动 物 学 研 究 2004, Jun. 25 (3): 191 - 197 CN 53 - 1040/Q ISSN 0254 - 5853
Zoological Research

Effect of Weak Noise on the Frequency Tuning of Mouse Inferior Collicular Neurons

TANG Jia[1], PI Jian-hui[2], WANG Dan[1], WU Fei-jian[1], CHEN Qi-cai[1,*]

(1. *School of Life Sciences, Central China Normal University, Wuhan 430079, China*;
2. *Department of Biology, Huaihua College of Hunan, Hunan 418008, China*)

Abstract: In order to study the effect of weak noise on the sound signal extraction of mouse (*Mus musculus* Km) inferior collicular (IC) neurons from environments, we examined the changes in frequency tuning curves (FTCs) of 32 neurons induced by a weak noise relative to 5 dB below minimum threshold of tone (reMT-5 dB) under free field stimulation conditions. The results were as follows: ① There were three types of variations in FTCs, sharpened (34.4%), broadened (18.8%), and unaffected (46.9%), nevertheless, only the alteration of sharpened FTCs was statistically different. ② Sharpness of frequency tuning induced by a reMT-5 dB noise was very strong. Q_{10} and Q_{30} of FTCs were increased by (34.42 ± 17.04)% ($P = 0.026$, $n = 11$) and (46.34 ± 22.88)% ($P = 0.009$, $n = 7$). ③ The changes of inverse-slopes (ISs, kHz/dB) between high (IS_{high}) and low (IS_{low}) limbs of FTCs were dissymmetry. The IS_{high} of FTCs decreased markedly ($P = 0.046$, $n = 7$), however, there was little change ($P = 0.947$, $n = 7$) in IS_{low}. Our data revealed for the first time that the weak noise could sharpen frequency tuning and increase the sensitivity on the high frequency of sound signal in IC neurons of mouse.

Key words: Weak white noise; Sharpening frequency tuning; Inferior collicular neurons; Mouse

弱噪声对小鼠下丘神经元频率调谐的影响

唐 佳[1], 皮建辉[2], 王 丹[1], 吴飞健[1], 陈其才[1,*]

(1. 华中师范大学 生命科学学院, 湖北 武汉 430079; 2. 湖南怀化学院 生物系, 湖南 怀化 418008)

摘要: 为探讨弱噪声对小鼠（*Mus musculus* Km）中脑下丘（inferior colliculus, IC）神经元声信号提取的影响，采用单位胞外记录方法，研究了加入弱白噪声（强度相当于纯音阈强度下 5 dB）前后神经元频率调谐曲线的变化。实验共记录到 104 个下丘神经元，测量了 32 个神经元的频率调谐曲线。结果显示：①弱噪声条件下神经元的频率调谐曲线表现出 3 种类型，即锐化（34.4%，11/32）、拓宽（18.8%，6/32）和不受影响（46.9%，15/32），其中锐化呈现有意义的变化；②频率调谐受弱噪声锐化的神经元，其 Q_{10}、Q_{30}平均分别增大（34.42 ± 17.04)%（$P = 0.026$，$n = 11$）和（46.34 ± 22.88)%（$P = 0.009$，$n = 7$），且 Q_{30}变化率大于 Q_{10}；③弱噪声对调谐曲线的高、低频边锐化度不一，神经元低频边的反转斜率基本不变［由 0.16 ± 0.08 变为 0.16 ± 0.07 kHz/dB（$P = 0.947$，$n = 7$)］，而高频边明显下降［由 0.52 ± 0.25 下降为 0.26 ± 0.13 kHz/dB，平均减小（43.81 ± 24.06)%，（$P = 0.046$，$n = 7$)］。上述结果表明，弱噪声可锐化小鼠 IC 神经元频率调谐，并强化神经元的声信号高频分析能力。

关键词：弱白噪声；锐化频率调谐；下丘神经元；小鼠
中图分类号：Q959.837；Q437 **文献标识码**：A **文章编号**：0254 - 5853(2004)03 - 0191 - 07

Signals about sound often occur in a background of noise in natural environments. Previous studies have demonstrated that the strong background noise could hinder the signal extraction of auditory neuron by ele-

