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Research Paper

Differences in velocity-information processing between two areas in the auditory cortex of mustached bats

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ABSTRACT

The bio-sonar pulse of the mustached bat, *Pteronotus parnellii parnellii*, consists of four harmonics of constant frequency (CF_{1-4}) and frequency-modulated (FM_{1-4}) components. The CF and FM components carry velocity and distance information, respectively. In the auditory cortex of mustached bats, the CC ("C" stands for constant frequency) and DIF (dorsal intrafossa) areas consist of CF/CF neurons tuned to a combination of pulse CF_1 and echo CF_n ($n = 2$ or 3). They show facilitative responses to pulse-echo stimuli with specific frequency differences, corresponding to Doppler shifts. Their facilitative responses are sharply tuned to a specific relative target velocity (best velocity). Compared with CC neurons, DIF neurons are tuned to higher velocities and to larger CF_1 amplitudes, and adapt faster to repetitive pulse-echo stimuli. The great majority of CC neurons are suited for the processing of velocity information during cruising and target-directed flight, whereas the majority of DIF neurons are suited for the processing of velocity information when the bat is emitting loud pulses at low repetition rates during cruising flight. CC and DIF neurons are broadly tuned to 0–2-ms echo delays and not suited for ranging.

1. Introduction

For echolocation, the mustached bat, *Pteronotus parnellii parnellii*, emits bio-sonar pulses, each of which consists of four harmonics of constant-frequency (CF_{1-4}) and frequency-modulated (FM_{1-4}) components (Schnitzler, 1970; Suga et al., 1983a; Henson et al., 1980, 1987). Therefore, there are 16 components in a pulse-echo pair (Fig. 1A). In target-directed flight, the bat lowers the pulse frequency to compensate for echo Doppler shifts, shortens pulse duration from ~30 ms to ~8 ms, and increases pulse emission rate from ~8/s to ~100/s (Novick and Vaisnys, 1964; Henson et al., 1980, 1987). Relative target velocity information is extracted from a pair of pulse CF and its Doppler-shifted echo CF (Schnitzler, 1968, 1970), whereas target distance information is extracted from the delay of echo FM from pulse FM (Simmons et al., 1975). Those information-bearing elements in a pulse-echo pair are separately processed in the auditory cortex of mustached bats (Fig. 1B). Namely, the CC area ("C" stands for constant frequency; previously called the CF/CF area) is specialized for the processing of velocity information (Suga et al., 1983a; Suga and Tsuzuki, 1985). The FF ("F" stands for frequency modulation; previously called the FM-FM area; Tang and Suga, 2008), dorsal fringe (DF) and ventral fringe (VF) areas are specialized for the processing of target-distance information (Suga and O'Neill, 1979; Suga et al., 1978, 1983a; O'Neill and Suga, 1979, 1982; Suga and Horikawa, 1986; Edamatsu et al., 1989). Anatomical studies have shown that the CC and Doppler-shifted CF (DSCF) areas project to the dorsal intrafossa (DIF) area which is much smaller than the CC area (Fitzpatrick et al., 1998). The CC and DSCF area are quite different from each other in response properties.

Our preliminary data indicated that, like CC neurons, DIF neurons were sharply tuned to a combination of Doppler shift-compensating CF_1 and Doppler-shifted CF_n ($n = 2$ or 3) and were very broadly tuned to 0–2 ms echo delays. It was likely that CF/CF combination-sensitive neurons clustered in the different cortical areas are different from each other in velocity-information processing. To test this hypothesis, we studied the response properties of DIF and CC neurons (i.e., CF/CF neurons in the DIF and CC areas) in detail with the same set of stimuli mimicking pulse-echo pairs. The aims of our current paper are to report the similarities and differences in response properties between DIF and CC neurons and to

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Abbreviations

CC	"C" stands for constant frequency
CF	constant frequency
CF_{1-4}	1st-4th harmonics of a constant frequency component
CF_n	2nd and 3rd harmonics of a constant frequency component of an echo stimulus
CF/CF	pulse CF and echo CF
dB SPL	decibels in sound pressure level
DF	dorsal fringe
DIF	dorsal intrafossa
DSCF	Doppler-shifted constant frequency
FF	frequency modulation-frequency modulation
FM	frequency modulation
FM_{1-4}	1st-4th harmonics of a frequency-modulated component
Hz	hertz, i.e., cycles per second
PST	post-stimulus time
VF	ventral fringe

propose potential functional differences between the CC and DIF areas.

2. Methods

The methods in the present experiments were the same as those described in a previous paper (Suga et al., 1983a), so that only the main portions of those are summarized below.

2.1. Surgery and recording of action potentials

Seven mustached bats, *Pteronotus parnellii parnellii*, from Jamaica were used for this study. Under Innovar-Vet analgesia (0.08 mg/kg Fentanyl and 4 mg/kg Droperidol, i.m.), the dorsal surface of the skull was exposed and a 15-mm-long metal post was mounted on it with cyanoacrylate gel. The bat was individually kept in a cage for recovery from the surgery for 3–4 days before electrophysiological experiments.

