THE TONOTOPIC ORGANIZATION OF THE AUDITORY THALAMUS OF THE SQUIRREL MONKEY *(SAIMIRI SCIUREUS)*

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SUMMARY

Single unit responses were recorded from the auditory thalamus of anesthetized squirrel monkeys. The microelectrode penetrations had an orientation perpendicular to the sagittal plane. The small cell division is tonotopically organized. The cells in the most lateral aspect of this division have their 'best frequencies' (BFs) in the low frequency range with a progressive shift in the BF toward the higher frequencies the further medially the sampling progressed. Dorsal to and extending ventromedially are large cells which are darkly stained. In addition there is a bulbous extension more ventrally of large cells less dense and perhaps less darkly stained. The large cells in these subdivisions did not always discharge spontaneously nor were they always responsive to tones. In the dorsal group, there is an initial low to high sequence of BF followed by one or more reversals in BF. Within the border region between the small cell division and both the ventromedial extension and bulbous extension of the large cells there starts a reversal, a high-to-low sequence which occurs within a comparatively short distance. Beyond the initial reversal, in both subdivisions, there are one or two additional reversals of BF.

INTRODUCTION

In the cat, the auditory thalamus has been subdivided into 3 major cellular subdivisions: pars principalis, pars magnocellularis and the posterior group by Rose and Woolsey[9,12], and into the dorsal, medial and ventral nuclei by Morest[6,7]. Each of these subdivisions has been shown to be tonotopically organized[1–4,8]. The data to be presented here show that in the squirrel monkey the auditory thalamus is also

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tonotopically organized, although it differs from that of the cat in respect to the organization of the dorsal large cell division.

METHODS

Squirrel monkeys, *Saimiri sciureus*, weighing between 500 and 600 g were used in the experiments. Anesthesia was achieved by injecting 30 mg/kg of ketamine hydrochloride (Ketalar) intramuscularly. When the animal became ataxic, 12 mg/kg of sodium pentobarbital (Nembutal) was injected intraperitoneally. Anesthesia was sustained by injection of small doses of either drug to effect.

The trachea was cannulated. Most of the pinna and the skin overlying the cranium were removed by electric cautery. The head was secured and then was turned by 90 ° and aligned so that the lower ridge of the orbit and the middle of the ear drum were in the same anterior–posterior vertical plane. Electrode coordinates were chosen relative to this plane. An ear speculum was fitted into the remaining portion of each pinna and then centered over the ear drum by direct visual inspection. Either the microphone probe tube or a dummy probe tube was then inserted through the center of the speculum. A polyethylene tube connected an acoustic coupler containing a PDR-600 phone to the speculum.

Intensity calibrations were made with the aid of a Brüel and Kjaer microphone (4134) and a General Radio Wave Analyzer (1900A). A computer program was used to collect calibration data from 0.1 to 25.6 kHz.

Most penetrations were made using glass micropipettes filled with 3 *M* NaCl, whose impedance was in the 10–40 MΩ range. The electrodes were advanced with the aid of a Baltimore Instrument Co. microdrive.

The potentials were amplified and filtered by a Grass P-15 amplifier and observed on a Tektronix oscilloscope (565). The discriminated potential was fed to a PDP-12 computer. Dot pattern and histogram programs were available for displaying the responses.

The pure tones were generated by a Wavetek function generator (115), fed through a tone switch and attenuator network and delivered to either or both earphones. Only data obtained from contralateral stimulation are included in the study.

After the initial auditory response was encountered, the electrode was advanced in 50 μm steps until there were no further responses to auditory stimulation. The penetration was continued at least 1 mm beyond the point of no response. If two units having thresholds within 6 dB were encountered at a particular location, both units were registered on the plot of frequency *vs.* depth of electrode.

When a responsive unit or group of units was found the following routine was employed in order to determine the 'best frequency' (BF). The entire acoustic range from 0.1 to 45.0 kHz was explored at a moderately high intensity. The intensity of the tone was then reduced and the frequency limits were redetermined. The response area was tracked in this manner until a BF was reached. The response threshold was determined for both ipsilateral and contralateral ears. During this procedure the computer display was observed to determine the effectiveness of the stimulus.

