of panels **A**, **B** and **C** show the patient's scan co-registered with an anatomical probabilistic map of HG derived from normal individuals (Penhune *et al*., 1996); the map is scaled to show voxels that have a probability of lying within HG of ⩾25%. The cross-hairs indicate the same position in standardized space as the arrow. Note the correspondence between the position of HG as determined from the map and the patient's partially excised HG region. The box in panel **C** indicates the region of the removal pictured in close-up in panel **D**, which illustrates the transition from intact, to undercut, to fully excised tissue (coronal sections taken at 3 mm intervals, posterior to anterior, from $y = -23$ to -14). Arrows again correspond to the cross-hairs in the other panels, and indicate the location of the HG region. This figure can be viewed in colour as supplementary material at Brain Online (http://brain.oupjournals.org).

Middle); and (iii) large difference (High–Low, Low–High). Each pairing was presented at all levels of F0 difference. Participants were instructed to judge whether the pitch of the second tone was the same as or different from the first tone, ignoring any timbre changes as much as possible. Participants completed 54 trials at their own pace.

Melodic context

In the melodic context condition, the task was to determine whether the last note of a melody was in tune. One of two melodies, familiar to all participants, was presented on each trial: 'Oh, Susanna' by Stephen Foster, or 'The Blue Danube Waltz' by Johann Strauss (Fig. 3). These melodies were chosen for their different endings; the four final notes of 'Blue Danube' all share the same pitch, and 'Oh, Susanna' ends in a downward scalar motion. Each melody, excepting the last note, was presented in tune in one of three keys, so that the last note should end on one of six whole steps from C4 to A4. Each melody was presented in one of the three spectral shapes described above. The last note could continue with the same spectral shape as the melody, or sound in one of the other two, thus creating the same three timbre pairs as the isolated condition (same, small difference, and large difference), and was 0 (same), 35 or 52 ¢ sharper than the correct final note. After the presentation of each melody, participants were instructed to indicate if the last note of the melody was in or out of tune, ignoring any timbre differences. Due to the differing melodic structures of the two melodies, listeners could perform the task by comparing the pitches of the final two notes when 'The Blue Danube' was presented, but processing of the interval information was necessary when 'Oh, Susanna' was presented (Fig. 3). Participants completed 54 trials of each melody at their own pace.

Results

We calculated percentage correct scores from the data and performed all statistical analyses on this measure. Due to the time constraints of the testing sessions, we were not able to collect enough replications within each cell from each participant to calculate a meaningful d′ index.

Isolated versus melodic context

The NC group replicated our previous study (Warrier and Zatorre, 2002) in that the isolated condition was performed poorly, and scores improved substantially in the melodic condition (Fig. 4). A three-factor analysis of variance (ANOVA) was performed with two levels of Context (isolated and melodic), three levels of Pitch (0, 35 and 52 ¢) and three levels of Group as a between-subjects factor (NC, LT and RT). Three main effects were found. A main effect of Context [$F(1,45) = 83.03$, $P < 0.001$] showed that scores were higher overall in the melodic condition, and a main effect of Pitch [$F(2,90) = 10.68$, $P < 0.001$] showed that scores were highest in the 52 ¢ condition. A main effect of Group was also found, the RT group attaining the lowest overall scores (Fig. 4, left) [$F(2,45) = 3.74$, $P < 0.05$]. Three interaction effects emerged: Context × Pitch [$F(2,90) = 5.99$, $P < 0.005$], Context × Group [$F(2,45) = 5.10$, $P = 0.01$] and Context × Pitch × Group [$F(4,90) = 4.24$, $P < 0.005$].

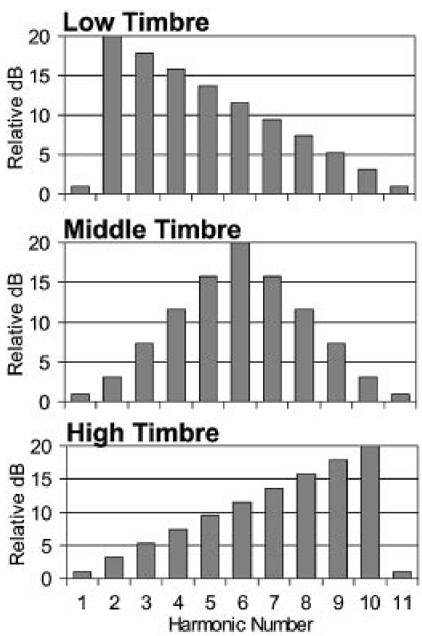

Fig. 2 Spectral shapes of timbres. Differences in intensity level of each harmonic are shown relative to the other harmonics.