For the experiments, the un-anesthetized bat was placed in a Styrofoam restraint suspended by an elastic band at the center of a soundproof, echo-attenuated room maintained at 30–31 °C. The head was immobilized by fixing the metal post mounted on the skull to a metal rod with setscrews. Small holes (50–100 μm diameter) were made in the skull with a sharpened needle with the aid of a dissection microscope. A tungsten-wire recording electrode with a 6-8-μm-tip diameter was inserted into the CC or DIF area through the hole. To avoid the sylvian artery when penetrating the DIF area (Fig. 1B), the recording electrode was tilted laterally ~40° from the vertical plane and posteriorly ~45° to the sylvian artery. A tungsten-wire indifferent electrode with a 20-30-μm-tip diameter was placed anterior to the sylvian artery, where no auditory responses were recorded. In each animal, neural responses to pulse-echo stimuli were recorded from the CC and DIF areas of the right and left cortices. At the end of a recording period, an electrolytic lesion was made to identify the recording site of the DIF area (Fig. 1C).

2.2. Acoustic stimuli

Two condenser loudspeakers were placed at 68 cm in front of the bat. One loudspeaker to deliver pulse stimuli was immediately above the other to deliver echo stimuli. They were 3° up and 3° down relative to the eye-nostril line, respectively. Acoustic stimuli were CF tones, FM sounds, and CF-FM sounds presented alone or in a pair. In CF-FM sounds, the FM component always followed the CF component. In FM_{1-4}, frequency swept downward 6, 12, 18 and 24 kHz, respectively. The durations of CF and FM stimuli were 30 and 3.0 ms, respectively, except otherwise stated. The rise and decay times of these sounds were 0.5 ms. Sound amplitudes were controlled with manual attenuators. All stimulus levels were expressed in dB SPL (decibels in sound pressure level re 20 μPa).

Acoustic stimuli were delivered in three different ways, termed standard stimulus, delay scan, and train of repetitive stimuli. **(1)** The standard stimulus was either a single sound or a pulse-echo

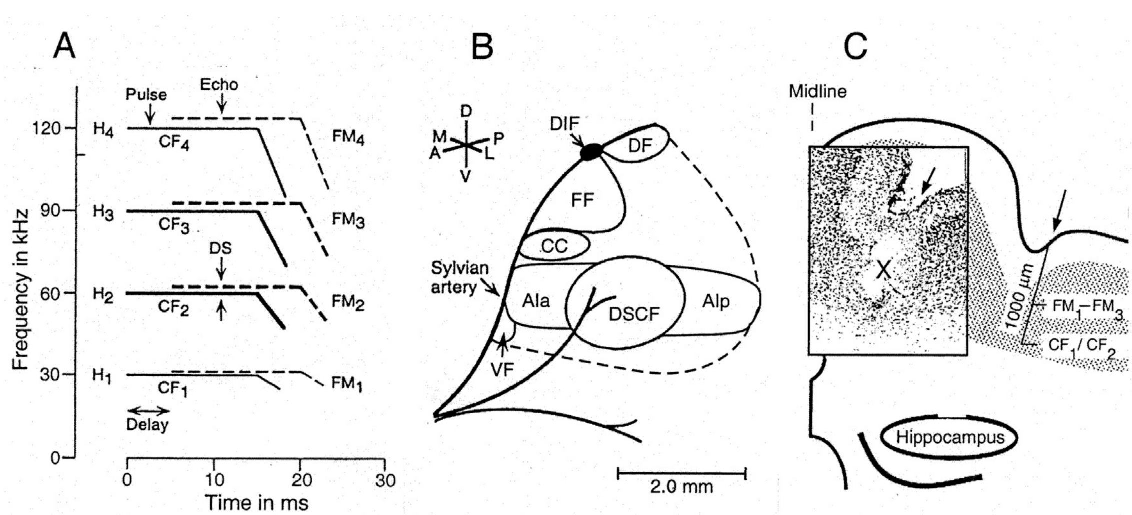

Fig. 1. Bio-sonar signal and cortical auditory areas. (**A**) Schematic sonograms of a mustached bat's bio-sonar pulse and a delayed, Doppler-shifted echo. The pulse (—) and echo (———) each consist of four harmonics (H_{1-4}) composed of constant frequency (CF_{1-4}) and frequency modulated (FM_{1-4}) components (Suga, 1990). (**B**) Dorso-lateral view of the left auditory cortex of the mustached bat (based on Suga et al., 1997a). (**C**) A frontal section across the DIF area that is located at the posterior bank of the dorsal portion of the sylvian fossa. The arrow indicates a recording electrode penetration and the depths where FM_1-FM_3 and CF_1/CF_2 neurons were recorded. The inset shows an electrolytic lesion where DIF neurons were recorded. $AI_{a\ and\ p}$: anterior and posterior portions of the primary auditory cortex; CC: constant frequency/constant frequency area; DF: dorsal fringe area; DIF: dorsal intrafossa area; DS: Doppler shift; DSCF: Doppler-shifted CF processing area within AI; FF: frequency modulation-frequency modulation area; VF: ventral fringe area.