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Review Article

Specialization of the auditory system for the processing of bio-sonar information in the frequency domain: Mustached bats

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A R T I C L E I N F O

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For echolocation, mustached bats emit velocity-sensitive orientation sounds (pulses) containing a constant-frequency component consisting of four harmonics ($CF_{1\text{-}4}$). They show unique behavior called Doppler-shift compensation for Doppler-shifted echoes and hunting behavior for frequency and amplitude modulated echoes from fluttering insects. Their peripheral auditory system is highly specialized for fine frequency analysis of CF_2 (~61.0 kHz) and detecting echo CF_2 from fluttering insects. In their central auditory system, lateral inhibition occurring at multiple levels sharpens V-shaped frequency-tuning curves at the periphery and creates sharp spindle-shaped tuning curves and amplitude tuning. The large CF_2-tuned area of the auditory cortex systematically represents the frequency and amplitude of CF_2 in a frequency-versus-amplitude map. "CF/CF" neurons are tuned to a specific combination of pulse CF_1 and Doppler-shifted echo $CF_{2\text{ or }3}$. They are tuned to specific velocities. CF/CF neurons cluster in the CC ("C" stands for CF) and DIF (dorsal intrafossa) areas of the auditory cortex. The CC area has the velocity map for Doppler imaging. The DIF area is particularly for Dopper imaging of other bats approaching in cruising flight. To optimize the processing of behaviorally relevant sounds, cortico-cortical interactions and corticofugal feedback modulate the frequency tuning of cortical and sub-cortical auditory neurons and cochlear hair cells through a neural net consisting of positive feedback associated with lateral inhibition.

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Abbreviations: AI, primary auditory cortex; AM, amplitude modulation; BA, best amplitude; BAF, BA for facilitation; BF, best frequency; BFF, BF for facilitation; BMI, bicuculline methiodide; CC, constant frequency/constant frequency; CF, constant frequency; $CF_{1\text{-}4}$, 1st-4th harmonics of CF; CF_n, $CF_{2\text{ or }3}$ of an echo; CF/CF, combination sensitive to overlapping pulse CF and echo CF; CM, cochlear microphonic response; dB, decibels; DIF, dorsal intrafossa; DS, Doppler shift; DSCF, Doppler-shifted CF; FF, frequency modulation-frequency modulation; FM, frequency modulation; $FM_{1\text{-}4}$, 1st-4th harmonics of FM; FM-FM, combination sensitive to non-overlapping pulse FM and echo FM; GABA, gamma-aminobutyric acid; ICc, central nucleus of the inferior colliculus in the midbrain; MGB, medial geniculate body in the thalamus; N_1, summated auditory nerve response; NMDA, N-methyl-D-aspartate; Q, quality factor indicating sharpness of a tuning curve; $Q_{10dB,\ 30dB\text{ and }50dB}$, Qs at 10, 30 and 50 dB above minimum threshold of a given neuron, respectively; SPL, sound pressure level

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1. Introduction

The frequency-tuning curves of peripheral auditory neurons are V-shaped, so that the bandwidth of the curves becomes broader at higher sound pressure levels. In the central auditory system, however, the bandwidth of the tuning curves of some neurons is narrow regardless of sound pressure levels, i.e., “level tolerant” (Suga, 1977, 1995). Peripheral auditory neurons monotonically increase a discharge rate to a plateau with an increase in sound pressure level (amplitude). They are not tuned to a specific amplitude. Some central auditory neurons, however, respond best to the sound at specific amplitude. They are tuned to a specific combination of frequency and amplitude (Grinnell, 1963; Suga, 1965, 1977; Suga and Manabe, 1982; Phillips and Orman, 1984; Langner and Schreiner, 1988). Behaviorally relevant sounds are generally complex and simultaneously stimulate multiple locations of the basilar membrane. Some central auditory neurons respond to a specific combination of simultaneously stimulated regions of the basilar membrane. They are “combination-sensitive” (Suga et al., 1978, 1979; Suga, 1990a). “Combination-sensitive” means that the response of a neuron to a complex sound is larger than the algebraic sum of the responses to individual components of the sound. Multiple components of a complex sound have a specific relation in frequency and amplitude. If these specialized neurons were found occasionally in the central auditory system and were not clustered, one would doubt their significance in auditory signal processing and auditory behavior. If those neurons are clustered at particular portions of the central auditory system, however, one may associate them with the processing of behaviorally relevant sounds.

