Int. J. Devl Neuroscience 48 (2016) 50–57

Contents lists available at ScienceDirect

International Journal of Developmental Neuroscience

journal homepage: www.elsevier.com/locate/ijdevneu

Encoding of sound envelope transients in the auditory cortex of juvenile rats and adult rats

Qi Lu, Cuiping Jiang, Jiping Zhang*

Key Laboratory of Brain Functional Genomics, Ministry of Education, Shanghai Key Laboratory of Brain Functional Genomics, NYU-ECNU Institute of Brain and Cognitive Science at NYU Shanghai, School of Life Science, East China Normal University, Shanghai 200062, China

ARTICLE INFO

Article history:
Received 1 September 2015
Received in revised form 3 November 2015
Accepted 18 November 2015
Available online 26 November 2015

Keywords:
Age-related
Rise–fall time
Sound level
Rats
Auditory cortex
Sound envelope

ABSTRACT

Accurate neural processing of time-varying sound amplitude and spectral information is vital for species-specific communication. During postnatal development, cortical processing of sound frequency undergoes progressive refinement; however, it is not clear whether cortical processing of sound envelope transients also undergoes age-related changes. We determined the dependence of neural response strength and first-spike latency on sound rise–fall time across sound levels in the primary auditory cortex (A1) of juvenile (P20–P30) rats and adult (8–10 weeks) rats. A1 neurons were categorized as “all-pass”, “short-pass”, or “mixed” (“all-pass” at high sound levels to “short-pass” at lower sound levels) based on the normalized response strength vs. rise–fall time functions across sound levels. The proportions of A1 neurons within each of the three categories in juvenile rats were similar to that in adult rats. In general, with increasing rise–fall time, the average response strength decreased and the average first-spike latency increased in A1 neurons of both groups. At a given sound level and rise–fall time, the average normalized neural response strength did not differ significantly between the two age groups. However, the A1 neurons in juvenile rats showed greater absolute response strength, longer first-spike latency compared to those in adult rats. In addition, at a constant sound level, the average first-spike latency of juvenile A1 neurons was more sensitive to changes in rise–fall time. Our results demonstrate the dependence of the responses of rat A1 neurons on sound rise–fall time, and suggest that the response latency exhibit some age-related changes in cortical representation of sound envelope rise time.

1. Introduction

The accurate perception of sound information involves processing of both amplitude envelope structure and spectral fine structure. It has been demonstrated that sound envelope cues are more important for speech perception (Shannon et al., 1995; Smith et al., 2002; Bertoncini et al., 2011), whereas the sound fine structure is more important for pitch perception and sound localization (Smith et al., 2002). Sound envelope can be described by the parameters amplitude, duration, rise time, and fall time. The rise time reflects how quickly the amplitude reaches a steady-state level whereas the fall time reflects how fast the amplitude decays from one level to another. Previous studies on dyslexia showed a correlation between impaired rise time perception and dyslexia (Goswami et al., 2002, 2011b; Huss et al., 2011; Beattie and Manis, 2013; Hamalainen et al., 2013), and suggested that phonological processing difficulties are associated with difficulties in processing acoustic cues to speech rhythm. During postnatal development, the ability of children (3–6 years old) in discriminating sound rise time improves with age (Corriveau et al., 2010), and adults showed better performance in rise time discrimination task than children (Thomson et al., 2006; Thomson and Goswami, 2008; Goswami et al., 2011a). However, the underlying neural mechanism of age-related changes in the ability of sound rise time discrimination is not fully understood.

Previous studies on the neural processing of sound envelope rise and/or fall time focused on the auditory neural activities of adult animals such as frogs, bats, and cats. In the anuran auditory system, the mean spike counts of frog auditory nerve fibers were largely independent of sound rise–fall time, showing all-pass response functions across rise–fall time (Feng et al., 1991); in contrast, some neurons in the superior olivary nucleus (Condon et al., 1991), dorsal medullary nucleus (Hall and Feng, 1991), midbrain

---

Abbreviations: A1, primary auditory cortex; CF, characteristic frequency; dB SPL, sound pressure level in decibel.

* Corresponding author.

E-mail addresses: Luluqisqi@163.com (Q. Lu), ginger517@163.com (C. Jiang), jpzhang@bio.ecnu.edu.cn (J. Zhang).