At the close of the experiment markers were made in the brain for shrinkage measurements. The animal was perfused, the brain after processing was cut at 30 μm and then stained with cresyl violet. All sections through the auditory thalamus were mounted for examination in order to locate the electrode tracks. Distances along the electrode tracks were measured, whenever possible, from the last visual responses obtained from the lateral geniculate body. The distances were corrected for shrinkage.

RESULTS

Data were obtained from 51 electrode penetrations of the auditory thalamus which involved 3 types of cells. In the lateral aspect of the auditory thalamus one finds numerous small cells which never stain darkly. Posterior to the start of the small cell division one finds a group of large cells just medial to the tip of the pulvinar. These cells have large nuclei and stain darkly. More anteriorly these cells become more numerous and form a cap over the small cell division. In addition, the same type of cells can be seen to extend ventro-medially and join with a third division which forms a bulbous extension. Within the third division, the cells are about the same size as those in the dorsal group, but do not stain quite as darkly and are less numerous.

There were 38 electrode penetrations of the small cell division. The tonotopic organization which emerges from the data is as follows: cells in the lateral aspect of the small cell division have BFs in the low frequency range and as the electrode penetrates further medially there is a progressive shift in BF toward higher and higher frequencies. At the boundary with the large cells one frequently finds a transitional zone where there is an intermixture of high and low BFs. In addition, the progression of BFs occurs more rapidly in the extremities where the small cell division is considerably reduced in the horizontal plane.

The information obtained from 3 animals is presented in support of these generalizations. Fig. 1A[1] shows one electrode track for animal 70-41:VII. The electrode track is located just above the solid line. A 1 mm calibration is also included but is not corrected for shrinkage.

In this case the electrode was found to have penetrated the auditory thalamus between 750 and 900 μm from the posterior limit of the small cell division. The electrode passes through both the small cell division and the ventromedial extension of the large cell division. The initial responses in this penetration as shown in the graph of Fig. 1A[2] are around 6.0 kHz. There follows a progressive rise in BF to approximately 30.0 kHz about 800 μm beyond the lateral boundary of the small cell division. Then there is a decrease in the BF with increased distance to about 0.5 kHz.