Several species of insectivorous bats perform unique behavior called “Doppler-shift (DS) compensation” for hunting fluttering insects near vegetations, i.e., in acoustically cluttered environments (Schnitzler, 1968, 1970; Neuweiler, 1990). DS compensation is the process by which the bat lowers the frequency of the emitted pulse according to the flight speed so that the echoes return at the same frequency regardless of the speed (described more fully below). Their auditory systems accordingly show unique features matching DS compensation. Since the orientation sound (bio-sonar pulse or pulse) used for DS compensation is species-specific, unique features of the auditory system are also species-specific in the frequency domain (Schnitzler and Denzinger, 2011). It is interesting and important to compare the auditory systems of different species of animals. However, I will focus on various neurophysiological findings made with the mustached bat, *Pteronotus parnellii**, which has highly specialized mechanisms for the processing of Doppler-shifted echoes and which has arguably been best studied neurophysiologically. (**P. parnellii rubiginosa* had been called *Chilonycteris rubiginosa*.)

In the mustached bat, neurons with sharp level-tolerant frequency tuning, neurons tuned to a specific combination of frequency and amplitude, and neurons tuned to a specific combination of multiple signal elements are clustered for the systematic representation of parameter values characterizing their tuning at certain portions of the central auditory system. They are directly related to the processing of Doppler-shifted echoes. Furthermore, cortical and subcortical neurons and cochlear hair cells directly related to the processing of these echoes are improved and adjusted in frequency tuning by cortico-cortical interactions and corticofugal feedback. The aim of this review article is to summarize all these findings made with the mustached bat. The mustached bat auditory system shows multiple specializations other than those in the frequency domain. For those multiple specializations and the comparative physiology of the auditory system, one may read “Hearing in Bats” edited by Popper and Fay (1995) and “Integrative Functions in the Mammalian Auditory Pathway” edited by Oertel et al. (2001).

2. Bio-sonar pulses and Doppler-shift compensation

For echolocation, the mustached bat emits bio-sonar pulses, each of which consists of four harmonics of a long constant-frequency ($CF_{1\text{-}4}$) and a short frequency-modulated ($FM_{1\text{-}4}$) component (Schnitzler, 1970; Henson et al., 1980, 1987; Suga et al., 1983a). Therefore, there are 16 components in a pulse-echo pair (Fig. 1A). The CF and FM components are suited for carrying velocity and distance information, respectively (Simmons et al., 1975).

In target (e.g., fluttering insect)-directed flight, the bat increases a pulse emission rate from ~6/s to 100/s and shortens pulse duration from ~30 to 8 ms after initial lengthening from 20 to 30 ms (Fig. 1C). So, the duty cycle increases (Novick and Vaisnys, 1964; Goldman and Henson, 1977). During flight, the bat lowers the pulse frequency to compensate for echo Doppler shifts evoked by its own flight (Schnitzler, 1970). This behavior called DS compensation has been best studied in the horseshoe bat, *Rhinolophus ferrumequinum* (Schnitzler, 1968; Schuller et al., 1974; Hiryu et al., 2008). The DS compensation of the mustached bat was studied in flight (Schnitzler, 1970) and also by placing it on a pendulum (Henson et al., 1980; Gaioni et al., 1990). The mustached bat on a pendulum shows DS compensation during a forward swing, but no DS compensation during a backward swing or DS compensation only at the beginning of a backward swing. It emits pulses at the “resting” frequency during a backward swing (Fig. 1D). The resting frequency is the frequency of CF_2 of bio-sonar pulses emitted by a bat in rest and not compensating for Doppler shifts. Since CF_2 is the predominant component of the pulse (Fig. 1B), DS compensation has been described in terms of a change in CF_2 frequency.

The resting frequency is different between individual bats. In the mustached bat from Panama (*P. p. rubiginosa*), the CF_2 resting frequency measured by D. Margoliash ranged from 59.69 to 63.33 kHz (61.250 ± 0.534 kHz for 58 males and 62.290 ± 0.539 kHz for 58

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