We then broke down the three-way interaction between Context, Pitch and Group by testing for group differences at each level of F0 difference, looking at each condition separately with Tukey's honestly significant difference (HSD) *post hoc* tests. The LT group did not differ from controls at any F0 deviation in either condition. The RT group did not differ from controls at any F0 deviation in the isolated condition, but scored significantly lower than controls on both the 35 and the 52 ¢ deviations in the melodic condition ($P < 0.05$ for both comparisons) (Fig. 4, right).

All groups improved with melodic context (Bonferroni-corrected t test, $P < 0.001$ all groups), but the degree of improvement differed between groups [one-way ANOVA, $F(2,45) = 5.10$, $P = 0.01$]. The RT group improved significantly less than the control group (*post hoc* Tukey's HSD test, $P < 0.01$), whereas the LT and NC groups showed equal improvement (Fig. 4, left).

In order to examine the contribution of HG excision, the RT group was split into two smaller groups: seven patients whose excision extended into HG, and 11 in whom this gyrus was entirely spared. Analyses of variance did not reveal any differences between these two subgroups. Due to the small number of patients with left temporal resections extending into HG ($n = 3$), we were unable to perform this analysis within the LT group.

Same-timbre trials

Restricting the data to include only same-timbre trials enabled us to remove the spectral analysis factor of the study. Data from same-timbre trials are shown in Fig. 5. Pitch discrimination in same-timbre trials could be completed with a simple comparison of F0 between two tones. These trials did not require extraction of pitch from tones of differing spectral shape, a task we predicted patients with lesions in right HG would have difficulty performing. We therefore predicted that this patient group would have difficulty on the different-timbre trials but not on the same-timbre trials. Because timbre influenced judgements so much at the small differences in F0 we used in this study, same-timbre trials were biased to be judged the same in pitch. This accounts for the low percentage correct scores seen in all groups on the 35

Fig. 3 Melodic contexts shown in musical notation.

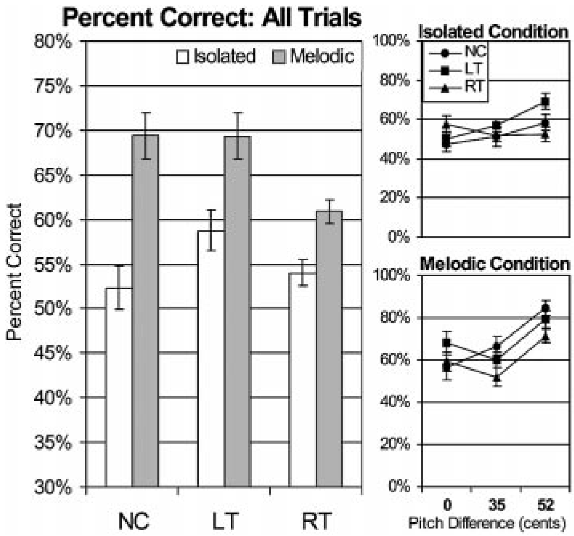

Fig. 4 Percent correct results averaged across same- and different-timbre trials. (*Left*) Average scores for both isolated (open bar) and melodic (shaded bar) conditions, shown by group. (*Right*) Average scores at each pitch difference of test tones, shown by group (circles, NC; squares, LT; triangles, RT) for the isolated (top) and melodic (bottom) conditions. Error bars are indicated.

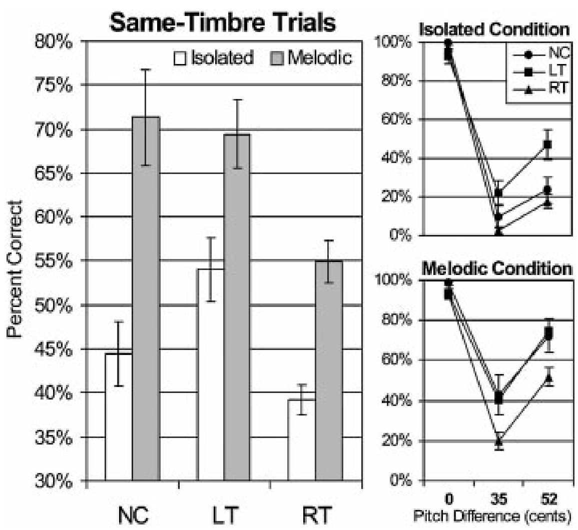

Fig. 5 Percent correct results averaged across same-timbre trials only. (*Left*) Average scores for both isolated (open bar) and melodic (shaded bar) conditions, shown by group. (*Right*) Average scores at each pitch difference of test tones, shown by group (circles, NC; squares, LT; triangles, RT) for the isolated (top) and melodic (bottom) conditions. Error bars are indicated.