* Received date: 2003 - 08 - 04; Accepted date: 2004 - 03 - 11
Foundation item: This work was supported by the National Natural Science Foundation of China (39970251)
* Corresponding author (通讯作者), Tel: 027 - 67867229, E-mail: qcchen2003@yahoo.com.cn
收稿日期：2003 - 08 - 04；接受日期：2004 - 03 - 11

vating the minimum threshold (MT), decreasing the discharge rate, and interfering with the sound localization (Furukawa & Middlebrooks, 2001; Ramachandran et al, 2000; Brugge et al, 1998; Jiang et al, 1997). And the interference degree of background noise is related to intensity, duration, and relative positions between noise and signal (Kawase et al, 2000; Rajan, 2001). However, the research of auditory neuron's response to sound signal under the condition of weak noise, has been largely ignored.

Many reports indicated that the effect of noise might be originated from the motion of the basilar membrane, i.e., periphery suppression. Nevertheless recent neurophysiological investigations performed in the auditory midbrain, thalamus, and primary auditory cortex (AC) have revealed that mechanism underlying the effect of noise on the sound signal processing was more from central auditory system than from cochlear suppression (Furukawa & Middlebrooks, 2001; Ratnam & Feng, 1998; Cunningham et al, 2002). For example, there were experiments indicating that the noise at times might enhance the ability to probe the sound signal (Cunningham et al, 2002; Zeng et al, 2000).

Frequency analysis is a fundamental function of the auditory system. Although a great number of data were focused on the intention to frequency selectivity along periphery to AC under different stimulus conditions, including in the presentation of background noise, there have been few reports of how the weak noise influenced the frequency tuning of central auditory neurons. In the present study, the weak background noise for simulating a natural acoustic environment was conducted by choosing a white noise intensity that was relative to 5 dB below minimum threshold (reMT-5 dB) of neuron response to tone burst, and the effect of the weak noise on the frequency tuning curves (FTCs) of inferior collicular (IC) neurons in mouse was explored.

1 Materials and Methods

1.1 Animal preparation, sound stimuli, and response recording

Eight adult healthy mice (*Mus musculus* Km) (20 – 25 g, b. wt.) in good hearing were used in the experiment. The animals were anesthetized with sodium pentobarbital (Nembutal 60 – 90 mg/kg, b. wt.) for surgery. The flat head of a 1.8 cm nail was glued onto the exposed skull of animal with Glue 502 and dental cement 1 day before the recording session. The mouse secured to an aluminum plate with a plastic band inside a sound-proof room (temperature 28 – 30 ℃). The ceiling and walls of the room were covered with 8 cm foam to reduce echoes. The mouse's head was immobilized by fixing the shank of the nail into a brass rod with a setscrew. The head was oriented with the eyes-nostril line pointed to 0° in azimuth and 0° in elevation with respect to the frontal auditory space. A small hole with diameter of 200 – 500 μm was made in the skull above the IC for inserting 2 mol/L NaCl glass pipette electrodes (impedance: 5 – 10 MΩ). An indifferent electrode (silver wire) was placed at the nearby temporal muscles. Each recording electrode was inserted as orthogonally as possible and the recording depth of each neuron was read from the small screen of a hydraulic driver (KOPF Model 640, DAVID KOPF INSTRUMENTS, USA). Additional doses of Nembutal were administered during later phases of recording if necessary. A local anesthetic (Lidocaine) was applied to the open wound area.

The electronic instruments used to generate acoustic stimuli were function generator (GFG-8016G, Good Will Instrument Co., LTD), white noise generator (ND-502, Nanjing University, China), tone burst generator (homemade), attenuator (LAT-45, LEADER, Japan), power amplifier (homemade), and ultrasonic loudspeaker (AKG model CK 50, 1.5 cm diameter, 1.2 g, frequency response 1 – 100 kHz). The loudspeaker was calibrated with sound pressure meter (HS-5660A, Jiangxi, China) positioned at mouse ear. Its output was expressed in dB SPL referred to 20 μPa root mean square. The loudspeaker was placed at 30 cm away from the mouse and 60° contra lateral to the recording site. Durations of tone burst and weak white noise burst used as sound stimuli were both 40 ms (2 ms rise-decay times) and delivered at 2 per second in free field.

