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Interdependent effects of sound duration and amplitude on neuronal onset response in mice inferior colliculus

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ABSTRACT

In this study, we adopted iso-frequency pure tone bursts to investigate the interdependent effects of sound amplitude/intensity and duration on mice inferior colliculus (IC) neuronal onset responses. On the majority of the sampled neurons (n=57, 89.1%), sound amplitude and duration had effects on the neuronal response to each other by showing complex changes of the rat-intensity function/duration selectivity types and/or best amplitudes (BAs)/durations (BDs), evaluated by spike counts. These results suggested that the balance between the excitatory and inhibitory inputs set by one acoustic parameter, amplitude or duration, affected the neuronal spike counts responses to the other. Neuronal duration selectivity types were altered easily by the low-amplitude sounds while the changes of rate-intensity function types had no obvious preferred stimulus durations. However, the first spike latencies (FSLs) of the onset response neurons were relative stable to iso-amplitude sound durations and changing systematically along with the sound levels. The superimposition of FSL and duration threshold (DT) as a function of stimulus amplitude after normalization indicated that the effects of the sound levels on FSLs are considered on DT actually.

1. Introduction

Two fundamental parameters of iso-frequency pure tones, amplitude/intensity and duration, affect the auditory neuronal responses. The interdependent effects of them have been studied widely in the bats (Casseday et al., 2000; Faure et al., 2003; Fremouw et al., 2005; Galazyuk and Feng, 1997; Mora and Kossl, 2004; Zhou and Jen, 2001; Zhou and Jen, 2002). They might take the advantage of these effects to identify their own echolocation calls and the distance to a reflecting surface (Lawrence and Simmons, 1982; Mora and Kossl, 2004). However, stimulus amplitude and duration affecting neuronal onset response to each other in the non-echolocation mammals are poorly studied.

Duration tunings, evaluated by using spike counts, have been found on the IC offset response neurons (Brand et al., 2000;

Abbreviations: FSL, first spike latency; IC, inferior colliculus; BA, best amplitude; BD, best duration; DT, duration threshold; CF, characteristic frequency; MT, minimum threshold

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Casseday et al., 1994, 2000; Ehrlich et al., 1997; Faure et al., 2003; Fremouw et al., 2005; Fuzessery and Hall, 1999; Luo et al., 2008; Perez-Gonzalez et al., 2006; Wang et al., 2006; Xia et al., 2000; Yin et al., 2008; Zhou and Jen, 2001) but other auditory nuclei below it (Casseday et al., 1994; Galazyuk and Feng, 1997; Gooler and Feng, 1992). Since most BALB/c mice IC neurons recorded in our previous studies fired at the sound onset (Liang et al., 2011; Qiu et al., 2007; Tan et al., 2008; Tang et al., 2008), we here tried to identify if the duration tunings also existed on them firstly.

Although peripheral auditory nerve fibers have amplitude-untuned spike counts responses (Kiang et al., 1965), the non-monotonic neurons tuned to specific sound levels via an inhibition to the high-amplitude stimuli have been widely found in the central auditory nuclei (the cochlear nucleus (Greenwood and Maruyama, 1965; Young and Brownell, 1976), the superior olivary complex (Grothe, 1994; Zheng and Hall, 2000), the inferior colliculus (IC) (Blatchley and Brugge, 1990; Wu and Jen, 1991), the medial geniculate body (Aitkin and Webster, 1972; Rouiller (1983)), and the auditory cortex (Barone et al., 1996; Phillips and Irvine, 1981)). Since the IC is the first nucleus in the ascending auditory pathway having both amplitude- and duration-tuned neurons, it becomes a perfect candidate for the investigation of the interdependent amplitude–duration effects.

