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Research paper

The role of the temporal pole in modulating primitive auditory memory

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HIGHLIGHTS

- A break in interaural correlation is used to study primitive auditory memory (PAM).
- Anterior temporal lobectomy (ATL) in humans does not abolish the PAM.
- Unilateral ATL shortens the temporal preservation of PAM of contralateral sounds.
- The temporal pole top-down modulates PAM of sounds entering the contralateral ear.

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ABSTRACT

Primitive auditory memory (PAM), which is recognized as the early point in the chain of the transient auditory memory system, faithfully maintains raw acoustic fine-structure signals for up to 20–30 milliseconds. The neural mechanisms underlying PAM have not been reported in the literature. Previous anatomical, brain-imaging, and neurophysiological studies have suggested that the temporal pole (TP), part of the parahippocampal region in the transitional area between perirhinal cortex and superior/inferior temporal gyri, is involved in auditory memories. This study investigated whether the TP plays a role in mediating/modulating PAM. The longest interaural interval (the interaural-delay threshold) for detecting a break in interaural correlation (BIC) embedded in interaurally correlated wideband noises was used to indicate the temporal preservation of PAM and examined in both healthy listeners and patients receiving unilateral anterior temporal lobectomy (ATL, centered on the TP) for treating their temporal lobe epilepsy (TLE). The results showed that patients with ATL were still able to detect the BIC even when an interaural interval was introduced, regardless of which ear was the leading one. However, in patient participants, the group-mean interaural-delay threshold for detecting the BIC under the contralateral-ear-leading (relative to the side of ATL) condition was significantly shorter than that under the ipsilateral-ear-leading condition. The results suggest that although the TP is not essential for integrating binaural signals and mediating the PAM, it plays a role in top-down modulating the PAM of raw acoustic fine-structure signals from the contralateral ear.

1. Introduction

1.1. Primitive auditory memory

In a reverberant environment, humans exhibit a remarkable ability to perceptually integrate the (time-leading) direct sound wave from a source with the time-delayed (and linearly filtered) reflections of the source: attributes of the time-delayed reflections are perceptually captured by the direct wave [1], resulting

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in a single fused image of the source whose perceived location is around the location of the source (the precedence effect) [2–4]. The perceptual integration between the leading direct wave and the lagging reflections plays a role in suppressing the perception of distinct echoes and facilitating the recognition and localization of the source.

More interestingly, the perceptual integration can occur over a few tens of milliseconds of the lead-lag delay [5–7], suggesting that a temporal storage of the leading direct-wave signals occurs in the central nervous system. Since auditory information is processed in a temporally sequential pattern, both an auditory storage and a temporal readout of sequential auditory information from the storage are critical for organizing acoustic stimuli into auditory-image units [8]. Without such a faithful temporal storage of raw fine-structure signals of the leading wave, neither the central computation of the similarity (correlation) nor the perceptual integration between the leading and lagging waves is possible. Thus, this faithful auditory storage of raw fine-structure signals has been termed *primitive auditory memory* (PAM) and recognized as the early point in the chain of the transient auditory memory system [6,7].

The PAM is different from the traditionally defined auditory sensory memory as investigated by the mismatch negativity (MMN) of event-related potentials [e.g.,9–11], because the MMN-probed auditory memory can last up to 2–10 s and be of a long-term nature in some circumstances [12]. Thus, the PAM of acoustic details occurs at the early end of the chain of the transient auditory memory system [6]. However, the sensory memory probed by MMN encodes sensory memory updating, reflecting the representation of inter-sound regularities based on feature- and temporally integrated sensory stimulus information that correspond to the subjective contents of perception [12].

1.2. How to measure the temporal preservation of PAM at the perceptual level?

Interaural correlation (IAC), which is defined as the maximum cross-correlation coefficient of these two sounds across the two ears, describes the similarity of the sound waves entering the two ears [13]. The auditory system is capable of processing the IAC and expressing the processing consequence perceptually. For example, when two identical (correlated) wideband noises are simultaneously presented at the left ear and the right ear, respectively, listeners will perceive a fused compact noise image at the center of the head. However, if the IAC gradually decreases from 1 to 0, the centrally located single image dramatically changes into two (left-right) separated images [14,15]. More importantly, when an interaural delay (i.e., interaural interval) is introduced without changing the IAC, the noise image becomes increasingly diffuse with the gradual increase of the interaural delay and eventually indistinguishable from the images of the binaurally presented independent (uncorrelated) noises [16,17].