1.2 Frequency tuning curve measuring of IC neurons

The action potential of IC neuron to sound stimuli was amplified (ISO-DAM, WPI, USA), then parallel-inputted into an oscilloscope (PM3084, FLUKE, USA) for visual observation, and an audio-monitor for audio discrimination (Grass, USA).

When a neuron responding to 40 ms tone was isolated, tone intensity and frequency were adjusted to determine the neuron's best frequency (BF) and MT audiovisually. Weak noise intensity of reMT-5 dB was used in the experiment. The FTC of each neuron sampled was measured audiovisually by changing tone frequency toward high frequency and low frequency at 10 dB steps. To compare with control, "reMT-5" denoting the chargs of FTCs during noise delivered was used in the Table and Figs. of results.

1.3 Data processing

The sharpness of a FTC was quantified by Q_n (Q_{10}, Q_{30}) values (Pollak & Casseday, 1989). They were determined by dividing the BF by the frequency bandwidth of a FTC at 10, 30 dB above the MT. In addition, inverse-slopes (ISs, IS = $\triangle F/\triangle I$ kHz/dB) (Sutter, 2000) measured by dividing the increasing or decreasing frequency values at high or low limbs of FTC by the 20 dB (10 – 30 dB intensity above the MT), were calculated for evaluating the sharpening on high and low frequency tuning. Statistical analysis and plotting of the data were conducted by softwares of Origin 6.0 and SigmaPlot2000. Mean ± standard deviation (*SD*), a common usage, was chosen to report data, and unpaired *t*-test was used for statistical analysis in this paper.

2 Results

A total of 104 IC neurons were recorded at depths of 479 – 1998 μm. BFs and MTs of these neurons were within 8.4 – 50.8 kHz (17.80 ± 8.08 kHz) and 21 – 64 dB SPL (42.18 ± 10.58 dB SPL), respectively.

2.1 Effect of weak noise on the Q_n values of FTCs of neurons

Data were obtained from 32 IC neurons' FTCs. Using a more than 20% variation of Q_{10} as the critical standard, three types of effect of noise on FTCs could be observed: inhibited, facilitated, and unaffected. 17 neurons' FTCs (53.1%) of 32 neurons were changed (Fig.1A and B) and the others (15, 46.9%) were not affected (Q_{10} changed from 1.98 ± 1.50 to 1.89 ± 1.35, P = 0.876) (Fig.1C). Among 17 neurons, FTCs of 11 (11/17, 64.71%) neurons were sharpened (Q_{10} increased from 1.13 ± 0.19 to 1.46 ± 0.37, P = 0.026) and FTCs of 6 (6/17, 35.29%) neurons were broadened (Q_{10} decreased from 2.97 ± 1.49 to 2.65 ± 1.76, P = 0.363).

In comparison with control, mean Q_{10} and Q_{30} variations induced by reMT-5 dB noise were showed in Table 1. Although the reMT-5 dB stimulation resulted in not only increase but also decrease of Q_n, only the increases of Q_{10} and Q_{30} were statistically different between control and noise addition. There were not significant changes in Q_{10} and Q_{30} of those neurons whose FTCs were broadened. No matter whether the FTCs were sharpened or broadened, it showed that Q_{30} altered more dramatically than Q_{10}. As showed in Fig.2A and B, percent increases in Q_{10} and Q_{30} of a representative neuron's FTC were 33.77% and 46.05%, respectively, during noise delivered. Statistical analysis showed that the Q_{10} increased from 1.13 ± 0.19 (control) to 1.46 ± 0.37 (P = 0.026, n = 11, Fig.2C) while the Q_{30} increased from 0.46 ± 0.12 (control) to 0.66 ± 0.11 (P = 0.009, n = 7, Fig.2D) during reMT-5 noise delivered. On average, mean percent increases in Q_{10} and Q_{30} were 34.42 ±

Table 1　Mean change (M ± *SD*) in Q_n

Q_n, n	Efficiency	Q_n (control)	Q_n (reMT-5)	% Q_n change	P (control vs reMT-5)
Q_{10}, 11	+	1.13 ± 0.19	1.46 ± 0.37	34.42 ± 17.04	0.026
Q_{10}, 6	–	2.97 ± 1.49	2.65 ± 1.76	– 31.34 ± 5.12	0.363
Q_{30}, 7	+	0.46 ± 0.12	0.66 ± 0.11	46.34 ± 22.88	0.009
Q_{30}, 5	–	1.58 ± 1.06	0.89 ± 0.55	– 40.11 ± 16.71	0.123

+: Increasing, –: Decreasing.