and 52 ¢ trials in the same-timbre trials in the isolated condition, while 0 ¢ deviation scores were near 100% correct (Fig. 5, top right).

A three-factor ANOVA was performed on the same-timbre trials with two levels of Context, three levels of Pitch, and three levels of Group as a between-subjects factor (NC, LT and RT). Three main effects were found. The main effect of Context indicated higher performance in the melodic

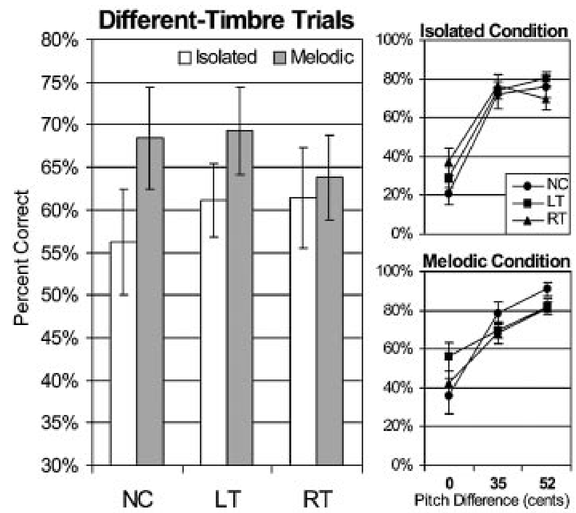

Fig. 6 Percent correct results averaged across different-timbre trials only. (*Left*) Average scores for both isolated (open bar) and melodic (shaded bar) conditions, shown by group. (*Right*) Average scores at each pitch difference of test tones, shown by group (circles, NC; squares, LT; triangles, RT) for the isolated (top) and melodic (bottom) conditions. Error bars are indicated.

condition [$F(1,45) = 72.18$, $P < 0.001$], and a main effect of Pitch showed differing scores for different F0 deviations [$F(2,90) = 268.49$, $P < 0.001$]. A main effect of Group was also found, the RT group demonstrating the lowest scores [$F(2,45) = 7.98$, $P = 0.001$] (Fig. 5, left). Two interaction effects were found: Pitch × Group [$F(4,90) = 4.35$, $P < 0.005$] and Context × Pitch [$F(2,90) = 38.03$, $P < 0.001$]. No Context × Group interaction was seen, indicating that all groups showed the same amount of improvement with melodic context.

We again broke down the interaction effects by testing for group differences at each level of F0 difference within each condition using Tukey's HSD *post hoc* tests. In the isolated condition, the only difference from controls was found in the LT group on the 52 ¢ trials, in which the LT group scored higher than the controls ($P < 0.05$). In the melodic condition, no differences were found between LT and NC groups. However, the RT group scored significantly lower than controls on both the 35 and the 52 ¢ condition ($P < 0.05$ both comparisons) (Fig. 5, bottom right).

Within the RT group, we again separated those patients whose lesions encroached upon HG from those in whom this area was spared, and looked at same-timbre trials only. A three-factor ANOVA was performed on these two groups (Context × Pitch × Group). No between-group differences were found.

