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The human 'pitch center' responds differently to iterated noise and

Huggins pitch

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Running head : Examining evidence for a human pitch center

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ABSTRACT

An MEG marker for pitch analysis (the pitch onset response, POR) has been reported for different types of pitch-evoking stimuli, irrespective of whether the acoustic cues for pitch are monaurally or binaurally produced. It is claimed that the POR reflects a common cortical representation for pitch, putatively in lateral Heschl's gyrus. The result of this fMRI study sheds doubt on this assertion. We report a direct comparison between iterated ripple noise and Huggins pitch in which we reveal a different pattern of auditory cortical activation associated with each pitch stimulus, even when individual variability in structure-function relations is accounted for. Our results suggest it may be premature to assume that lateral Heschl's gyrus is a universal pitch center.

Keywords : Functional imaging; auditory; monaural diotic pitch; binaural dichotic pitch.

INTRODUCTION

Pitch is one of the most important auditory sensations, having a vital role in speech perception, music perception, and in the perceptual segregation of concurrent sounds. The fact that sounds with very different physical characteristics can be matched in terms of their pitch [1] suggests that at some stage in the auditory pathway there is a common neural representation of pitch.

A recent primate neurophysiological study has suggested that a region immediately anterolateral to the primary auditory cortex may act as a pitch center, with an individual neuron in the region sensitive to a characteristic fundamental frequency (F_0) irrespective of the spectral characteristics of the eliciting stimulus [2]. It is argued that this result is consistent with the many human neuroimaging studies demonstrating a pitch-sensitive region in the homologue of the primate pitch center; lateral Heschl's gyrus [3]. One concern however is that the majority of these studies have used iterated ripple noise as a pitch-evoking stimulus [4-11]. Reliance on mapping a pitch-related neural response that is evoked by only one class of stimulus does not provide a robust test of a claim for a general pitch center.

Two recent magnetoencephalographic (MEG) studies have gone some way to addressing this issue by making within-subject comparisons of the responses to two different classes of pitch-evoking stimulus. Both studies compared the pitch onset response (POR) to a binaurally produced (dichotic) pitch with that to a monaural (diotic) pitch, either a tone in noise [12] or iterated ripple noise [8].

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The dichotic stimulus was a Huggins pitch in which the input to the two ears is an identical white noise except in a narrow frequency region. In this frequency region the input to the two ears is decorrelated. Listeners hear a pitch corresponding to the decorrelated region, and this pitch has been shown to support the production of musical melodies [13], thereby satisfying the most conservative definition of pitch. In a Huggins pitch, the input to each ear alone is simply white noise. This contrasts sharply with the pitches of single frequency tones, complex tones and iterated ripple noise, that do not depend on binaural integration. Huggins pitch is therefore a potentially useful test of the generality of a supposed neural pitch center.

The POR is defined as the deflection in the measured signal at the transition from a spectrally controlled noise to the pitch stimulus. In both studies [8, 12], the POR for Huggins pitch was similar to that for the monaurally produced pitch and the principal generating dipole was proposed to originate in the proximity of Heschl's gyrus. The spatial precision of MEG is rather coarse and interpretations are generally guided by other information, such as results gained from fMRI. Nevertheless, the PORs reported by Chait [12] are at least consistent with a common generating dipole in lateral Heschl's gyrus for both types of pitch; see also [11]. In order to test this assumption, we presented dichotic and diotic pitch signals to a set of listeners. The present fMRI experiment addressed two predictions arising from the MEG evidence:

1. With respect to a matched noise, Huggins pitch and iterated ripple noise produce comparable pitch-related fMRI responses

2. Both pitch-related responses are co-located in lateral Heschl's gyrus.

METHODS

Subjects: We recruited five female and four male, normally hearing listeners (≤ 25dB HL between 250 Hz and 6 kHz). Their mean age was 24½ years old, ranging from 18 to 40 years. All except one listener (#1) was strongly right handed and all except one listener (#8) was musically trained. Listeners gave written informed consent and the study was approved by the Nottingham University Medical School Ethics Committee.

