Hearing Research 350 (2017) 189–204

Contents lists available at ScienceDirect

Hearing Research

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

Research Paper

Acuity in ranging based on delay-tuned combination-sensitive neurons in the auditory cortex of mustached bats

Masakiyo Suzuki [1], Nobuo Suga *

Department of Biology, Washington University, One Brookings Drive, St. Louis, MO 63130, USA

ARTICLE INFO

Article history:
Received 17 December 2016
Received in revised form
7 April 2017
Accepted 28 April 2017
Available online 2 May 2017

Keywords:
FM-FM neurons
Simulation of neural activity
Peak location of neural responses
Center location of neural responses
Weighted sum of neural responses

ABSTRACT

A 1.0-ms echo delay from an emitted bio-sonar pulse at 25 °C corresponds to a 17.3-cm target distance. In the auditory cortex of the mustached bat, *Pteronotus parnellii*, neurons tuned to a specific delay (best delay) of an echo from an emitted pulse are clustered in the FF, dorsal fringe and ventral fringe areas. ("FF" stands for the frequency-modulated components of a pulse and its echo.) Those delay-tuned neurons are systematically arranged in the FF area according to their best delays and form a 18-ms-long delay axis. Using the neurophysiological data, the theoretical acuity at a 75% correct level was computed as just-noticeable changes in (a) the location of maximally responding delay-tuned neurons, (b) the location of the center of all responses in the FF area, and (c) the weighted sum of responses of all delay-tuned neurons. The acuity is range-dependent: the shorter the target range, the higher the acuity is. The just-noticeable changes in target range are 7.57–46.2, 0.50–2.32 and 0.22–2.53 mm at the target ranges of up to 140 cm for (a), (b) and (c), respectively. When the dorsal and ventral fringe areas are included in the computation, the just-noticeable changes become smaller than those in the FF area alone. Those acuities computed are comparable to certain behavioral acuities.

1. Introduction

The mustached bat, *Pteronotus parnellii*, emits bio-sonar pulses for echolocation. Each pulse consists of four harmonics of a constant frequency ($CF_{1\text{-}4}$) and a frequency modulated ($FM_{1\text{-}4}$) component (Fig. 1, A and B). During a target-directed flight, the bat starts to change pulses in duration and emission rate at 3–4 m distances to a target (Novick and Vaisnys, 1964). These distances correspond to 17–23 ms echo delays from an emitted pulse. In the auditory cortex of the mustached bat, FM-FM neurons are tuned to a pulse-echo pair with a specific echo delay (best delay). They are delay-tuned and combination-sensitive. "Combination-sensitive" means that the response of a neuron to a pair of two sounds is larger than the algebraic sum of the responses to individual sounds in the pair. The essential components of the pulse-echo pair for their excitation (facilitative response) are pulse FM_1 and echo FM_n ($n = 2$, 3 or 4). They are clustered in the FF ("F" stands for frequency modulation), DF (dorsal fringe) and VF (ventral fringe) areas (Fig. 1C; Suga, 2015). The FF area was previously called the FM-FM area (Tang and Suga, 2008). Among those three areas, the FF area is the largest and has an axis systematically representing echo delays from 0.4 ms to 18 ms, rarely, to 24 ms (Fig. 1D). Along the delay axis, the best delay of a neuron changes at a rate of 0.116 ms per cortical mini-column (i.e., per neuron) up to 8.0 ms of the delay axis (Suga and O'Neill, 1979). Each mini-column contains ~45 neurons (Suga, 1990). The delay axis is up to 9 ms in the DF area (Suga and Horikawa, 1986) and up to 5 ms in the VF area (Edamatsu et al., 1989).

The delay tuning and combination-sensitivity of FM-FM neurons studied with simulated pulse-echo pairs in a soundproof room are the same as those studied with a mustached bat emitting pulses in the open air and listening to simulated echoes triggered by those vocalized pulses. Therefore, their facilitative responses are indeed evoked by a combination of a vocal self-stimulation by pulse FM_1

Abbreviations: BD, best delay; CF, constant frequency; dB, decibels; DF, dorsal fringe; FF, frequency modulation-frequency modulation; FM, frequency modulation; $FM_{1\text{-}4}$, 1st-4th harmonics of a FM signal; FM_n, 2nd-4th harmonics of an echo FM signal; VF, ventral fringe

* Corresponding author. Current address: 7455 Stratford Ave., University City, MO 63130, USA.
E-mail addresses: masakiyo@mail.kitami-it.ac.jp (M. Suzuki), sugahn@att.net (N. Suga).
[1] Current address: Department of Computer Sciences, Kitami Institute of Technology, 165 Koen-cho, Kitami, Hokkaido 090-8507, Japan.