Due to the sensitivity to changes in IAC, listeners with normal hearing can easily detect an interaurally uncorrelated noise fragment embedded in the interaurally correlated noises [18], i.e., a change of IAC from 1 to 0, then back to 1, so called "break in interaural correlation", BIC. More relevant to this study, in younger adults with normal hearing, the detection of the BIC well remains even when a short interaural interval (interaural delay) up to 20–30 ms is introduced [6,7,19], indicating that the noise fine-structure signals from the leading ear are sufficiently maintained in the PAM system during the delay period. In other words, when an interaural delay is introduced, the BIC is detectable only when the contrast in IAC between the central representation of the BIC and that of the BIC markers (the noise sections flanking the BIC) is sufficiently large, indicating that the fine-structure signals of the BIC markers are sufficiently maintained due to the PAM system during the delay period Table 1.

Moreover, according to the PAM theory [6,7,20], when the interaural delay between the binaurally presented identical (correlated) noises is progressively increased, the PAM trace of fine-structure signals from the leading ear progressively decays (i.e., the central representation of the fine-structure signals of the noise entering the leading ear becomes more and more diminished with time), causing a progressive reduction in both the IAC of the central representation of the noises from the two ears and the perceptual salience of the BIC. Thus, the longest interaural delay at which the BIC is just detectable can be used to indicate the temporal preservation of the PAM of acoustic fine-structure signals from the leading ear. Note that introducing a BIC does not alter the energy and spectrum of the monaural noise signals, but modifies the auditory image, i.e., the perceptual compactness/diffuseness, number, placement, loudness, and the pitch of the noise object.

1.3. The temporal pole is part of the pathways modulating auditory memories

As mentioned above, PAM can be recognized as the early point in the chain of the transient auditory memory system [6,7]. Although it has been known that the maximum maintaining time (the temporal preservation) of PAM traces can be up to 20–30 ms in some younger-adult individuals with normal hearing and the PAM traces decay quickly over time [6,7,19,20–22], the neural mechanisms underlying the dynamic PAM are largely unknown. One of the investigation strategies is to examine whether the central pathways involved in auditory memories are also involved in mediating/modulating the PAM.

It has been reported that auditory sensory memories are stored in the auditory cortex including the superior temporal gyrus (STG) [23], and predominantly in the auditory cortex contralateral to the ear of sound presentation [24]. Also, the neural connections between the auditory cortex and medial temporal cortex (which comprises the hippocampal formation and the parahippocampal region) are involved in both short-term episodic auditory memory [25] and long-term auditory memory [26]. Particularly, it has been reported that the temporal pole (TP), as part of the parahippocampal region in both humans and nonhuman primates, is a transitional area between memory-associated perirhinal cortex and the neocortical areas of the adjacent superior and inferior temporal gyri [27], and involved in both auditory perception and auditory memories [28]. More specifically, the dorsal part of the TP receives inputs from the auditory processing areas of the rostral part of the STG (which is also part of the "what" pathway concerned with the identification of specific features of sounds) [27,29–31], projects to both the rhinal cortex and the entorhinal cortex (EC) of the medial temporal lobe [27,31], and is involved in auditory memories in both humans and monkeys [28,32,33]. The TP is also recognized as a cortical convergence zone integrating signals between auditory, somatosensory, visual, paralimbic, and default-semantic networks [34].

1.4. Patients with temporal lobe epilepsy and unilateral anterior temporal lobectomy

Epilepsy is one of the most common and serious neurologic disorders. Many patients with temporal lobe epilepsy (TLE) are refractory to drug medication [35]. Unilateral anterior temporal lobectomy (ATL, including the removal of the TP) has been widely used as an effective treatment for TLE [36–39]. Surprisingly, although delayed middle-latency auditory evoked potentials and a few mildly impaired auditory cognitive functions exhibit in patients with TLE [40,41], the ability in short-term memorization of non-verbal sounds is reduced but not abolished by ATL

Table 1
Clinical Information for individual patients.