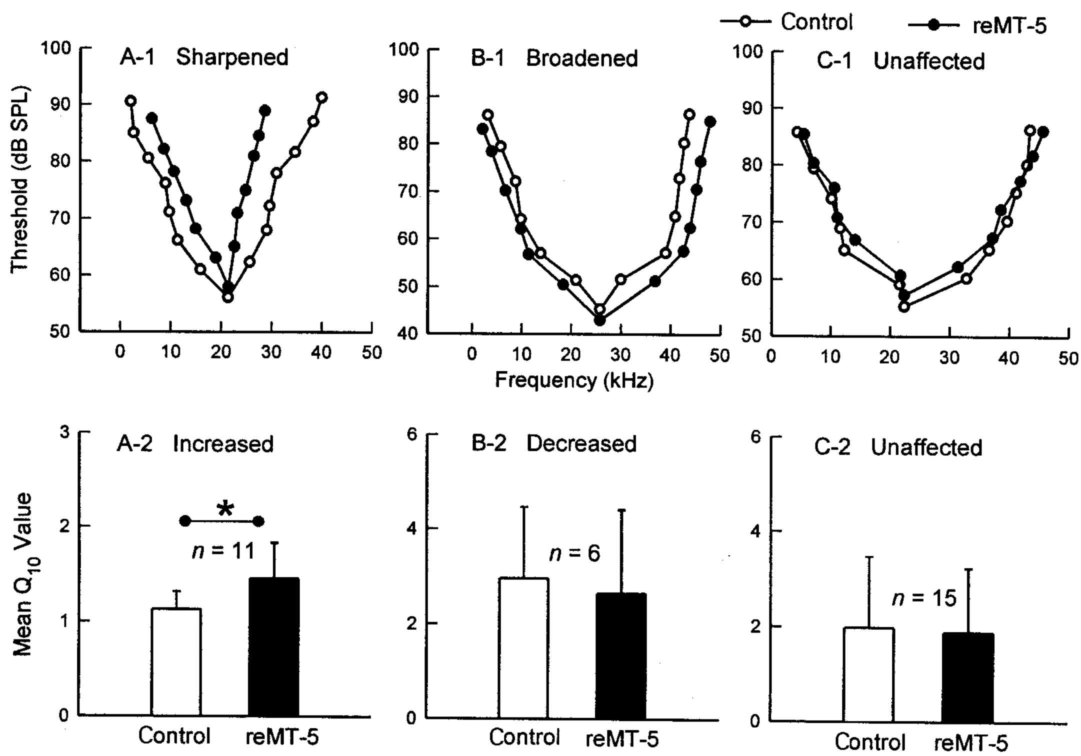

Fig.1 Effects of noise on FTCs of IC neurons

Three representative neurons showing three types of FTC variations, i. e., sharpened (A-1), broadened (B-1), and unaffected (C-1). The mean Q_{10} changes (A-2, B-2, and C-2) of same 3 types with A-1, B-1, and C-1 during the presentation of noise (shaded columns). Note that Q_{10} increased significantly (*: $P=0.026$) in A-2, but the variations in B-2 ($P=0.363$) and C-2 ($P=0.876$) were not significant. The vertical line on the top of each column is ± *SD*. *n*: Number of neurons. The recording depth (μm), BF (kHz), and MT (dB SPL) of 3 representative neurons are 898, 21.4, 56 (A-1); 1 173, 25.8, 45 (B-1); 1 818, 22.4, 55 (C-1), respectively.