Stimuli: Stimulus conditions each comprised a 15.5 s repeating sequence of stimulus bursts presented at a rate of 2 Hz. Each burst had a fixed duration of 450 ms (including 10 ms onset and offset ramps). To avoid artifacts due to repeated presentation of identical noise portions, sequences contained different noise exemplars.

In the baseline condition, we presented a Gaussian noise that was lowpass filtered at 2 kHz. Two different pitch-evoking stimuli were generated by manipulating this noise carrier. Neither pitch-evoking stimulus contained any spectral cues for pitch and both stimuli were matched to the noise in terms of their spectral envelope and spectral energy. We also confirmed, through cochlear simulation, that the energy of the neural excitation pattern in the auditory nerve was equivalent to that of the noise control.

The dichotic pitch was a Huggins stimulus in which the waveforms of the noise at the two ears differed only in the phases of a narrow band of frequencies from 190 to 210 Hz (200 Hz +/- 10%), generating a pitch corresponding to a pure tone of 200 Hz. This frequency region was given a progressive phase shift, linear in frequency between 0 and 2π, in the left ear only. The sensation of dichotic pitch does not require extensive training [13]. Nevertheless, to ensure that our listeners were able to determine the pitch we first exposed them to a 2 interval-2AFC pitch discrimination task using the experimental stimulus as a reference. After one practice run, the threshold for the group reached an acceptable level of performance; 16 Hz (7.8 %) averaged over four adaptive tracks. Thresholds were not related to musicianship.

The diotic pitch was an iterated ripple noise which contains regular intervals between successive peaks in the temporal waveform of the noise. The waveforms were identical at the two ears. This stimulus was created by adding a copy of the noise segment back onto itself after a delay of 10 ms had been imposed onto the copy and then repeating this delay-and-add process for 16 iterations to generate a salient pitch percept. The pitch of the iterated noise corresponds to a pure tone with a frequency equal to the reciprocal of the delay; in this case, 100 Hz. All listeners reported that they could immediately perceive this type of pitch.

Spectrally-complex pitch stimuli often contain peaks in spectral energy corresponding to the fundamental frequency and its higher multiples, even when they are not physically present in the original stimulus. These are

generated by the nonlinear mechanics of the basilar membrane and can contribute to the perception of complex pitches [14]. Given the hypothesis about a common central representation of pitch that responds irrespective of the spectral region, it is imperative that the contributions of peripheral mechanisms to neural responses are discounted before a central mechanism can be proposed. To avoid the effect of spectral distortion products, the iterated ripple noise was created using only the 1-2 kHz frequency band, while the 0-1 kHz band contained a Gaussian noise matched in spectral energy to act as an energetic masker.

Procedure: Scanning was conducted using a Philips 3 T Intera equipped with an 8-channel SENSE head coil. Sequences used a SENSE factor of 2 to reduce image distortions and a SofTone factor of 2 to reduce the background scanner noise level by 9 dB. For each participant, a high resolution (1 mm^3) anatomical scan was used to position the functional scan centrally on Heschl's gyrus. Functional scans consisted of 20 slices taken in an oblique-axial plane, with a voxel size of 3 mm^3. We took care to also include the entire superior temporal gyrus and to exclude the eyes. Scans were collected at regular 8 s intervals, with the stimulus presented predominantly in the quiet periods between each scan ('sparse imaging' [15]). Each pitch stimulus was presented in a separate scanning run, but the same noise and silent baseline conditions were repeated in each run to provide a quantitative basis for comparison. Listeners were requested to attend to the sounds and to listen out for the pitch,

but were not required to perform any task. A custom-built MR-compatible system delivered distortion-free sound using high-quality electrostatic headphones. Sound levels were equal loudness (~ 90 dB SPL measured at the ear).

Data processing: Image analysis was conducted using SPM (**www.fil.ion.ucl.ac.uk/spm**) separately for each listener. Pre-processing steps included within-subject realignment and spatial normalization. For each listener, normalized images were up-sampled to a voxel resolution of 2 mm^3 and smoothed by a Gaussian kernel of 4 mm full width at half maximum. This procedure meets the smoothness assumptions of SPM without compromising much of the original spatial resolution, so preserving the precise mapping between individual brain structure and function. Individual analyses were computed for the two runs, specifying the two pitch and the two noise conditions as separate regressors in the design. In the individual analysis, we specified separate statistical contrasts for each sound condition relative to the silent baseline that was implicitly modeled in the design.

