



Research paper

Responses of inferior colliculus neurons to sounds presented at different rates in anesthetized albino mouse

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ABSTRACT

We recorded extracellular activity from 402 single units located in the inferior colliculus (IC) of barbiturate-anesthetized albino mice. The stimuli were pure tones at characteristic frequency (CF) with durations of 10, 40 and 100 ms and intensities ranged from 5 to 25 dB above unit's minimum threshold (MT). The tones were presented with different repetition rates (RRs) ranging from 0.2 to 20.0 Hz. At low intensities (5 dB above MT, determined at RR of 0.5 Hz) the great majority of units exhibited a strong decline of their responses when the stimulus RR was increased. About one-half of the units did not respond to 40 ms tones when they were stimulated with the RR of 3.0 Hz. This effect was even more pronounced for 100 ms tones. Generally, the increase in stimulus intensity led to an increase in the high-frequency border of RR. Nevertheless, even at intensities of 20–30 dB above MT, some units showed no response when the RR exceeded 5.0 Hz. In many cases the band-pass or high-pass duration tuning of the single unit was transformed to low-pass or all-pass when the rate was low enough to guarantee the independence of successive presentations of the stimuli. Responses of a very small group of IC units, however, were enhanced when the RR was increased. Our data have shown that the changes in the RR radically modify many features of the neural response (number of spikes, latency, discharge pattern, duration selectivity). We suggest that long-lasting inhibitory processes may be induced by low intensity stimuli in many units of the IC.

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1. Introduction

It is generally accepted that temporal features of sounds are vitally important for their identification and/or classification. They are fundamental components of communication sounds such as human speech and animal vocalizations. For many ecologically important sounds the most evident temporal features are the duration and time interval between successive sound elements – repetition rate (RR). There are several methods to code these temporal parameters. For example, sound duration could be encoded by duration of the firing or by the excitation of specialized neurons showing duration selective response. The RR may be also encoded either by time-locked responses or by the response selectivity to a particular rate.

Most previous studies using click trains or amplitude-modulated tones have demonstrated that synchronization boundaries

in primary auditory cortex range from 10 to 300 Hz in various species and preparations (Anderson et al., 2006; Barlett and Wang, 2004; Burger and Pollak, 1998; Eggermont, 1991, 1999; Lu et al., 2001). The cause of this variation is not well understood. In the inferior colliculus (IC) neurons of mouse, an earlier study showed that the mean discharge rate is inversely proportional to the stimulus rate (Willot and Demuth, 1986). Interestingly, Pinheiro et al. (1991) observed that there were three types of IC neurons (low-pass, band-pass, and high-pass neurons) in the big brown bat according to their preference for RRs. There might be multi tactics for coding RR in the central auditory system. For instance, in the light of the two-stage model (Barlett and Wang, 2004; Lu et al., 2001), at low RRs sequential sounds can be coded explicitly by the neuronal temporal discharge pattern in the primary auditory cortex. The representation of rapid inter-stimulus intervals (high RRs) may be by a rate measure (implicit coding).

Duration tuning neurons have been observed in different central auditory regions of different animals (Bibikov, 1973; Brand et al., 2000; Cassaday et al., 1994, 2000; Chen, 1998; Ehrlich et al., 1997; Fremouw et al., 2005; Fuzessery and Hall, 1999; Galazyuk and Feng, 1997; Wu and Jen, 2006a; Xia et al., 2000). These studies show that duration selective neurons are only detected at

Abbreviations: CF, characteristic frequency; GABA, γ -aminobutyric acid; HRR, highest repetition rate; IC, inferior colliculus; MT, minimum threshold; PSTH, peristimulus time histograms; RR, repetition rate

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or above the level of the IC in all of the species studied. Generally, the duration tuned neurons are classified as short-pass, band-pass, and long-pass neurons. The best durations were observed usually in the range of 2–8 ms. In a few specialized animals (mice – Brand et al., 2000; rats – Perez-Gonzalez et al., 2006; frogs – Potter, 1965; Bibikov, 1973) the best durations could be far longer – of the order of tens and hundreds of milliseconds.

Faure et al. (2003) reported that duration tuned neurons in the bat experienced suppression under the condition of forward and backward masking, suggesting that the responses of these neurons are also determined by the temporal content. In another study, Jen and Zhou (1999) observed that when pulses trains were relieved at different RRs, the number of short-pass and band-pass neurons progressively increased with increasing RR. They also confirmed that this transformation was correlated with increasing GABAergic inhibition (Wu and Jen, 2006b). However, there are far fewer studies concentrating on rate coding of relatively long tone bursts (Bibikov, 1971; Chen and Jen, 1994; Piesman et al., 1994). When duration coding was investigated, it was generally assumed that rate of presentation was low enough to avoid interference of unit's response to the preceding stimulus. The relationships between duration and rate sensitivity have not been systematically investigated. The exceptions to this occur mainly in frogs (Bibikov, 1981; Gooler and Feng, 1992) and bats (Pinheiro et al., 1991). In addition, in the majority of studies, only one carrier level (20–30 dB above MT or “optimal intensity”) was used.