Patients	Age	M/F	Lesion Regions (BA)	Current Medication
Left Hemishpere				
P01	29	M	38, 20	CBZ, LEV
P02	34	M	38, 20	OXC, LEV
P03	20	M	38, 36, 21, 20	LEV, OXC
P04	14	M	38, 36, 22, 21, 20	SV
P05	25	M	38, 20	OXC, LEV
P06	27	M	38	OXC
P07	20	F	38	OXC, LEV
P08	16	F	38, 20	SV
P09	30	M	54, 53, 38	OXC, LEV
P10	20	M	38	CBZ, SV, CZP
P11	31	M	38, 20	OXC, LEV
P12	22	M	54, 53, 38, 36, 22, 21, 20	OXC
P13	36	F	54, 53, 38, 20	OXC, LTG
Right Hemishpere				
P14	18	M	38, 20	LTG
P15	26	M	38, 20	OXC, PHY, SV, LEV
P16	35	F	54, 53, 38, 20	LTG
P17	23	M	38, 20	OXC
P18	23	M	54, 53, 38, 20	CBZ, PHB, LTG
P19	19	F	38, 20	OXC
P20	19	M	54, 53, 38, 20	OXC, LEV
P21	22	M	54, 53, 38, 20	CBZ
P22	23	M	38, 20	SV
P23	31	M	30, 20	OXC
P24	25	M	54, 53, 38, 20	none
P25	25	M	38, 20	OXC, LEV
P26	21	M	54, 53, 38, 20	OXC, PHB

P, patient; M/F, male/female; LTG, lamotrigine; LEV, levetiracetam; OXC, oxcarbazepine; CBZ, carbamazepine; SV, Sodium Valproate; PHB, Phenobarbitone; PHY, Phenytoin; CZP, Clonazepam; BA, Brodmann area.

[42], suggesting that the TP is mainly involved in memory modulations. This view is supported by a recent study showing that ATL provokes functional modifications of the auditory pathway as indicated by altered auditory brain-stem responses and middle-latency responses [43].

1.5. The goal of this study

Since hospitalized patients with both unilateral ATL and normal hearing offer a rare and precious opportunity for investigating whether the TP plays a role in mediating/modulating the PAM, this study was to examine the difference in the longest interaural interval (interaural delay threshold) for detecting the BIC between the ipsilateral-ear-leading stimulation condition (related to the ATL site) and the contralateral-ear-leading stimulation condition in patients with unilateral ATL centered on the TP.

2. Material and methods

2.1. Participants

Twenty-six TLE patients with the unilateral neurological damage to the TP area, recruited in the Affiliated Bayi Brain Hospital, participated in this study. Thirteen patients (aged between 14–36 years) received the ATL in the left hemisphere and the other 13 patients (aged between 18–31 years) received the ATL in the right hemisphere. Thirteen healthy controls (aged between 19 and 39 years), who were recruited from the communities surrounding the hospital, participated in this study for establishing the normal baseline performance in the testing environments. Confirmed by tuning fork tests, all the participants had normal pure-tone hearing thresholds at each ear between 0.125 and 4 kHz.

Each of the patient participants underwent a standard lobectomy with the removal of the anterior temporal lobe in one hemisphere. In a few patients, the lobectomy also removed the amygdala, anterior half of the hippocampus, and/or the anterior one third of the parahippocampal gyrus (see Section 3). These patients participated in perceptual testing at least three months after the lobectomy when they fully recovered from surgery.

All the participants provided informed consent for their participation. The experimental procedures were approved by the Ethics Committee of the Military General Hospital of Beijing PLA.

2.2. Apparatus and stimuli

Gaussian wideband-noise stimuli were synthesized using the MATLAB function at the sampling rate of 48 kHz with 16-bit amplitude quantization and low- pass filtered at 10 kHz. The stimulus duration was 2000 ms including the 10-ms rise/fall time. All the stimuli were transferred using Creative Sound Blaster (Creative SB X-Fi Surround 5.1 Pro, Creative Technology Ltd., Singapore) and presented to participants with insert earphones (*ER*-3, Etymotic Research, Elk Grove Village, IL) at the sound pressure level (SPL) of 65 dB. Calibration of the sound level was carried out with the Larson Davis Audiometer Calibration and Electroacoustic Testing System (AUDit and System 824, Larson Davis, Depew, NY).