Different-timbre trials

In order to directly assess performance on trials requiring a pitch comparison of tones differing in spectral shape, we restricted the next analysis to include different-timbre trials only. Data from different-timbre trials are shown in Fig. 6. A three-factor ANOVA was performed on the different-timbre trials with two levels of Context, three levels of Pitch and three levels of Group as a between-subjects factor (NC, LT and RT). Two main effects were found. The main effect of Context again indicated higher performance in the melodic condition [$F(1,45) = 29.12$, $P < 0.001$], and a main effect of Pitch showed differing scores for different F0 deviations [$F(2,90) = 51.14$, $P < 0.001$] (Fig. 6). A Context × Pitch interaction was also found [$F(2,90) = 6.00$, $P < 0.005$]. Of particular relevance to our hypotheses, a Context × Group interaction indicated that the groups differed in the amount of improvement gained with melodic context [$F(2,45) = 3.98$, $P < 0.05$]. Specifically, the NC and LT groups gained significantly from the presence of melodic context and the RT group showed no improvement [$t(11) = 4.10$, $P < 0.01$; $t(17) = 3.87$, $P = 0.001$, $t(17) = 1.06$, $P > 0.3$ for NC, LT and RT, respectively, computed as Bonferroni-corrected *t* tests] (Fig. 6, left). This result contrasted with performance on same-timbre trials, in which all groups showed a similar amount of improvement due to the melodic context.

We further examined the RT group's responses to different-timbre trials by separating the group into those patients whose lesions encroached upon HG and those in whom this area was spared. A three-factor ANOVA (Context × Pitch × Group) was performed on these two groups. As in the previous analyses comparing these two groups, no between-group differences were found.

Differences between melodic stimuli

In all previous analyses, responses to both melodies were averaged together to create a generic index of performance in a melodic context. Differences in responses to the two melodies were assessed by comparing overall responses to each melody with paired *t* tests for each group. Melody-related differences were seen in the RT group only ($t = 3.04$, $P < 0.01$), with poorer performance on the 'Oh, Susanna' melody (Fig. 7). Based on the previous analyses in which the RT group was found to have trouble utilizing melodic context only in different-timbre trials, we investigated this difference further by separating the RT group's responses into same- and different-timbre trials for each melody and analysed them separately. Differences between melodies were apparent in the different-timbre trials only.

Gender

Because the three groups differed significantly in male/female ratio ($\chi^2 = 9.44$, $P < 0.01$), and we did not have enough observations of each gender in each group to successfully disentangle any potential effects of gender from those of group, gender effects could not be assessed. However, exploratory statistics did not reveal a significant role of gender. Additionally, previous studies of tonal auditory processing that tested patient populations similar to those in the present study report no significant effects of gender (Zatorre, 1985; Samson and Zatorre, 1988).

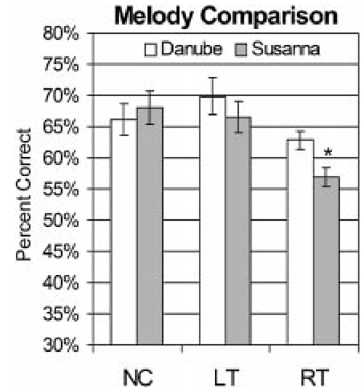

Fig. 7 Percent correct results of the melodic condition separated by melody. Average scores for 'The Blue Danube Waltz' ('Danube,' open bar) and 'Oh, Susanna' ('Susanna,' shaded bar) melodies, shown by group. Error bars are indicated.

Discussion

As in our previous behavioral study, all participants had difficulty performing the pitch extraction task in the isolated condition. Placing the test tones within the context of a melody improved performance for all three groups, but the degree of improvement varied between groups. In particular, and consistent with the predictions, patients with right temporal lobe damage did not achieve the same level of improvement as controls, but patients with corresponding lesions in the left hemisphere did. Within the RT group, performance did not differ if the lesion included or excluded HG.

Role of the right temporal lobe in utilizing contextual cues

The difficulty shown by all groups in the isolated condition mimics data from a previous study in which normal listeners were unable to ignore timbre differences when judging pitch differences in that condition (Warrier and Zatorre, 2002). At the small fundamental frequency differences used in both this and the previous study, differences in timbre were interpreted as differences in pitch, such that tones in same-timbre trials were judged as having the same pitch and those in different-timbre trials were judged as having different pitches, whether the F0 changed in that trial or not. It is only in the melodic condition that, although pitch judgements are still influenced by timbre, listeners are better able to focus on the fundamental frequency dimension and extract pitch from the spectral information of the tones.