The effects of sound amplitude and duration on the neuronal spike counts responses to each other have been studied in the IC of echolocation bats (Casseday et al., 2000; Faure et al., 2003; Fremouw et al., 2005; Galazyuk and Feng, 1997; Mora and Kossl, 2004; Zhou and Jen, 2001; Zhou and Jen, 2002). The stimulus durations alter the type, dynamic range and slope of rate-intensity function and best amplitude (BA, the sound amplitude eliciting the highest spike counts) on some big brown bat IC neurons (Zhou and Jen, 2002). On the other hand, it has been proven that the neuronal duration selectivity types could be affected by the sound levels (Fremouw et al., 2005; Mora and Kossl, 2004; Zhou and Jen, 2001). In the IC of big brown bat (Faure et al., 2003; Zhou and Jen, 2001) and the auditory cortex of little brown bat (Galazyuk and Feng, 1997), the types of duration selectivity change along with the stimulus amplitudes. Furthermore, this phenomenon has been also found in the outbred non-albino mouse (Brand et al., 2000) indicating that it might be common in non-echolocation mammals. Therefore, we attempted to verify the existence of these effects on the BALB/c mice IC onset response neurons in this study. Then, we analyzed the detailed patterns of the stimulus amplitude/duration affecting the duration selectivity/rate-intensity function types by identifying the types at the minimal and maximal tested amplitudes/durations and the sound amplitudes/durations inducing the changes. On the neurons with fixed rate-intensity function/duration selectivity types, the changing patterns of the BA/best duration (BD, the sound duration eliciting the highest spike counts) along with sound duration/amplitude were studied.

In addition to spike counts, neuronal acoustic response could be evaluated by the first spike latency (FSL). It shortens along with the increasing sound levels and shows the paradoxical latency shift in some cases (Chase and Young, 2007; Heil, 1997; Heil and Irvine, 1997; Heil, 2004; Tan et al., 2008; VanRullen et al., 2005). However, the effect of sound duration on the FSL–amplitude function is unclear. To study that, we plotted all the iso-duration FSL–amplitude responses together. Since the FSL varies systematically along with the sound duration on the offset response neurons (Brand et al., 2000; Ehrlich et al., 1997; Faure et al., 2003; Fuzessery and Hall, 1999), we tried to test if it is the case on the neurons fire at sound onset. Then, the effects of the sound levels on the FSL–duration functions and the duration threshold (DT, the minimum stimulus duration to evoke at least one spike) were investigated. Finally, we tried to reveal the relationship between FSL and DT by plotting the FSL– and DT–amplitude functions together.

2. Results

2.1. General

In this study, sixty-four neuronal single units in the BALB/c mice IC firing at the sound onset were recorded extracellularly. The recording depths were from 100 to 1618 μm beneath the brain surface. The minimum thresholds (MTs, the stimulus amplitude at which a neuron was elicited at least one spike with the probability of 0.1 (Keithley and Feldman, 1983)) and characteristic frequencies (CFs, the frequency at which a neuron responded to the sound at MT) were 18–80 dB SPL (53.5 ± 17.5 dB SPL) and 11–42 kHz (22.4 ± 7.1 kHz), respectively. The spontaneous spike activities (less than 2/s) and the basic features of IC neurons were similar to the previous results (Aitkin and Martin, 1990; Liang et al., 2011; Qiu et al., 2007; Tan et al., 2008; Tang et al., 2008).

2.2. *Features of the spike counts responses to the standard stimulation*

2.2.1. *Duration selectivity types under standard amplitude condition*

Based on the "50% threshold" criterion similar to those proposed previously (Fuzessery and Hall, 1999; Narins and Capranica, 1980; Wang et al., 2006), a duration-untuned ("all-pass") neuron was identified if its spike counts reached a peak when it is responding to a particular sound duration (best duration, BD), and never decreased by more than 50% of the peak at others. In this study, twenty-six neurons (40.6%) showed all-pass under the standard amplitude condition (at/near 10 dB above MT, Fig. 1A).

Spike counts decreased by more than the 50% criterion at the sounds shorter or longer than the BD were defined as long- or short-pass, respectively. The long-pass neurons represented the majority of the IC duration-tuned neurons ($n = 20$, 52.6%, Fig. 1B), and only six short-pass neurons (15.8%, Fig. 1C) were found at the standard stimulus amplitudes. Meanwhile, we identified five band-pass (13.2%, Fig. 1D) and seven band-reject neurons (18.4%, Fig. 1E). The spike counts of a band-reject neuron dropped more than 50% of the max when a certain range of sound durations was given while a band-pass neuron was in the opposite situation.