2.3. Design and procedures

The participant was seated in a quiet room in the hospital during the behavior tests. The experiment was programmed in MATLAB environment with Psychtoolbox (http://www.psychtoolbox.org). The design and procedures followed our previous studies [6,7,21]. Each trial included two binaural presentations of 2000-ms noises: In one presentation, the left-earphone noise was an exact copy of the right-earphone noise; in the other presentation, the left-earphone noise was also identical to the right-earphone noise except that its temporal middle section (900–1100 ms from the onset) was substituted with an interaurally uncorrelated fragment (i.e., the BIC) with a fixed duration of 200 ms. The offset-to-onset

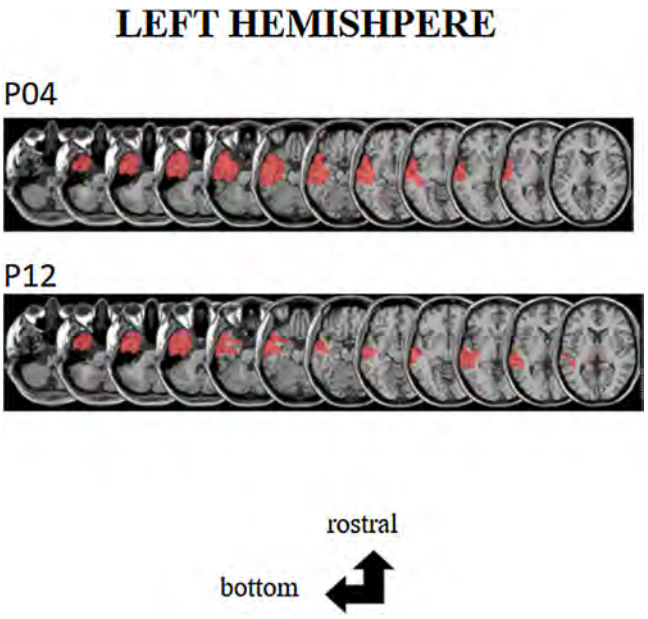

Fig. 1. Reconstruction of the extent of unilateral anterior temporal lobectomy (ATL) surrounding the temporal pole (TP, centered in Brodmann Area 38) in individual patients P04 and P12, whose perceptual testing results were not included data analyses.

interval between the two presentations was 1000 ms. Frozen noises were used for each trial.

The interaural delay, with either the leaf-ear leading (50% chance) or the right-ear leading (50% chance), was systematically increased from 0 ms using an adaptive two-interval, two-alternative, forced-choice (2AFC) procedure [19]. The participant's task was to identify which of the two noise presentations contained the BIC by pressing either the left or the right button of a computer mouse. The delay threshold for detecting the BIC was tracked using a three-up-one-down paradigm [44].

For both healthy participants and patient participants, comparisons in the delay threshold for detecting the BIC were conducted between the left-ear-leading condition and the right-ear-leading condition. For patient participants, comparisons in the delay threshold were also conducted between the ipsilateral-ear-leading (related to the hemisphere with ATL) condition and the contralateral-ear-leading condition. Moreover, for patient participants, comparisons in the delay threshold were conducted between patients with ATL in the left hemisphere and those with ATL in the right hemisphere.

2.4. Data analyses

The recordings of patient's lesion location and extent, obtained from both MRIs and CT films, were transcribed onto an averaged template in MNI space using MRIcron.

Mixed two-way ANOVA, *t*-tests, Pearson correlation, and Bonferroni post-hoc tests were used with IBM SPSS Statistics 20 (SPSS Inc., Chicago, Illinois 60606). The null-hypothesis rejection level was set at 0.05.

3. Results

Anatomical analyses showed that the ATL completely removed the unilateral TP (BA38) (Table 1, Supplementary material) Fig. 1. In 2 patients (P04 and P12), the surgically removed structures also included the amygdala, anterior half of the hippocampus, and anterior one third of the parahippocampal gyrus (Fig. 1, Supplementary material)). Thus, the behavioral results of P04 and P12 were not included in data analyses. Fig. 2 shows the reconstruction of the extent of ATL surrounding the temporal pole in 24 individual patient participants (also see Supplementary material), whose perceptual testing results were included data analyses.

In this study, the delay threshold for detecting the BIC was measured under both the left-ear-leading stimulation condition and the right-ear-leading stimulation condition. Fig. 2 shows individual participants' thresholds in the healthy-control group (left panel) and the patient group (right panel). In each panel, individual-participants' threshold values under the left-ear-leading condition distribute along the abscissa, and individual-participants' threshold values under the right-ear-leading condition distribute along the ordinate. The diagonal line represents the positions of value points in the panel when threshold values under the two leading conditions were identical.

