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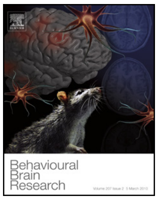

Research report

Response properties of neurons in the cat's putamen during auditory discrimination

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HIGHLIGHTS

- Neural activities of putamen are studied in the cats engaged in auditory tasks.
- Putamen neurons showed multiple spike patterns in response to sound stimuli.
- A large part of neurons encoded the sound signals like envelope or repetition rate.
- A small part of neurons encoded the signals predicting reward or not.
- These neurons cooperate to transform auditory signals to stimulus-reward association.

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ABSTRACT

The striatum integrates diverse convergent input and plays a critical role in the goal-directed behaviors. To date, the auditory functions of striatum are less studied. Recently, it was demonstrated that auditory cortico-striatal projections influence behavioral performance during a frequency discrimination task. To reveal the functions of striatal neurons in auditory discrimination, we recorded the single-unit spike activities in the putamen (dorsal striatum) of free-moving cats while performing a Go/No-go task to discriminate the sounds with different modulation rates (12.5 Hz vs. 50 Hz) or envelopes (damped vs. ramped). We found that the putamen neurons can be broadly divided into four groups according to their contributions to sound discrimination. First, 40% of neurons showed vigorous responses synchronized to the sound envelope, and could precisely discriminate different sounds. Second, 18% of neurons showed a high preference of ramped to damped sounds, but no preference for modulation rate. They could only discriminate the change of sound envelope. Third, 27% of neurons rapidly adapted to the sound stimuli, had no ability of sound discrimination. Fourth, 15% of neurons discriminated the sounds dependent on the reward-prediction. Comparing to passively listening condition, the activities of putamen neurons were significantly enhanced by the engagement of the auditory tasks, but not modulated by the cat's behavioral choice. The coexistence of multiple types of neurons suggests that the putamen is involved in the transformation from auditory representation to stimulus-reward association.

1. Introduction

An important research theme in auditory neuroscience is to reveal the neural substrate of sound discrimination behavior, that is, how the brain transforms auditory information into a behavioral response. The contribution of auditory cortices (AC) in the goal-directed behavior has been investigated before, but the results suggest that they are primarily associated with the neural representations of acoustic stimuli [1–4]. In contrast, the neural activities in prefrontal cortex (PFC) were demonstrated to reflect the behavioral choices that the monkeys made during an auditory task [5,6]. Except for AC and PFC, auditory information is processed and relayed to a number of cortical and subcortical structures, such as inferior colliculus, striatum and amygdala. The roles of these brain regions in sound discrimination remain unclear.

Abbreviations: AC, auditory cortex; ED, Euclidian distance; PFC, prefrontal cortex; PU, putamen; VS, vector strength; RS, Rayleigh statistic; PSTH, peri-stimulus time histogram; SPL, sound pressure level; SDM, spike distance metric.

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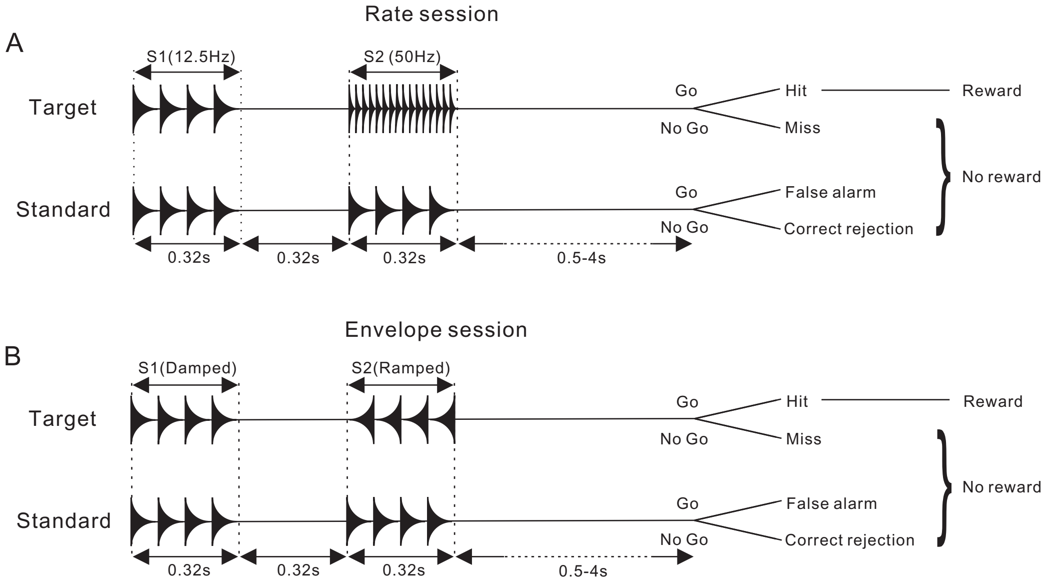

Fig. 1. Schematic diagrams of the sound stimuli and cat's behavioral responses in the rate (A) and envelope (B) sessions.