RESULTS

Average responses: The outputs of the individual statistical contrasts were entered into a within-subjects correlated-measures ANOVA that accounted for the variability across listeners. Both the pitch-evoking stimuli and the noise generated widespread bilateral auditory responses (Table 1). Activation was

highly reliable since it survived a statistical threshold of $p < 0.05$ (corrected for false discovery rate and an extent of at least 10 voxels). Peak responses were mostly in Te1.0 (40-80% probability [17]).

** Table 1 **

The observed activation represents multiple classes of neural computation including not only the representation of pitch, but also that of the spectral content and the sound level of the signals. To test the specific hypothesis that both Huggins pitch and iterated noise access a common representation for pitch, it is desirable to eliminate the effects of all other neural computations that are common to both pitch and non-pitch stimuli. This was achieved by subtracting the matched noise from the pitch. The resulting pattern was very different across the two pitch contrasts (Table 1). The diotic pitch engaged Heschl's gyrus, planum polare (-54 -2 -12 and 50 -8 -4 mm) and anterior planum temporale (-60 -22 4 and 62 -24 6 mm). The dichotic pitch reached significance only at an uncorrected threshold in left medial planum temporale (-40 -42 10 mm).

Individual responses: The group-averaged results are difficult to resolve with the dominant view of pitch coding in lateral Heschl's gyrus [3]. However, it is well known that averaged data can obscure what is happening in individual listeners. For example, the position of a peak in the group data is not necessarily the location where a majority of the individuals all exhibit the same

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peak; instead, it can represent a location where activation from individuals overlaps in some way [10].

** Figure 1 **

To get a clearer picture, each pitch condition was contrasted with its noise baseline for each listener. To enable data exploration we chose lenient threshold criteria (p<0.01). These maps were converted into binary images and then summed across the group to generate a map of the probability distribution for each pitch-related activation (Figure 1). For every listener, we observed a significant bilateral response to iterated noise. Its location was reasonably consistent across listeners; reaching a maximum overlap at the posterior boundary of Heschl's gyrus (7/9 listeners in the left at -47 -17 3 mm and 6/9 listeners in the right at 56 -9 1 mm). In contrast, the amount of pitch-related activation was significantly smaller for Huggins pitch (Wilcoxon signed rank test computed using the extent of activation across individual listeners, Table 2, z=2.98, p<0.01). It was also much more variable in its location. As Figure 1 illustrates, the effect of Huggins pitch occurred in Heschl's gyrus, posterior planum temporale, planum polare and the superior temporal sulcus, but was never present in the same voxel for more than two listeners.

** Table 2 **

If there was a shared representation of pitch, then one would predict that fMRI responses to both types of pitch-evoking stimuli should engage the same brain region. However, typically there was no intersection between the two pitch effects (Table 2).

DISCUSSION

The present study reports the first demonstration of an auditory cortical response to a dichotic pitch measured by fMRI. While Huggins pitch produced activity in various auditory cortical sites, iterated noise activity was focused on lateral Heschl's gyrus. Typically, the two pitch-related effects were non-overlapping. Our data do not support the claim for a common neural substrate suggesting that it may be premature to assume that lateral Heschl's gyrus is a universal pitch center. Although we observed no response to Huggins pitch in lateral Heschl's gyrus, listeners did respond in other auditory regions. Hence, the absence of an Huggins pitch effect in lateral Heschl's gyrus is unlikely to be due to a generalized response reduction which might be reasoned to stem from Huggins pitch's lower perceptual salience.