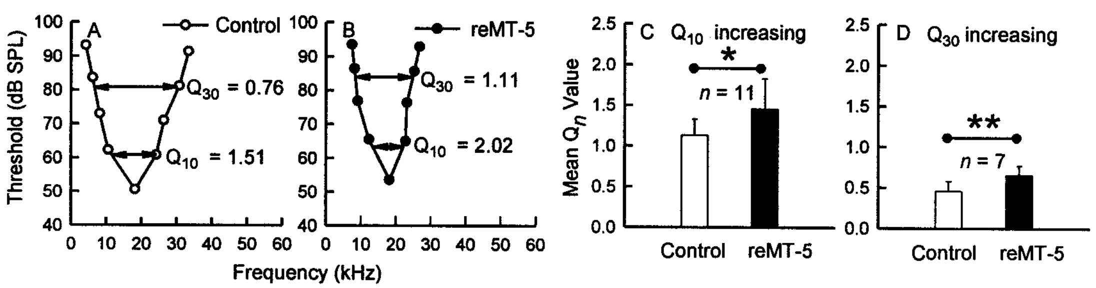

Fig.2 Sharpened FTCs of neurons by weak noise

FTCs before (A) and during (B) noise delivered. Mean increases of Q_{10} (C, *: $P=0.026$) and Q_{30} (D, **: $P=0.009$) induced by reMT-5 dB noise. The vertical line on the top of each column is ± *SD*. *n*: Number of neurons and ± *SD*, respectively. The recording depth (μm), BF (kHz), and MT (dB SPL) of this representative neuron are 1 881, 18.2, 51.

17.04% and 46.34 ± 22.88%, respectively. And the sharpness at high intensities was obvious.

2.2 Effect of the weak noise on the high and low frequency tunings of neurons

For comparing the sharpening effect of noise on high and low frequency tuning of IC neurons, the inverse-slopes (ISs, kHz/dB) of sharpened FTCs from 10 to 30 dB above MT were calculated (Fig.3A) during noise delivered. Using more than 20% of variation as a critical standard, there were three different types of variations in IS_{low}: increased (Fig.3B, 1/7, 14.28%), unchanged (Fig.3C, 5/7, 71.44%), and decreased

(Fig.3D, 1/7, 14.28%), however, IS_{high} of all sharpened FTCs decreased (Fig.3B, C and D).

There was no statistical significance (Fig.4A) for IS_{low} changes [0.16 ± 0.08 (control) to 0.16 ± 0.07 kHz/dB, $P = 0.947$, $n = 7$], however, IS_{high} reduced from 0.52 ± 0.25 to 0.26 ± 0.13 kHz/dB (43.81 ± 24.06%, $P = 0.046$, $n = 7$, Fig.4B) significantly.

2.3 Effect of the noise on the neuronal MTs

During a reMT-5 dB noise delivered, there were three types of variations in MTs (Fig.5). For most of neurons (28/32, 87.5%), the weak noise induced their MTs up-shifted. Few neurons' MTs unchanged (9.4%). There was only one neuron's MT down-shifted under the condition of noise stimulation.

3 Discussion

In general, the complex temporal sound is always encompassed in competing background noise. Therefore, numerous psychophysical and physiological investigations associated with the effect of noise on acoustic response have been performed during last two decades (Furukawa & Middlebrooks, 2001; Ramachandran et al, 2000; Brugge et al, 1998; Jiang et al, 1997; Kawase et al, 2000; Rajan, 2001). However, in all of these studies, a potentially important area that involves the issue of the response of central auditory neuron to sound signal under the condition of weak noise, has been largely ignored. Compared with earlier researches (Ratnam & Feng, 1998; Cunningham et al, 2002; Zeng et al, 2000), the present study investi-

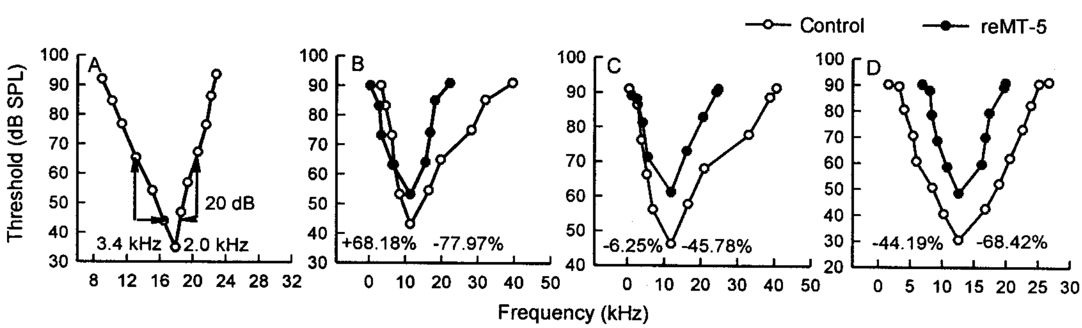

Fig.3　Effect of the reMT-5 dB noise on the high and low frequency tunings of neurons