The data obtained from animal 71-44:VII are presented in Fig. 1B. The electrode track was found between 1050–1200 μm from the posterior limit of the small cell division and the electrode also penetrated the ventromedial division. In this case there is a progressive rise in the BF from 3.0 to 36.3 kHz at about 1000 μm from the lateral boundary of the small cell division. In the border region between the small cells and the large cells of the ventromedial extension, there starts an incomplete reversal of BFs, which decreases to about 10 kHz. No spontaneous discharge nor further responses were recorded beyond this point.
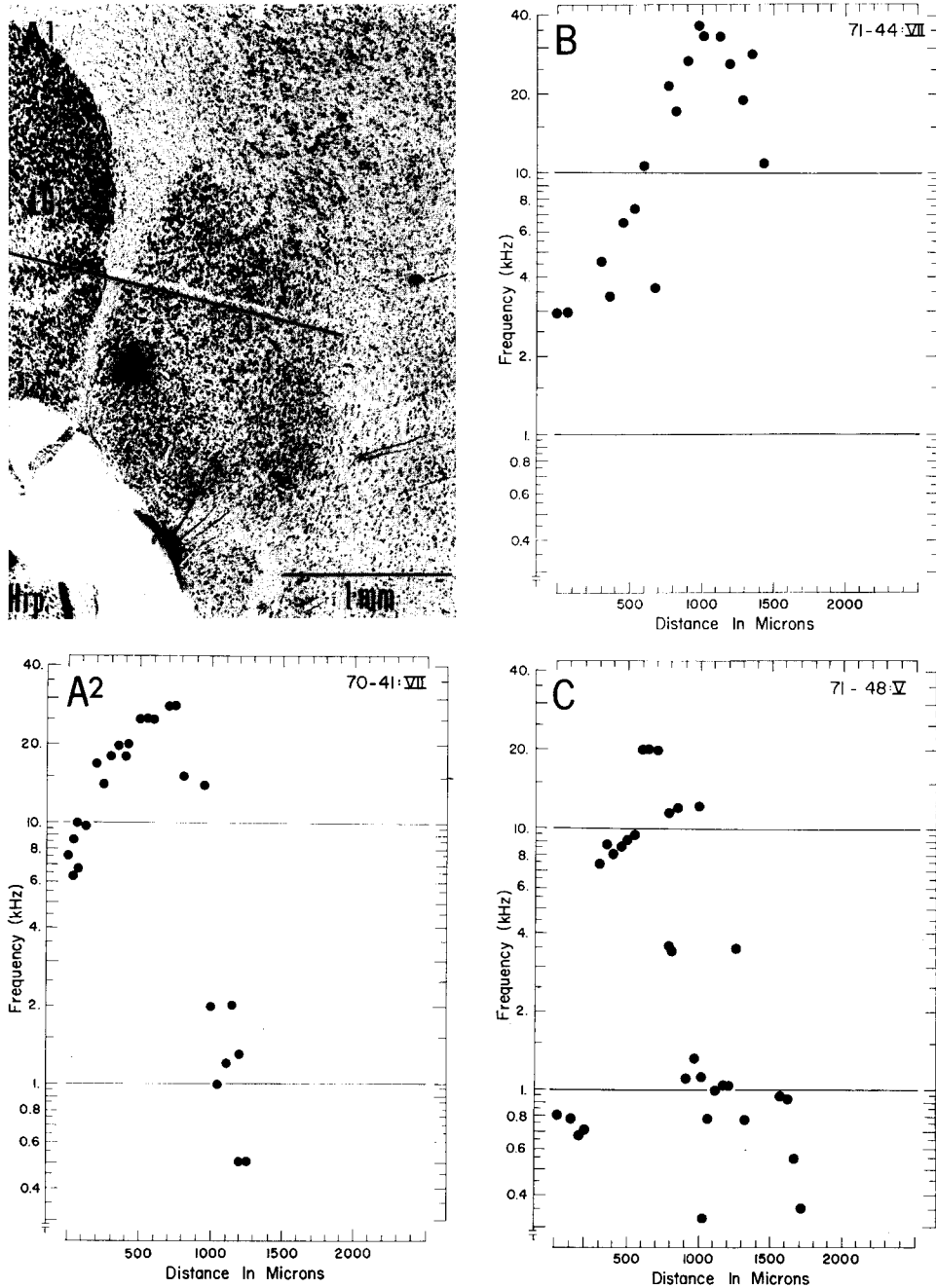
Fig. 1. A[1]: coronal section through part of the thalamus of an animal 70-41:VII. LG $=$ lateral geniculate body; Hip. $=$ hippocampus. The electrode track is dorsal to the solid line. A[2]: BF data for increments along the track. B: BF data for animal 71-44:VII. C: BF data for animal 71-48:V.
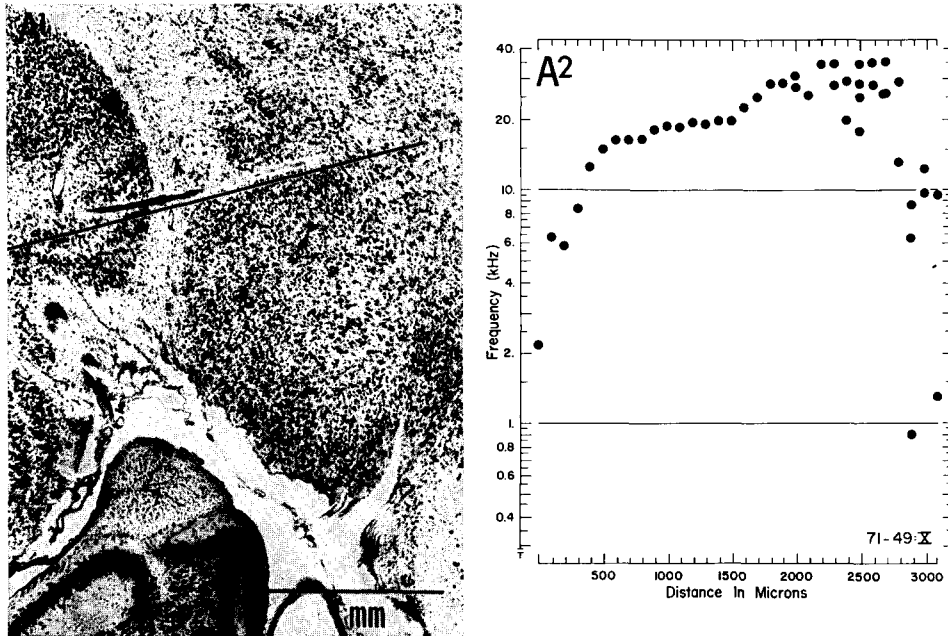
Fig. 2. A[1]: coronal section through part of the thalamus of animal 71-49: X showing the electrode track. A[2]: BF data along the track.