We consider the apparent contradiction between our fMRI result and previous MEG reports of a common POR for both Huggins and other pitch signals, such as iterated ripple noise. It cannot be ruled out that different neural populations give rise to a similar POR. In support, although Hertrich [8] reported that the main POR dipole had the same response shape for Huggins pitch and iterated noise, important stimulus differences were present in the orthogonal response components. Thus, the dipole fits to the POR were consistent with different spatial distributions for the different pitch signals. It is entirely feasible that, like the N100, the pitch effect captured by the POR is not best represented by a single dipole [18]. Rather the dipole could simply represent a center of activity for multiple sites of pitch-specific activity.

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Three key methodological differences are also noteworthy. The first point is simple to explain. MEG selectively detects tangential sources, notably in grey matter perpendicular to the skull, and so not necessarily all the neural activity revealed by fMRI has an MEG correlate. EEG comparisons of the POR to different pitch signals might be informative here since EEG detects sources at different orientations to the skull. The second point concerns the stimuli. The MEG reported the transient deflection associated with individual pitch onsets in the absence of a change in the signal energy, while our fMRI reported the integrated response to a sequence of pitch bursts punctated by quiet intervals. Given that the energy onset response and the POR interact with one another in such a way that the POR becomes refractory when it occurs close to the energy onset [19], it would be informative to compare these MEG results to an fMRI study in which the noise baseline was presented continuously during the pitch sequence. However, one would have to assume different refractory states for the two pitch signals to fully account for the differences reported in the present study. This would be unlikely. The final point concerns whether the transient and sustained pitch-related responses represent the same neural phenomena. A common source in lateral Heschl's gyrus has been demonstrated by simultaneous modeling of both the transient response and the sustained field evoked by regular click trains [20]. This result holds promise that the MEG and fMRI are probably measuring different manifestations of the same neural coding of pitch even though the dipole source is not definitive.

CONCLUSION

Our results provide novel evidence that the spatial organization of activity for a dichotic pitch differs from that for a diotic pitch. This is evidence against the claim for a single pitch center located in lateral Heschl's gyrus.

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LEGENDS

Table 1. Location and extent of sound-evoked activation, including the degree to which three anatomical subdivisions of HG (central: Te 1.0, medial: Te 1.1 and lateral: Te 1.2 [16]) respond to each stimulus contrast. These values are reported as a percentage of the total volume of each region, calculated using the SPM anatomy toolbox [17]. The pitch > noise contrasts reached cluster-level significance ($p<0.001$) using statistics corrected for the volume of the main effect, except for those results presented in italics which reached only an uncorrected voxel-level significance ($p<0.001$) within the same functional volume.

Table 2. Number of suprathreshold voxels ($p<0.01$) in the superior temporal gyrus for each pitch effect and the intersection.