Pearson correlation tests showed that for both healthy-control participants and patient participants, the delay threshold under the left-ear-leading condition was significantly correlated to that under the right-ear-leading condition across participants (Fig. 3), suggesting that the PAM of left-ear signals and the PAM of right-ear signals shared a common underlying mechanism.

To examine both the laterality effect of left-right ear leading and the group effect on the interaural delay threshold, a 2 (leading ear: left, right) by 3 (participant group: healthy control, left-ATL patient, right-ATL patient) mixed two-way ANOVA showed that neither the two main effects nor the interaction of the two factors were significant (all $p > 0.10$). Thus, the left-right leading-ear laterality effect was not significant for the three participant groups.

Also, for both patients with the left ATL and patients with right ATL, after averaging individuals' delay thresholds under the left-ear-leading condition and the right-ear-leading condition, the difference in group-mean delay threshold between left-ATL patients and right-ATL patients was not significant ($t_{22} = 1.317$, $p = 0.201$).

Finally, in patient participants, to examine the effects of ipsilateral-contralateral (relative to the site of ATL) leading-ear laterality on the delay threshold, the behavioral results of left-ATL patients and right-ATL patients were combined and their delay thresholds for detecting the BIC under the condition of ipsilateral-ear leading (relative to the side of ATL) were compared with those under the condition of contralateral-ear leading.

The left panel of Fig. 4 shows individual patient participants' delay thresholds for detecting the BIC under the ipsilateral-ear-leading condition (values along the abscissa) and those under the right-ear-leading condition (values along the ordinate). Apparently, for the majority of patient participants, their data points distribute beneath the diagonal line, indicating that the longest interaural intervals for detecting the BIC under the ipsilateral-ear-leading condition were generally larger than those under the contralateral-ear-leading condition.

The right panel of Fig. 4 compares the group-mean delay threshold of patients under the ipsilateral-ear-leading condition and that under the contralateral-ear-leading condition. Obviously, the threshold under the ipsilateral leading condition, which was also close to the group-mean threshold for healthy controls (represented by the horizontal broken line), was larger than that under the contralateral leading condition. A paired *t*-test confirmed that the difference in delay threshold between these two listening conditions for patients was significant ($t_{23} = 2.731$, $p = 0.012$). Thus, for patients with unilateral ATL, the PAM of noise fine-structure signals entering the ipsilateral ear lasted longer than that entering the contralateral ear.

Also across patient participants, the delay threshold under the ipsilateral leading condition was significantly correlated to that under the contralateral leading condition (Fig. 4, left panel), sug-