The data from animal 71-48:V are presented in Fig. 1C. The electrode penetration was found between 1200–1350 μm from the posterior limit of the small cell division. The electrode also penetrated the ventromedial division of the large cells. In this case there is progressive rise in BF from about 0.70 kHz to approximately 20.0 kHz about 600 μm from the lateral border of the small cell division. In the border region between the small cells and the large cells there is an intermixture of BFs, but there is a trend for the BF to decrease. The BF drops to 0.3 kHz about 1000 μm medially. There appears to be a reversal at this point with the BF rising to 4.0 kHz, 400 μm more medially and there is a reduction in BF once again as the electrode was advanced still more medially.

There were 10 electrode penetrations of the dorsal group of large cells. The data from animal 71-49:X are presented in Fig. 2. In this case the initial BF is 2.09 kHz, followed by a progressive rise in the BF to 35.2 kHz. There follows an intermixture of intermediate and low frequencies, with the lowest BF being 0.9 kHz.

There were 3 penetrations of this region which yielded neither spontaneous activity nor response to pure tones. In an additional case there was only an initial ascending phase of BF followed by no spontaneous activity or additional responses. In the remaining 5 cases the ascending phase was present, followed by at least one reversal in BF. In two of these cases the BF progressions were interrupted by regions of no spontaneous activity and no auditory responses.

There were 16 electrode penetrations which passed through the small cell region and through the ventromedial extension of the large cells. The data from animals
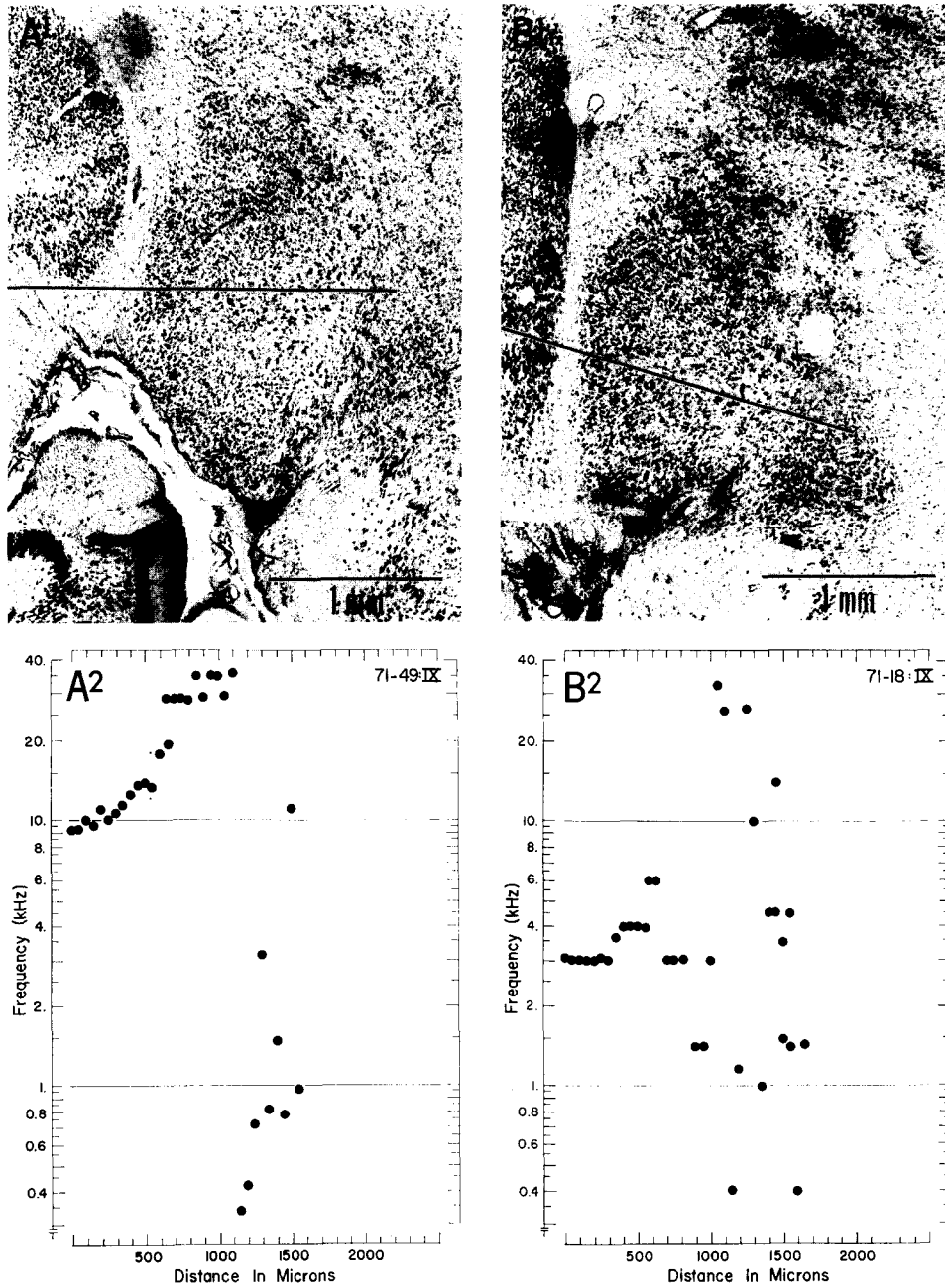
Fig. 3. A[1]: coronal section through the thalamus of animal 71-49:IX showing electrode track. A[2]: BF data along the track. B[1]: coronal section through the thalamus of animal 71-18:IX showing the electrode track. B[2]: BF data along the track.