A showing the method of calculating inverse-slope (IS = △F/△I) of FTC. When intensity increased from 10 to 30 dB (absolute intensity = 20 dB) above MT, IS_{high} (high frequency limb of FTC) and IS_{low} (low frequency limb of FTC) are 0.1 kHz/dB and 0.17 kHz/dB, respectively. B, C and D showing the three types of FTC variations in IS_{low}, which were increased, unchanged, and decreased, however, the IS_{high} decreased only. The percentages of FTCs bottom in B, C and D are percent IS increase (+) or decrease (–) both limbs of FTCs. The recording depth (μm), BF (kHz), and MT (dB SPL) of these four neurons are 838, 17.9, 35 (A); 1 075, 11.4, 43 (B); 1 424, 12.0, 46 (C); 520, 12.6, 31 (D), respectively.

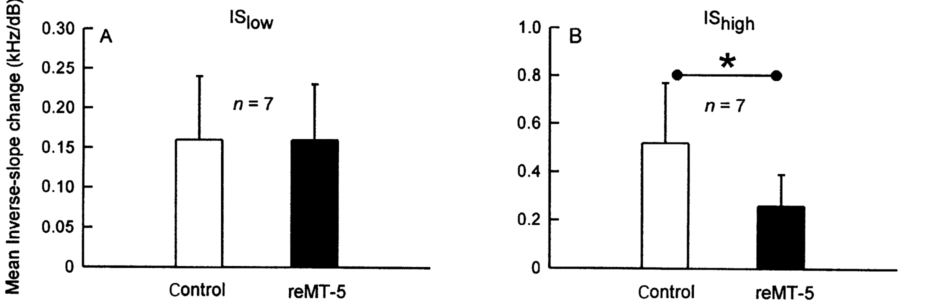

Fig.4　Comparison of IS_{low} (A) and IS_{high} (B) of neuronal FTCs obtained before (control) and during presentation of noise

The vertical line on the top of each column is ± *SD*. Note that only the change of IS_{high} (*: $P = 0.046$) in B is significant. *n*: Number of neurons.

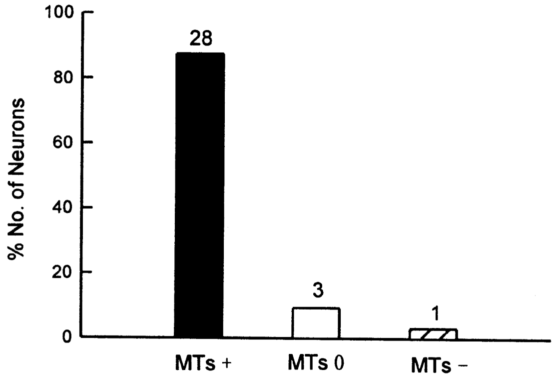

Fig.5 Percent distribution of three types of variations in MTs of IC neurons

The label above each column is the number of neurons.

gated the effect of a weak white noise on the frequency tuning of IC neurons for simulating the natural acoustic environment.

The results demonstrated that the weak noise induced three types of variations in neuronal FTCs: sharpened, broadened, and unaffected. It is tempting to speculate that the responses of IC neurons to sound signal could be inhibited or facilitated by the weak noise. As for the unaffected neurons, the poor response of IC neurons to noise addition possibly resulted from two factors: 1) The noise intensity used in the experiment was probably too weak to produce an effect; 2) These neurons perhaps belonged to noise tolerant units. In mouse IC, Barsz et al (2000) reported that the neurons could be classified as background noise resistant (BNR) or background noise sensitive (BNS).