Figure 1. Probability-weighted distribution of pitch-related activity across the nine listeners; overlaid on axial slices. Colour scale represents the percentage of listeners with significant activation.
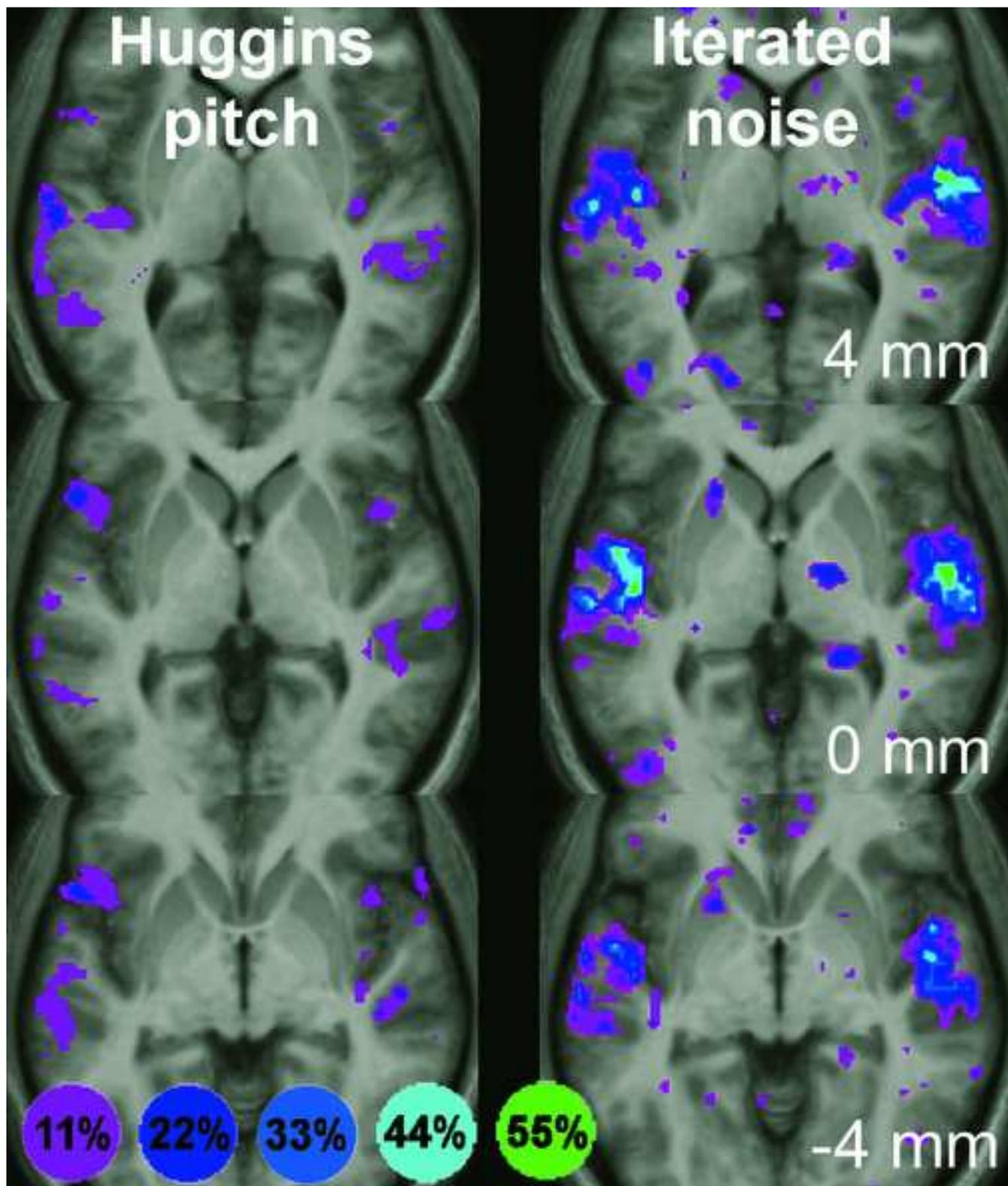
Table 1

Peak MNI coordinate mm			Z value	Cluster size (#voxels)	Side	Te1.0	Te1.1	Te1.2
x	y	z						
Huggins pitch								
-56	-14	6	5.63	1044	L	88	89	46
60	-6	2	5.01	846	R	87	62	53
Gaussian noise								
-48	-16	0	5.57	977	L	87	87	38
60	-6	2	5.37	682	R	79	47	52
Effect of dichotic pitch (Huggins pitch > noise)								
-40	*-42*	*10*	*3.44*	*10*	*L*	*0*	*0*	*0*
Iterated ripple noise								
-42	-22	8	6.74	1670	L	96	96	66
60	-10	6	6.02	1395	R	98	82	78
Gaussian noise								
-42	-22	8	6.45	1186	L	98	95	0
46	-18	8	5.62	1182	R	95	85	44
Effect of diotic pitch (Iterated ripple noise > noise)								
-54	-2	-12	4.31	206	L	21	40	7
66	-18	-2	4.04	269	R	19	0	32
-60	*-22*	*4*	*3.48*	*37*	*L*	*0*	*0*	*0*

Table 2.

Subject	Huggins pitch		Iterated noise		Both pitches	
	L	**R**	**L**	**R**	**L**	**R**
1	612	485	648	829	242	70
2	652	252	571	597	148	28
3	159	66	155	295	0	4
4	102	2	204	84	0	0
5	78	119	218	135	0	0
6	0	161	571	597	0	0
7	371	3	713	554	20	0
8	204	186	41	185	0	0
9	3	19	573	414	0	22
Median	**159**	**119**	**571**	**414**	**0**	**0**

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As suggested by the Section Editor, I have substantially reduced the use of abbreviations. The following abbreviations are now written in full throughout.