71-44:VII and 71-48:V have already been discussed. An additional example is provided by the data obtained from animal 71-49:IX presented in Fig. 3A[1] and A[2]. There is a progressive rise in BF from 9.17 to 35.5 kHz 800 μm more medially. There follows a precipitous drop in BF to 0.34 kHz and at least one additional reversal in BF.

In two cases only the rising phase of BFs was recorded and there was neither spontaneous activity nor responses to auditory stimulation in the large cell portion of the electrode penetration. In 8 cases there was only a high to low reversal in BF and within the remainder of the track there was neither recordable spontaneous discharge nor response to tones. In 6 cases there were always two reversals in the ordering of BF within the large cell division.

There were 6 penetrations which involved both the small cell division and the bulbous extension of the large cells. The electrode track is seen in Fig. 3B[1] for animal 71-18:IX. The initial responses were at 3.0 kHz as seen in B[2] and after an irregular course the BF peaks around 30 kHz. There is then an intermixture of units of high, intermediate and low BF within the large cell division.

No responses could be elicited within the large cell division in 3 animals. In two other animals there was only the descending order of BFs and in one of these cases there was a region of neither spontaneous activity nor responses within the track.

DISCUSSION

Within all divisions of the auditory thalamus thresholds were lower for contra-lateral stimulation than for ipsilateral stimulation. There were, however, units which responded exclusively to ipsilateral stimulation. The discharge pattern varied consider-ably from unit to unit being influenced by various patterns of inhibition, related to monaural stimulation or dichotic stimulation. Only data obtained from contralateral stimulation are presented.

Within the small cell division all units discharged spontaneously and discharged in response to auditory stimulation. This division showed a consistent tonotopic organization. Cells in the most lateral aspect are most responsive to low tones and there is a progressive shift to higher tones more medially. The highest BF is correlated with the medial border of the small cell division. This progression was seen in all animals. It is clearly seen in the data from animal 70-41:VII, but less clearly seen in animal 71-18:IX. There were very few data which showed this irregular course. Around 1000 μm, however, the BF does reach the 30–35 kHz range. (Response to tones below 1 kHz were frequently missed because of the mechanical problem related to dimpling and piercing of the pia mater.)