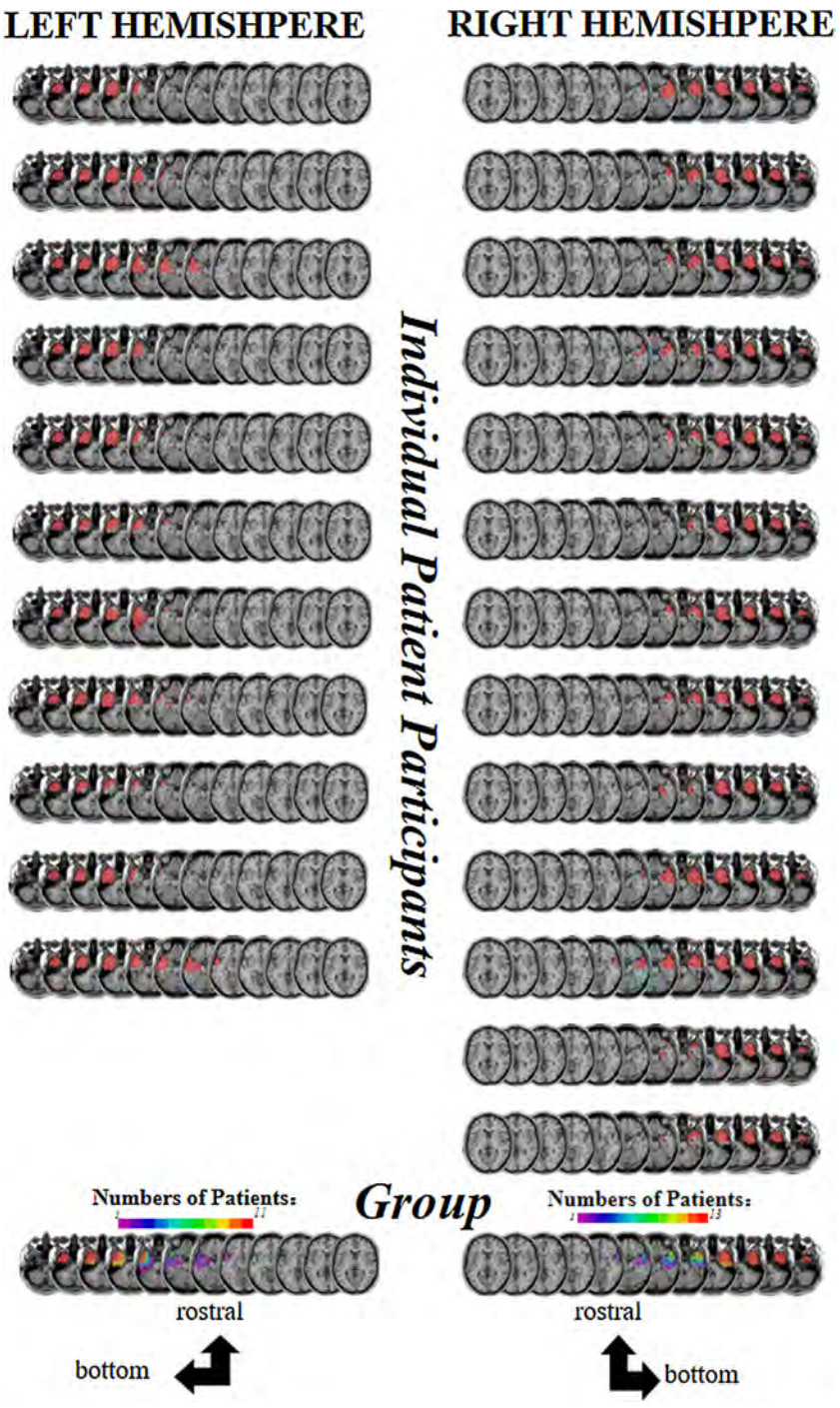

Fig. 2. Reconstruction of the extent of unilateral ATL surrounding the TP in 24 individual patient participants, whose perceptual testing results were included data analyses.

gesting that the PAM of ipsilateral-ear signals and the PAM of contralateral-ear signals shared a common underlying mechanism.

4. Disscussion

The results of this study showed that both healthy controls and patients with unilateral ATL centered on the TP (due to their unilateral TLE) were able to detect a transient BIC when an interaural delay is introduced. Also, in both healthy controls and patients, although there were no significant differences in the delay threshold for detecting the BIC between the left-ear-leading condition and the right-ear-leading condition, the delay threshold under the left-ear-leading condition was significantly correlated to that under the right-ear-leading condition. Thus, the hemispheric laterality of the temporal preservation of PAM is not evident.

Both previous brain-imaging studies and previous neurophysiological recording studies have shown that activities of the dorsal part of the TP are associated with auditory memories in both humans and monkeys [28,32,33]. However, people with ATL can still retain the ability in short-term memorization of non-verbal sounds [42]. Also, the ATL appears to produce no or only minor auditory-processing deficits when it improves the seizure control in patients with TLE that is refractory to drug medication [41,43]. Clearly, there is a need to integrate the findings from studies based