HP: Huggins pitch
IRN: Iterated ripple noise
PT: Planum temporale
PP: Planum polare
HG: Heschl's gyrus
STG: Superior temporal gyrus

1) The reviewer suggested that we were mainly guided by primate studies. While the introduction does cite 2 primate studies of pitch coding (only of which is a report of novel data – the other is a review), we do in fact cite 9 human imaging studies in the same section [refs 4-12]. Thus we feel the weight of our Introduction is guided more by human neuroimaging evidence than by the primate neurophysiology.

This focus now clarified by stating 'This result is consistent with the many human neuroimaging studies demonstrating a pitch-sensitive region in the homologue of the primate pitch centre'

Pitch is a very diverse field. Some researchers study pitch as a musical phenomena which contributes to melody. As part of this research focus they can also consider the relationships between pitch and timbre. Some researchers use pitch differences between sounds as a way to explore the effects of training on frequency or pitch discrimination. In contrast, other researchers study the psychoacoustics and physiology of pitch coding, for example to address the contribution of spectral and/or temporal mechanisms of pitch coding and to address whether there is a common representation of pitch.

The current manuscript deals with the latter approach. Therefore we do not consider it really appropriate to expand the Introduction to include the suggested references which address pitch processing from one of these other perspectives.
EG Meyer M, Baumann S, Jancke L: Electrical brain imaging reveals spatio-temporal dynamics of timbre perception in humans NEUROIMAGE 32 (4): 1510-1523 1 2006 This paper deals with the processing of complex instrumental tones.
EG Jancke L, Gaab N, Wustenberg T, Scheich H, Heinze HJ Short-term functional plasticity in the human auditory cortex: an fMRI study COGNITIVE BRAIN RESEARCH 12 (3): 479-485 2001
This paper deals with pitch discrimination and training listeners using sequences of pure tones of 950 Hz (standard) and deviant tones of 952, 954, and 958 Hz.

2) How does musicianship influence pitch perception?

Added the sentence
Thresholds were not related to musicianship.

3) The reviewer asked about the task. The task was the same for both pitch conditions. We have used this type of task widely, in a range of published papers, for stimulus mapping of the auditory cortex in well-motivated listeners.

Procedure :
Listeners were requested to attend to the sounds and to listen out for the pitch, but were not required to perform any task.

4) The reviewer asked about the quality of the sound signals delivered to the listeners

Procedure :
A custom-built MR-compatible system delivered distortion-free sound using high-quality electrostatic headphones.

5) The reviewer disagreed with the first sentence of the Discussion "The present study reports the first demonstration of an auditory cortical response to a dichotic pitch measured by fMRI." by referring to a study of dichotic tone perception by Jancke et al (2003). As we explain below, dichotic listening and dichotic pitch perception are very different processes. Therefore we are confident that our initial claim still holds true.

We would like to clarify the difference between a dichotic listening task (as used by Jancke) and dichotic pitch coding. Dichotic listening refers to the presentation of two separate signals that are presented monaurally, one to each ear. Hence, there are two simultaneous sound percepts. The listener can be instructed to listen out for a target signal presented in either the left or the right ear. This is a useful paradigm for investigating focused attention (e.g. as in the Jancke study).
Dichotic pitch refers to a single signal that is presented binaurally to both ears and the result is a single stimulus percept.. In a dichotic pitch, the pitch information can _only_ be extracted by a process of integration between the signals at the two ears.
These characteristics of a dichotic pitch are described in the Stimuli section. And to highlight the difference between this and the diotic pitch (the iterated ripple noise) we have added the following sentence when describing the diotic pitch.
 '_The waveforms were identical at the two ears._'

To clarify this a little I have expanded the keywords the include the phrase '_monaural diotic and binaural dichotic pitch_'.

6) The reviewer suggested that we mention the probabilities obtained from the Rademacher-Morosan atlas.

For brevity, we summarise the results as follows :

'Peak responses were mostly in Te1.0 (40-80% probability [17]).'