http://dx.doi.org/10.1016/j.ijdevneu.2015.11.004

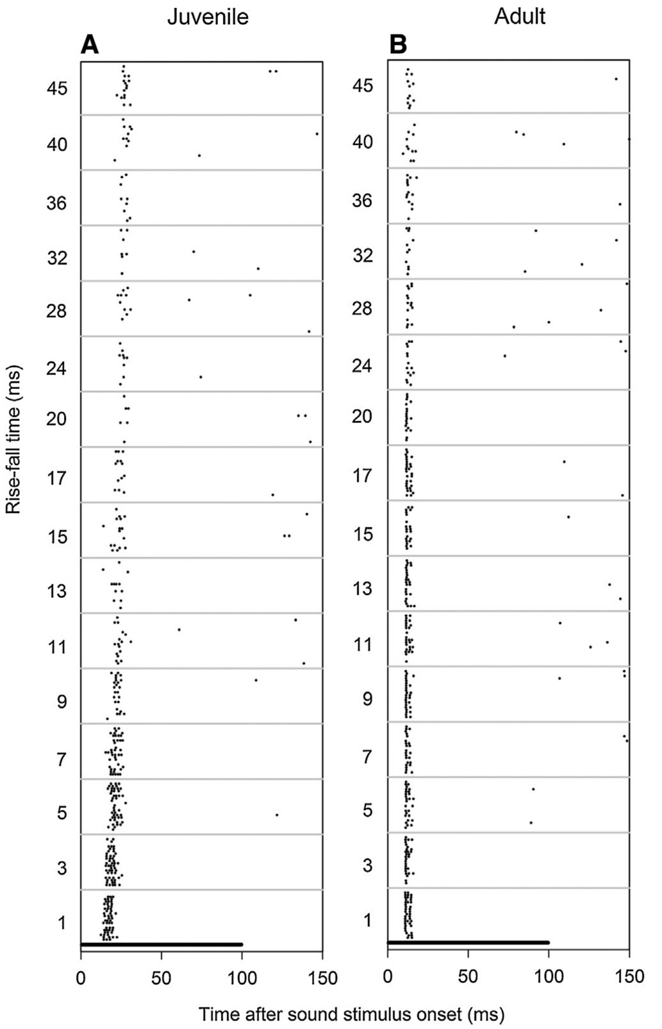

Fig. 1. Dot raster display for the responses of two A1 neurons to 20 trials of tone stimuli with various rise–fall times. The data shown in A and B are for the neurons from the juvenile group and the adult group, respectively, determined at 60 dB SPL and the CF of each neuron. The tone bursts are represented as thick black lines under the dot raster at 1 ms rise–fall time condition. Each dot represents an action potential. Note that the variation of the response latencies for neuron A was greater than those for neuron B as a function of sound rise–fall time.

(Gooler and Feng, 1992), and thalamus (Hall and Feng, 1988) of frogs preferentially responded to stimuli with shorter envelope rise–fall times, exhibiting short-pass response functions. The response vs. rise–fall time functions of a minority of neurons in the superior olivary nucleus of the leopard frog changed from all-pass to short-pass when the sound level was decreased, indicating dynamic modulation of both level and rise–fall time sensitivity (Condon et al., 1991). Studies in cats have shown that variation of sound rise time had profound effects on first-spike latency (Heil, 1997a), response strength (Heil, 1997b), and the features of rate-level functions (Phillips, 1988) and latency-level functions (Heil, 2003) of neurons in the auditory cortex. Onset rise time also affected the response threshold and frequency tuning of neurons in the bat inferior colliculus (Suga, 1971) and cat auditory cortex (Phillips et al., 1995). These studies in adult animals have demonstrated that variation of sound envelope transients can affect the response strength and (or) response latency of auditory neurons. However, the differences in neural encoding of sound rise–fall time between adult and juvenile animals have not been elucidated.

Rats are frequently used in auditory research; however, the neural encoding of sound envelope rise–fall time in auditory system of rats has not been investigated. The goal of the present study is to investigate how the neurons in the rat primary auditory cortex (A1) represent sound envelope rise–fall time, and whether cortical representation of sound envelope rise–fall time show age-related changes during postnatal development.

2. Materials and methods

2.1. Ethics statement

Animal care and experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of East China Normal University, and were in accordance with the National Institute of Health Guide for the Care and Use of Laboratory Animals (NIH Publications No. 80-23, revised in 1996). All efforts were made to minimize the suffering and the number of animals (rats) used. Rats were anesthetized by sodium pentobarbital throughout the experiment, and were sacrificed by an overdose injection of sodium pentobarbital (70 mg/kg body weight) at the end of the experiment.

2.2. Animals and surgery

Two age groups of Sprague-Dawley healthy rats (juvenile group: postnatal day 20–30, 15 females and 14 males, living with their mother rats before experiment; adult group: 8–10 weeks, 13 females and 11 males) were obtained from an in-house breeding stock that originated from breeding pairs purchased from Shanghai SLAC Laboratory Animal Co., Ltd. (Shanghai, China).

The surgical procedure for recording cortical neural activity was similar to that used in our previous studies (Peng et al., 2010, 2012). Rats were anesthetized with an intraperitoneal injection of sodium pentobarbital (40 mg/kg body weight) before surgery, and the anesthesia was maintained throughout the experiment by continuous intraperitoneal infusion of sodium pentobarbital (2% solution, 0.1–0.3 ml/h) via an automatic microinfusion pump (WZ-50C6, China). Body temperature was monitored by an animal temperature regulator through a rectal probe and maintained at 37.5 °C using a feedback-controlled heating blanket. The rats also received a single subcutaneous dose of atropine sulfate (0.01 mg/kg body weight) to reduce bronchial secretion at the beginning of surgery. After the trachea was cannulated, the dorsal and temporal skull was exposed and cleaned. A nail (4 cm long) was attached to the dorsal surface of the skull with 502 super glue and dental cement. The rat head was then immobilized by the nail to a head holder attached to a stainless steel platform. A craniotomy was performed over the temporal cortex and the auditory cortex was exposed. The position of the auditory cortex were Warm saline was applied to the cortex during the experiment to prevent drying.

2.3. Recording system

Experiments were carried out in a sound-insulated double-walled room with its inside walls and ceiling covered by three inches of sound-absorbing foam to reduce acoustic reflections. Single-neuron recording in the auditory cortex were obtained with glass electrodes filled with 3 M KCl (3.0–5.0 MΩ impedance). A remote controlled microdrive (SM-21, Narishige, Japan) was used to advance electrodes orthogonally to the pial surface of A1. The electrode signal was amplified (1000×) and filtered (0.3–3.0 kHz) by a DAM80 pre-amplifier (WPI, USA), digitized by a RZ-5 Bioamp data processor (Tucker-Davis Technologies, TDT3, USA), and stored in computer for online and off-line analyses. The electrode signal was also simultaneously monitored via a digital oscilloscope (TDS 2024, USA) and an audio speaker (TDT3, USA).