Contrary to the theory that the noise is a nuisance for detecting sensory signal, recent studies achieved in crayfish receptors, rat mechanoreceptors, and central visual neurons have discovered that neuronal responses to weak subthreshold signals could be, at first sight, paradoxically enhanced by the addition of noise (Ivey et al, 1998). In auditory system, there was an experiment showing that human hearing could be improved by addition of an appropriate amount of noise (Zeng et al, 2000). These observations have led to a new concept that the noise might not only suppress but also increase the acoustic responses. The broadened FTCs found in this paper provided a further support to it. That the variations of broadened FTCs having no statistical significance probably was due to the insufficient effect of weak noise or few sampled neurons, here it remains to be fully explored.

For the sharpened FTCs by noise, the previous studies have demonstrated that the sharpness of FTC might be in relation to nonlinear and automatic tuning oscillations in cochlea and complex modulation in central auditory system (Frisina et al, 1996; Camalet et al, 2000). In this study, a weak noise resulted in the FTCs sharpened of 34.4% neurons. Analyzing their Q_{10} and Q_{30} showed a significant change. Moreover, the mean increasing in Q_{30} of FTCs was more significant than in Q_{10}, suggesting that the sharpness of frequency tuning by weak noise at higher intensity had more efficiency than at lower intensity. Our data are consistent with the finding by Suga et al (1997) that the sharpening variation at the skirt-edge of a central auditory neuron's FTC is more significant than at the tip. On frequency domain, after we calculated the IS_{high} and IS_{low} of sharpened FTCs, there was a difference between high and low frequency sides of FTC. The IS_{high} decreased dramatically while the IS_{low} almost had no changes, indicating that the sharpening for high frequency tuning was basically stronger than for low frequency tuning. In combination with the observation by Wang et al (1996) that the damage of the peripheral sensory receptors associated with frequencies above the neuron's BF caused a dramatic widening of level-tolerant and upper-threshold tuning curves at high sound intensities, which suggested that the response properties of central neurons with extremely narrow tuning curves were shaped by an inhibitory circuit that was activated by frequencies above the high-frequency flank of FTC, it gives a strong hint that the effect of weak noise on FTC was not symmetrical in frequency domain.

Frequency discrimination is one of the most important acoustic perception. There is vast literature showing that frequency tuning of the central auditory neurons is differentially modulated by neural inhibition. For instance, the earlier studies have showed that the level-tolerant and upper-threshold tuning curves of neurons at high intensities were broadened after GABAergic disinhibition, however, they changed little at low intensities (Suga et al, 1997; Wang et al, 1996; Suga & Tsuzuki, 1985). On the other hand, the studies on the ICs or/and ACs in bats, cats, and frogs have revealed that there were inhibitory areas at high or/and low flanks of excitatory FTC (Chen et al, 2001, 2002; Fuzessery & Hall, 1996; Hall, 1999). On AC neurons of big brown bat, we have proved that GABAergic inhibition could sharpen FTC (Chen et al, 2001). Thus, a hypothesis for explanation of our results could be advanced. It is that the sharpness of FTC by weak noise was related with the activation of central GABAergic inhibition, which originated from the ascendent afferent of random oscillation in the cochlea induced by noise. We guess that the activated GABAergic inhibition should provide an inhibitory input for sharpening FTCs in the auditory center so as to make the IC neurons more precisely analyze the frequencies near BFs of neurons. Our data revealed for the first time that the weak noise could sharpen frequency tuning and increase the sensitivity on the high frequency of sound signal in the IC neurons of mouse, which presented an evidence at cellular level for interpreting why human and animal could extract or capture behavioral related sound from the environment with competing noise.

Acknowledgement: We would like to thank two anonymous reviewers for their helpful comments and suggestions on the manuscript.

References:

Barsz K, Wilson WW, Walton JP. 2000. Background noise differentially effects temporal coding by tonic units in the mouse inferior colliculus [J]. *Hear. Res.*, **150** (1-2): 149-160.

Brugge JF, Reale RA, Hind JE. 1998. Spatial receptive fields of primary auditory cortical neurons in quiet and in the presence of continuous background noise [J]. *J. Neurophysiol.*, **80** (5): 2417-2432.

Camalet S, Duke T, Julicher F, Prost J. 2000. Auditory sensitivity proved by self-tuned critical oscillations of hair cells [J]. *Proc. Natl. Acad. Sci. USA*, **97** (7): 3183-3188.