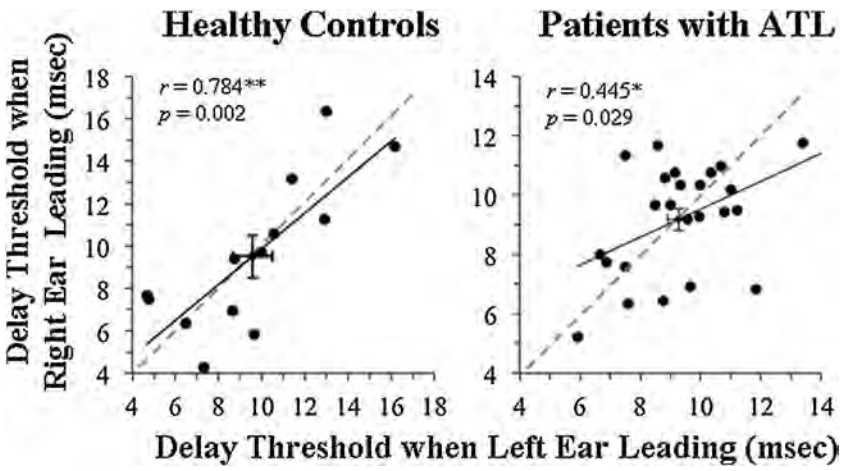

Fig. 3. Individual participants' longest interaural delays (the delay thresholds) for detecting a 200-ms break in correlation (BIC) in the healthy-control group (left panel) and in the patient group (right panel) under either the left-ear-leading condition (values along the abscissa) or the right-ear-leading condition (values along the ordinate). In each of the 2 participant groups, the delay threshold under the left-ear-leading condition was significantly correlated with that under the right-ear-leading condition (the solid line, both *r* and *p* values are presented). The broken diagonal line represents the data positions at which delay thresholds under the left-ear-leading condition were identical to those under the right-ear-leading condition.

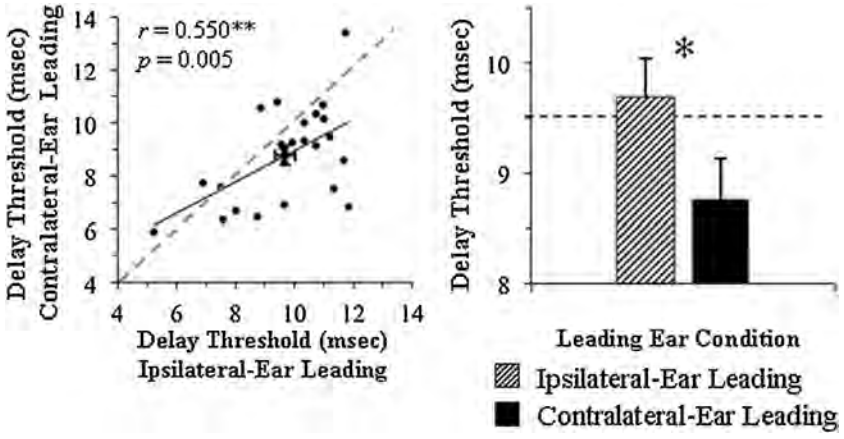

Fig. 4. Comparisons of the delay threshold for detecting the BIC in patients with unilateral ATL between the ipsilateral-ear-leading condition and the contralateral-ear-leading condition (relative to the side with ATL) for patient individuals (left panel) and patient-group means (right panel). The delay threshold under the ipsilateral-ear-leading condition was significantly correlated with that under the contralateral-ear-leading condition (the solid line, both *r* and *p* values are presented). The broken diagonal line represents the data positions at which delay thresholds under the ipsilateral-ear-leading condition were identical to those under the contralateral-ear-leading condition. *, $p < 0.05$.

on brain ablation and the findings from studies using brain-imaging and neurophysiological recordings.

This study for the first time reveals that although the unilateral ATL (with the resection of either the left or right TP) does not abolish the auditory ability to detect the BIC when an interaural delay is introduced, it significantly reduces the longest interaural interval for detecting the BIC under the listening condition with contralateral ear leading (related to the side of ATL). Moreover, the results of this study showed that the group-mean delay threshold in patients with unilateral ATL under the ipsilateral leading condition was more or less equal to that in healthy controls, and the delay threshold under the ipsilateral-ear-leading condition was also correlated to that under the contralateral-ear-leading condition across patient individuals. Thus, the TP plays a role in modulating the PAM of acoustic fine-structure signals from the contralateral ear but not in mediating the PAM.

5. Conclusions

This study for the first time provides evidence that in patients with unilateral ATL, the PAM of noise fine-structure signals from the ipsilateral ear lasted longer than that from the contralateral ear, indicating that the TP plays a role in top-down modulating the PAM of temporal fine-structure acoustic signals from the contralateral ear. In addition to the ascending pathways from the auditory cortex to the TP, the TP has descending functional connectivity to the brain structures mediating the PAM. The PAM-mediating regions and their connections with the TP will be important issues for future studies.

Moreover, the unilateral ATL-induced asymmetrical changes in transient storage of fine-structure sound information (i.e, the PAM) are useful for monitoring and estimating the effects of ATL on auditory perception.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neulet.2016.03.025.

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