In the present study, with different stimulus durations and intensities, we examined the role of RR in the response characteristics of single units located in the inferior colliculus (IC) of barbital-anesthetized albino mice. We report here that the changes in the RR radically modify many features of the response (number of spikes, latency, and discharge pattern). Increase in the tone burst duration usually strongly affected the unit's capability to respond to signals presented with comparatively low RRs (0.2–3.0 Hz). Therefore, some long-lasting inhibitory processes may be induced in many units of the IC by low intensity stimulus. In some units the strong dependence upon the comparatively low RRs was maintained at moderate intensities.

2. Materials and methods

2.1. Surgical procedures

Experiments were conducted on 26 male albino mice (*Mus musculus* Km) weighing 20–40 g. Before surgery, animals were anesthetized with an initial intraperitoneal injection of pentobarbital sodium (50–80 mg/kg, b. wt.). The skin was deflected from the upper part of the skull to allow a metal rod to be mounted using cyanoacrylate and dental cement. The rod was later used to secure the mouse's head during recordings. A small hole (1.0–1.5 mm diam.) was cut into the skull above the IC. Each mouse was used in one to six recording sessions on separate days. The animals were placed in soundproof chamber. Each session was <8 h in duration. During the experiments we kept body temperature at 37–38 °C by maintaining the temperature of the sound-attenuated chamber at 26–30 °C. Heart rate was monitored on the oscilloscope. No more than ten electrode penetrations were made in one animal.

A micropipette electrode was inserted according to coordinates from the stereotaxic atlas of the mouse brain (Franklin and Paxinos, 1997). During the recording session the mouse received supplemmental pentobarbital sodium injections to keep no signs of pain or discomfort. Extracellular recordings were made from neurons located mainly in the central nucleus of the IC at the following coordinates: 8.5 to –9.5 mm caudal and 1.5–3.0 mm lateral from bregma (Franklin and Paxinos, 1997).

After each experiment animals were returned to a colony and received water and food ad libitum. After the experimental session, the animals were given a lethal injection of pentobarbital intraperitoneally (150 mg/kg). All experimental procedures were approved by The Ethical Council of Central China Normal University.

2.2. Stimulus parameters

To generate sound stimuli, continuous sine waves from a function generator (GFG-8016G, Good Will Inst. Co., Ltd., Malaysia) were formed into tone pulses (3 ms rise-fall times) by custom-made tone burst generator (electronic switch) driven by a stimulator (SEN-7203, Nihon Kohden Co., Japan). The tone pulses were then passed to a decade attenuator (LAT-45, Leader, Japan) and a custom-made power amplifier before they were fed into a small loudspeaker (AKG CK 50, 1.5 cm in diameter, 1.2 g, frequency response range: 1–100 kHz). The loudspeaker was situated 60° contralateral to the recording site at the distance of 30 cm away from recording site. Sound intensity was measured near the animal's outer ear with a calibrated condenser microphone (4939, B&K, 1/4 in. diameter, Denmark) using a measuring amplifier (2610, B&K, Denmark). The transfer function of the loudspeaker in the range of 7–50 kHz was relatively flat (± 6 dB SPL). The output of the loudspeaker was expressed in dB SPL referred to 20 μ Pa root mean square. The stimuli were presented at nine different RRs (0.2, 0.5, 1.0, 2.0, 3.3, 5.0, 6.7, 10.0 and 20.0 Hz). Search stimuli were 40 ms tone bursts that varied in frequency presented at the rate of 0.5 Hz and at the intensity of 70–80 dB SPL. In some cases the RR of the search stimuli was 0.2 Hz.

2.3. Recording and acquisition

Extracellular recordings of cells exhibiting acoustically induced excitation were taken mainly from the central nucleus of the IC. The micro-electrodes with a diameter 1–2 μ m contained a 2.5 M NaCl were used for extracellular recordings.

The electrodes were advanced with a hydraulic drive (David Kopf 640, USA) controlled from outside the recording chamber. Bioelectrical activity was fed via a recording amplifier (WPI, ISO-DAM, USA) with a band-pass filter (0.3–3 kHz) to an AD converter and stored on a personal computer. The unit's minimum threshold (MT) and characteristics frequency (CF) were audio-visually determined by systemically changing amplitude and frequency of sound stimuli. The frequency that elicited the unit's response with lowest intensity is defined as the CF, and the MT was defined as the intensity at which the probability of responding to CF sounds was about 50%. For each unit its CF and discharge pattern were determined during the action of such tone burst at the intensity of 5 dB above MT and at low RR (usually 0.5 Hz).

Single unit's discharges were isolated by means of an amplitude discriminator. Spike timings to stimulus onset were recorded by custom-made program. These data were stored in computer files from which raster displays (dot patterns), peristimulus time histograms (PSTHs), and latency histograms were plotted. Only a few units showed spontaneous activity, so the number of spikes usually was counted over the entire period of recording. In spontaneous units we restricted an acquisition time to a time period corresponded to the evoked firing. PSTHs were usually generated using 25–50 stimuli presentations, with a bin width of 0.5 or 0.2 ms. The first spike latency was defined as a first considerable peak of the PSTHs. As an additional control raster displays of neuronal responses were visually monitored.

All quantitative values in the text are expressed as mean \pm SD. Comparisons between different responses were evaluated with paired Student's *t*-tests. Results were usually considered significant at the 99% confidence level ($P < 0.01$).

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