The present study showed that the capability of melodic context to help listeners ignore timbral differences is considerably weaker in the RT group. This group was not able to use the facilitating information contained in the melodic context to the same extent as controls or patients with left temporal lesions. Additionally, patients in the RT group performed relatively poorly on both melodies of the melodic condition, but were better when it was possible to perform the task by simply comparing the last two notes of the melody (i.e. 'The Blue Danube Waltz'). In other words, they had the most difficulty when the task absolutely relied on adequately processing the melodic context. This difference in performance between the two melodies was only seen in the RT group, and supports the notion that these patients have difficulty fully utilizing the melodic information. In order to make full use of the melodic context, it is necessary to consider pitch relative to contextual tones that were heard previously. Given that the RT group had difficulty on this task and the LT group did not, it appears that the right temporal lobe plays an important part in at least some of the processing necessary to fully utilize tonal context in this way. It is in this area of cortex that we propose that tones are analysed with respect to those that came previously, a process that must of necessity involve a tonal working memory function.

Previous lesion literature has shown patients with right temporal lobe lesions to exhibit impairments when the task requires holding tones in memory over a short period of time (Zatorre and Samson, 1991; see also Chao and Knight, 1997). Therefore, the RT group may have difficulty holding the contextual tones in memory long enough for them to affect perception of the test tones, and thus do not obtain the full benefit of the context.

The RT group's impairment may also be due in part to inadequate processing of the melodic structure. By not being able to fully process the melodies that make up the melodic context, these patients would not have all the melodic information available to them that the LT and NC groups did. Previous research has shown that patients with right-hemisphere lesions exhibit impaired performance on tasks requiring them to process melodic contours or interval information within the melodies (Zatorre, 1985; Liégeois-Chauvel *et al*., 1998; Peretz, 1990). However, these studies also find patients with left hemisphere lesions to have difficulty processing interval information. Therefore, difficulty processing the melodic contour, a deficit apparently specific to patients with right-hemisphere lesions, is a more likely candidate for contributing to the decreased performance in the RT group. By not processing contour information effectively, the RT group may not obtain the same facilitating information from the contextual melodies as the other groups did.

Another possible explanation for the RT group's decreased use of melodic cues relates to the fact that the melodies used were highly familiar. As a result, listeners could have judged whether the final note of the melody was correct by comparing it with an internal representation of the correct final tone or interval held in long-term memory storage. Impaired recognition of familiar melodies has been related to damage in right hemisphere structures (Griffiths *et al*., 1997; Steinke *et al*., 2001), although this is not always the case (Peretz, 1990; Liégeois-Chauvel *et al*., 1998). Consequently, we cannot rule out the possibility that the surgery performed on the RT patients disrupted access to this long-term melody storage or degraded the melodic memories themselves.

Spectral shape

The RT group did not show the expected effect of spectral shape. Trials differing in timbre required extraction of pitch from differing spectral shapes. We predicted that the RT group would perform better on same-timbre trials when this extraction was not necessary. To assess the effect of spectral shape directly, we looked at scores in the isolated condition only. If spectral processing affected their performance, the RT group should have scored better on same-timbre trials in the isolated condition than on different-timbre trials. In fact, the RT group's scores in the isolated condition did not differ from the NC group's when either same- or different-timbre trials were compared (white bars in Figs 5 and 6). In addition, contrary to our prediction, no effect was seen on same- or different-timbre trials in the isolated condition when dividing the RT group into two subgroups: patients whose excisions extended into HG or did not do so.

Although the RT group was not deterred by changes in spectral shape in the isolated condition, this factor did affect the way they utilized melodic context. Patients with right temporal lesions showed a similar amount of improvement due to the presence of melodic context as the other two groups when the timbre of the tones to be compared did not change (Fig. 5). However, when a change in timbre required extraction of pitch from tones of differing spectral shapes, melodic context did not benefit the RT group's performance, although the other two groups showed significant improvement (Fig. 6). Again, the two RT subgroups based on extent of surgical excision showed similar results. This suggests that the RT group does experience some degree of difficulty in processing spectral shape, and that lesions anterior to or including HG are sufficient to induce this deficit.

Auditory cortex on lateral aspect of HG vs. anterior regions

One of the main goals of this study was to assess the involvement of the primary auditory cortex versus the more anterior auditory areas in spectral analysis and the utilization of tonal contextual cues. No dissociation of responses was found between RT patients whose excision included or spared HG, the medial aspect of which contains the primary auditory cortex. The deficits seen in the RT group can therefore be attributed to the excision of more anterior areas of the temporal lobe, excised in all RT patients. This implies that anterior portions of the auditory cortex are involved in making pitch judgements relative to tones that were heard previously.