http://dx.doi.org/10.1016/j.heares.2017.04.017
0378-5955/

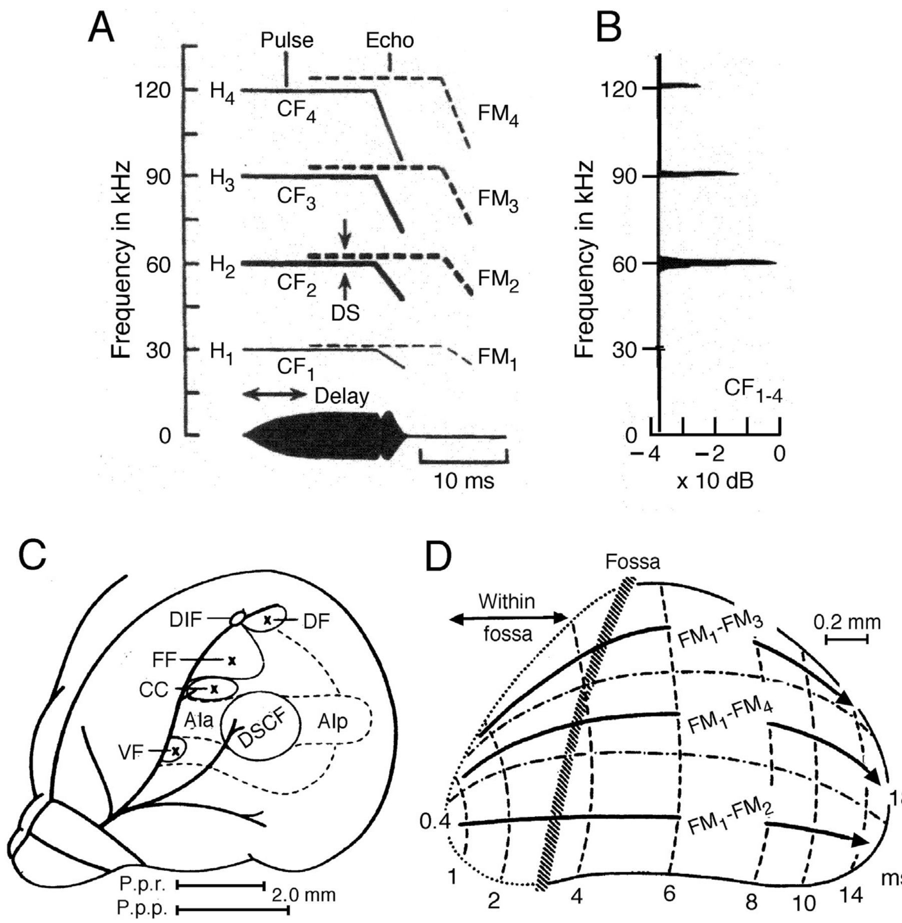

Fig. 1. Bio-sonar signal and the auditory cortex of mustached bats. **(A)** Schematized spectrograms of a pulse (un-dashed lines) and a Doppler-shifted (DS), delayed echo (dashed lines). The pulse contains four harmonics (H_{1-4}) consisting of a constant frequency (CF_{1-4}) and frequency modulated (FM_{1-4}) components. The envelope of the pulse is shown at the bottom. **(B)** Amplitude spectrum of the CF component of the pulse. **(C)** Dorsolateral view of the left cerebral cortex. The auditory cortex consists of several areas. DF (dorsal fringe), FF (frequency modulation-frequency modulation) and VF (ventral fringe) areas are specialized for the processing of distance information. CC (constant frequency/constant frequency) and DIF (dorsal intrafossa) areas are specialized for the processing of velocity information. DSCF (Doppler-shifted CF) area over-represents CF_2. AIa and AIp (anterior and posterior divisions of the primary auditory cortex) is tonotopically organized. **(D)** Echo-delay representation in the FF area consisting of three subdivisions: FM_1-FM_2, FM_1-FM_3, FM_1-FM_4. The horizontal arrows indicate delay axes from 0.4 to 18 ms. The vertical dashed lines indicate iso-best delay lines. P. p. r.: *Pteronotus parnellii* rubiginosus. P. p. p.: *P. parnellii parnellii* (A, based on Suga et al., 1983; B, Suga, 1984; C, Based on Suga et al., 1995; D, Suga and O'Neill, 1979).

and echo FM_n (Kawasaki et al., 1988).

The reversible bilateral inactivation of the FF area with muscimol temporarily impairs the bat's ability to detect a small (1.0 ms) difference in time interval between paired sounds, mimicking pulse-echo pairs, without affecting the bat's ability to detect a small (0.08%) frequency difference. Hence the FF area is indeed involved in the perception of small time intervals such as echo delays (Riquimaroux et al., 1991, 1992).

Acuity in ranging has been behaviorally studied in various test situations over many years (Simmons, 1973, 1979; Simmons et al., 1975; Moss and Schnitzler, 1995). However, neurophysiological correlates to it have not yet been examined. Since the neurophysiological data summarized above indicate that cortical FM-FM neurons are involved in perception of echo delays (i.e., ranging), it is an important and interesting subject to explore how high acuity in ranging is theoretically achieved with excitation of cortical FM-FM neurons. To obtain an answer to this question, we computed the theoretical acuity in ranging as just-noticeable changes at a 75% correct level in (a) the location of maximally responding neurons along the delay axis in the FF, DF and/or VF areas; (b) the location of a center of responses of all FM-FM neurons in these areas; and (c) the weighted sum of responses of all FM-FM neurons in those areas. We found that the theoretical acuities computed are comparable to the behavioral data indicating that four species of bats can discriminate 12–29-mm differences in target range (Simmons, 1973) and 0.5-μs echo jitters corresponding to 0.087-mm range jitter (Simmons, 1979). The aims of our current paper are to present the data obtained from our computer simulation experiments and to compare those with the behavioral acuities.

2. Methods

Neurophysiological data obtained from three cortical areas (FF, DF and VF) consisting of FM-FM neurons are suited to computer simulation experiments that evaluate theoretical acuity in ranging. The common response properties of FM-FM neurons and the topographical arrangement of neurophysiological properties were chosen for the computer simulation as described below.

2.1. Response properties of FM-FM neurons

Most cortical FM-FM neurons show background discharges and facilitative responses to pulse-echo paired stimuli (hereafter, stimuli). That is, they show action potentials (spike discharges) at a rate higher than a rate of background discharges. Their responses