The sequential ordering of BFs, low frequencies laterally and high frequencies medially, is also in evidence within pars principalis (ventral division) of the auditory thalamus of the cat[2–4]. The coronal plane of this division in the cat is more extensive and the ordering of BFs was found to be more gradual. There were far fewer inversions in the ordering of BFs in the cat and there was less evidence of a mixture of high inter-mediate and low units in the border region with the large cell divisions.

The physiological characteristics of both groups of large cells differ from those

of the small cells. The large cells did not always discharge spontaneously, and corre-
lated with this was the lack of responsiveness to tones. Within a single penetration a
segment could be without spontaneously discharging units and no responses to tones
or the entire track could be unresponsive. The level of activity is most probably related
to the depth of anesthesia.

Within the large cell division which lies dorsal to and caps the small cell division
there is an initial rise in BF followed by at least two reversals in the ordering of BFs.

There does exist the problem of deciding how many reversals in BF occur
within the large cell subdivisions. In some cases no data were available since tracks
within these regions were unresponsive within segments or throughout. In other cases,
the changes in BFs within the border region and within the large cell divisions occur
very rapidly; within 50–100 μm as in animal 71-49:IX. In this case the BF drops from
about 35 kHz to about 0.35 kHz with no intermediate responses between these limits.
There then follows a second rising phase in BF, although complicated by the presence
of units having BFs in the low and intermediate ranges. Likewise, an analysis of the
data from the large cell divisions for animals 71-18:IV and 71-48:V present similar
problems. It would appear that in some cases the functional subgroups within the
large cell divisions have well defined limits and the progression of BFs is orderly and
the reversals are uncomplicated. Where the borders are less well defined one finds the
intermixture of cells of divergent BFs and the reversals are less well defined. Examina-
tion of all the data would support the conclusion that at least two reversals in BF can
be found in the large cell division of the auditory thalamus.

Functionally the organization of the large cell division which extends ventro-
medially differs from the dorsal group. After the rising phase of the BFs associated
with the small cell group, there is a reversal in the ordering of BF from high to low
which starts in the border region between the small and large cells. There then follows
one or two additional reversals.

In the cat one finds a group of cells which have been designated as the posterior
group (dorsal nuclei), lying medial to the small cell group[6,7,9,10]. The cells are similar
in their response characteristics to the large cells under discussion. One finds in both
cases reversals in the ordering of BF. In both cases within a segment or throughout
a track, neither spontaneous activity nor tone elicited responses could be recorded.
The similarities in these properties are then fairly striking. However, there is a major
physiological difference between these cells in the cat and squirrel monkey in that the
large cells of the dorsal group of the squirrel monkey do have an initial rising phase
of BFs which one does not find within the posterior group (dorsal division) of the cat.

In the cat there is evidence that the cells of the posterior group (dorsal nuclei)
project to more than one subdivision of the auditory cortex[10–12]. Since the cortical
auditory area of *Macaca mulatta* has also been shown to be divided into subareas[5], it
would seem reasonable to assume that the same organization would be found for
Saimiri sciureus. If so, the reversal in BFs within the nuclei of the auditory thalamus
probably represent the subgroupings from which these projections originate.

In the border region between the small cell division and the large cells within
the bulbous extension, there starts a reversal in the ordering of BF from high to low.

After this there are one or two additional reversals in BF. Again, absence of spontaneous discharge and response in sections or throughout a track was encountered. Functionally the organization of this group of cells would appear to be similar to the organization of the magnocellular region of the cat[1,4]. These subdivisions could also project to subareas of the auditory cortex.

It is concluded that the auditory thalamus of the squirrel monkey is tonotopically organized. It is further concluded that the sensory epithelium of the cochlea is represented several times in the auditory thalamus as demonstrated by the reversals in the ordering of the BF. The auditory thalamus receives projections from lower auditory centers which are tonotopically organized. In addition, the auditory thalamus projects to the auditory cortex which has been subdivided into several subareas, each of which is tonotopically organized. The reversals in the ordering of BF could represent the origin of the projections to these subdivisions of the auditory cortex[5,11,12].

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