The anterior portion of the superior temporal gyrus (STG) contains auditory belt and parabelt areas with cortico-cortical connections to the superior temporal sulcus, as well as frontal and paralimbic areas (Pandya and Yeterian, 1985; Pandya, 1995; Kaas *et al.*, 1999; Chiry *et al.*, 2003). This region is particularly interesting in relation to the present study due to its connections with dorsolateral and inferior frontal regions, areas known to be involved in working memory (Petrides and Pandya, 1999; Romanski *et al.*, 1999). These connections could be involved in holding the contextual tones of melodic context in memory while listeners wait for the final tone. Prior lesion and imaging studies support the view that anterior temporal and frontal cortical regions are involved in tonal working memory (Zatorre and Samson, 1991; Zatorre *et al.*, 1994).

The role of anterior regions of the STG in the processing of melodic pitch has been suggested by two recent functional MRI (fMRI) studies (Schmithorst and Holland, 2003; Warren *et al.*, 2003). More direct support comes from an fMRI study comparing blood oxygenation level-dependent (BOLD) responses when listeners made same/different pitch judgements in different tonal contexts (Warrier *et al.*, 1999). When subtracting the BOLD response to judgements made in an isolated context from those made in a melodic context (contexts similar to those used in the present study), only one area of cortex showed a significant difference: the anterior portion of the right superior temporal gyrus. This is the same region excised in all of the RT patients in the present study. Given this convergence of results, it is reasonable to conclude that the neural computations necessary for bringing about the facilitating effects of tonal context recruit this anterior area of the auditory cortex.

Another fMRI study strengthens the idea that the anterior portion of the right superior temporal gyrus performs a distinct role compared with HG in melodic processing (Patterson *et al.*, 2002). That study found HG to be activated to the same extent bilaterally when a series of regular interval (RI) tones evoking fixed, random or melodic pitches was compared with noise, although a slight increase in activity in a region lateral to the primary auditory cortex was evident in the individual data. This study also examined the level of neural activity evoked when listeners heard either melodic or random RI tone sequences compared with sequences in which the pitches of RI tones did not change. No difference in the amount of activity in HG was seen in that contrast. However, an anterior portion of the right STG (planum polare), in addition to the right superior temporal sulcus, was more active when the pitch of subsequent tones changed. These results prompted the authors to suggest that HG is involved in short-term pitch processing, and that auditory regions outside HG handle longer-term pitch processing involving comparisons across sequences of tones. The data from the present study support this view.

The functional hemispheric asymmetry found in the present study, and reported in many prior studies, indicates a preferential role for right auditory cortical structures in the processing of pitch patterns. One account of this phenomenon (Zatorre *et al.*, 2002) argues for a relative specialization of the auditory cortices, such that those on the left are specialized for processing rapidly changing temporal information and those on the right are specialized for spectral processing (see also Poeppel, 2003; Tallal *et al.*, 1993). According to this model, specialization in one domain entails a cost in the other, leading to a trade-off in temporal versus spectral analysis. This idea may help to explain the unexpected finding that the LT group performed better than controls in one condition (Fig. 5, top right). Assuming that the right auditory cortices are optimized for processing spectral information and that the left auditory cortices have a coarser spectral resolution, one could speculate that in an intact brain the contribution of the left auditory cortices to performing our pitch discrimination task may be analogous to adding a certain level of noise to the necessary neural computations. Removal of the left auditory cortices may thus allow those on the right to execute the task unimpeded, therefore resulting in better performance than if both cortices were intact. Although it is unusual to see an improvement in function with removal of cortical tissue, it is not unprecedented. For example, in the study by Johnsrude and colleagues, patients with large resections of left auditory cortical regions obtained lower discrimination thresholds than controls in judging pitch direction, although this result was not statistically significant (Johnsrude *et al.*, 2000). Therefore, although this effect is subtle, it is possible that under appropriate circumstances one may be able to demonstrate a type of enhancement in pitch processing from left auditory cortical disruption.

Conclusion

This study examined pitch constancy as an example of perceptual constancy and explored how context can affect this perception. In particular, we investigated how the auditory cortex can use contextual cues to facilitate pitch constancy. Although a melodic context greatly facilitated pitch constancy both in controls and in patients with left temporal lobe lesions, it helped patients with right temporal lobe lesions much less. We propose that the auditory processing necessary for judging tones relative to those that were heard previously requires neural systems located in the right anterior auditory cortex.

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