Chen QC, Jen P, Wu FJ. 2001. Effect of GABAergic inhibition on properties of AC neurons in response to sound stimulation [J]. *Acta Biophysica Sinica*, **17** (1): 79-85. (in Chinese)

Chen QC, Jen P, Wu FJ. 2002. GABAergic inhibition can sharpen frequency tuning of auditory cortical neurons in big brown bat, *Eptesicus fuscus* [J]. *Acta Zoologica Sinica*, **48** (3): 346-352. (in Chinese)

Cunningham J, Nicol T, King C, Zecker SG, Kraus N. 2002. Effect of noise and cue enhancement on neural responses to speech in auditory midbrain, thalamus and cortex [J]. *Hear. Res.*, **169** (1-2): 97-111.

Frisina RD, Karcich KJ, Tracy TC, Sullivan DM, Walton JP, Colombo J. 1996. Preservation of amplitude modulation coding in the presence of background noise by chinchilla auditory nerve fibers [J]. *J. Acoust. Soc. Amer.*, **99** (1): 475-490.

Furukawa S, Middlebrooks JC. 2001. Sensitivity of auditory cortical neurons to locations of signals and competing noise sources [J]. *J. Neurophysiol.*, **86** (1): 226-240.

Fuzessery ZM, Hall JC. 1996. Role of GABA in sharping frequency tuning and creating FM sweep selectivity in the inferior colliculus [J]. *J. Neurophysiol.*, **76** (2): 1059-1073.

Hall JC. 1999. GABAergic inhibition shapes frequency tuning and modifies response properties in the auditory midbrain of the leopard frog [J]. *J. Comp. Physiol. A.*, **185** (5): 479-491.

Ivey C, Apkarian AV, Chialvo DR. 1998. Noise-induced tuning curve changes in mechanoreceptors [J]. *J. Neurophysiol.*, **79** (4): 1879-1890.

Jiang D, McAlpine D, Palmer AR. 1997. Responses of neurons in the inferior colliculus to binaural masking level difference stimuli measured by rate-versus-level functions [J]. *J. Neurophysiol.*, **77** (6): 3085-3106.

Kawase T, Ogura M, Hidaka H, Sasaki N, Suzuki Y, Takasaka T. 2000. Effects of contralateral noise on measurement of psychophysical tuning curve [J]. *Hear. Res.*, **142** (1-2): 63-70.

Pollak GD, Casseday JH. 1989. The Neural Basis of Echolocation in Bats [M]. Berlin: Springer-Verlag. 30-32.

Rajan R. 2001. Noise priming and the effects of different cochlear centrifugal pathways on loud-sound-induced hearing loss [J]. *J. Neurophysiol.*, **86** (3): 1277-1288.

Ramachandran R, Davis KA, May BJ. 2000. Rate representation of tones in noise in the inferior colliculus of decerebrate cats [J]. *J. Assoc. Res. Otolaryngol.*, **1** (2): 144-160.

Ratnam R, Feng AS. 1998. Detection of auditory signals by frog inferior collicular neurons in the presence of spatially separated noise [J]. *J. Neurophysiol.*, **80** (6): 2848-2859.

Suga N, Tsuzuki K. 1985. Inhibition and level-tolerant frequency tuning in the auditory cortex of the mustached bat [J]. *J. Neurophysiol.*, **53** (4): 1109-1145.

Suga N, Zhang YF, Yan J. 1997. Sharpening of frequency tuning by inhibition in the thalamic auditory nucleus of the mustached bat [J]. *J. Neurophysiol.*, **77** (4): 2098-2114.

Sutter MI. 2000. Shapes and level tolerances of frequency tuning curves in primary auditory cortex: Quantitative measures and population codes [J]. *J. Neurophysiol.*, **84** (2): 1012-1025.

Wang J, Salvi RJ, Powers N. 1996. Plasticity of response properties of inferior colliculus neurons following acute cochlear damage [J]. *J. Neurophysiol.*, **75** (1): 171-183.

Zeng FG, Fu QJ, Morse K. 2000. Human hearing enhance by noise [J]. *Brain Res.*, **869** (1-2): 251-255.