The striatum receives inputs from the thalamus, AC and PFC [7–9], and forms original outputs of basal ganglia to influence the activity in the motor thalamus as well as superior colliculus. These neural circuits enable the striatum to integrate sensorimotor, cognitive, and motivational/emotional information. A growing body of evidence established that plasticity within the striatum is necessary for the acquisition of response-outcome associations during instrumental conditioning [10–12]. However, the auditory functions of striatum are less studied. Several electrophysiological studies in anaesthetized and passively listening animals have found that a number of neurons in the dorsal striatum, putamen (PU), could be elicited by sound stimuli, and the auditory neurons usually exhibited a well-defined frequency receptive field comparable with that in AC neurons [13–16]. These results indicate that neurons in the PU have some ability to encode the physical information of auditory stimuli. Furthermore, recent optogenetic studies in rats demonstrated that auditory cortico-striatal projections influence behavioral performance during a frequency discrimination task [17,18]. To date, there is only one study systematically analyzed sensory-related neural activity in the PU during a somatosensory perceptual task [19], no study about the PU neural activities during sound discrimination has been done.

We addressed this issue by recording the activity of single neurons in PU while trained cats were performing a sound discrimination task to obtain reward. The task required cats to report the difference between two successively presented sound stimuli, whether the modulation rate of sound wave was increased (12.5 Hz vs. 50 Hz) or the modulation envelope was reversed (damped vs. ramped). We systemically analyzed the activities of individual PU neurons concerning about the neural coding of acoustic information and about potential contributions of PU to reward-association and decision-making can be addressed in this task.

2. Materials and methods

All animal work was carried out in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health. The Committee on the Ethics of Animal Experiments of the University of Yamanashi approved the protocol (permit number No.19-15). All surgery was performed under sodium pentobarbital anesthesia, and all efforts were made to minimize suffering.

2.1. Apparatus

The behavioral experiments were conducted in a custom-built acoustically-transparent behavioral cage (54 × 44 × 49 cm) that was placed in an electrically-shielded and sound-attenuated chamber. The cats were able to move freely in the cage, and a video camera and photoelectric sensors were used to monitor their position and movement. Custom-built software implemented in the MATLAB (Mathworks) environment was used to interact with the apparatus via digital input–output hardware (PCI-6052E; National Instruments). Sound signals were digitally created by using custom-built software, generated with a D/A converter at a sampling rate of 100 kHz, and then passed through an amplifier (PMA-2000; Denon). The sounds were delivered via an earphone (NW-STUDIO PRO W; Ninewave), which was screwed into the earphone holder fixed on the cat's skull during the surgery (see below). The placement of the earphone was adjusted to 1 cm from the ear canal without causing discomfort to the cat. Sound calibration was conducted using a Bruel & Kjaer 1/2" condenser microphone with a preamplifier 2669 positioned 1 cm in front of the earphone. Sound pressure level (SPL) was expressed in decibels relative to 20 μPa.

2.2. Behavioral task

The cats were trained to use their head to block a photoelectric sensor for at least 3 s to trigger the onset of the sound stimulus. As shown in Fig. 1, the sound stimuli were damped or ramped noises, which were generated by modulating a white noise carrier with an exponential function. The total duration of noise carrier was 320 ms and the modulation rate was 12.5 or 50 Hz (the periodicity was 80 or 20 ms). The half-life of the exponential function determined the time course of the amplitude modulation of the stimulus. It was 15.4 or 7.1 ms for the stimuli with 80 or 20 ms periodicity, respectively. The peak amplitude of stimulus was adjusted to subjective intensity equal to 60 dB sound pressure level (SPL) of 4 kHz pure-tone. Subjects were required to perform two Go/No-Go tasks to discriminate the difference between two successively presented stimuli. The first task was the rate discrimination task (Fig. 1A), wherein the first stimulus (S1) was always a 12.5 Hz damped noise, while