



Research paper

Narrow sound pressure level tuning in the auditory cortex of the bats *Molossus molossus* and *Macrotus waterhousii*



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ABSTRACT

In the auditory system, tuning to sound level appears in the form of non-monotonic response-level functions that depict the response of a neuron to changing sound levels. Neurons with non-monotonic response-level functions respond best to a particular sound pressure level (defined as "best level" or level evoking the maximum response). We performed a comparative study on the location and basic functional organization of the auditory cortex in the gleaner bat, *Macrotus waterhousii*, and the aerial-hawking bat, *Molossus molossus*. Here, we describe the response-level function of cortical units in these two species. In the auditory cortices of *M. waterhousii* and *M. molossus*, the characteristic frequency of the units increased from caudal to rostral. In *M. waterhousii*, there was an even distribution of characteristic frequencies while in *M. molossus* there was an overrepresentation of frequencies present within echolocation pulses. In both species, most of the units showed best levels in a narrow range, without an evident topography in the amplitude organization, as described in other species. During flight, bats decrease the intensity of their emitted pulses when they approach a prey item or an obstacle resulting in maintenance of perceived echo intensity. Narrow level tuning likely contributes to the extraction of echo amplitudes facilitating echo-intensity compensation. For aerial-hawking bats, like *M. molossus*, receiving echoes within the optimal sensitivity range can help the bats to sustain consistent analysis of successive echoes without distortions of perception caused by changes in amplitude.

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1. Introduction

Successfully using a biosonar system requires specialization both for broadcasting biosonar pulses and for decoding the information in the returning echoes. It has been reported that the auditory cortex (AC) of bats contains numerous specializations that supposedly help to extract echo information that is used to build up complex acoustic scenes. Probably the most common cortical specialization appears in the form of a large overrepresentation of neurons that are "tuned" to characteristic features of the species-specific biosonar signal, such as sound frequency (Suga, 1977; Esser and Eiermann, 1999; Hoffman et al., 2008; Macías et al.,

2009), sound duration (Galazyuk and Feng, 1997), echo-delay (i.e. the time interval between call emission and echo arrival) and echo-amplitude (Suga and O'Neill, 1979; Hagemann et al., 2010; Hechavarría et al., 2013). For example, in the AC of CF-FM bats (bats with sonar calls that contain long constant-frequency (CF) and short downward frequency-modulated (FM) segments, like the mustached bat *Pteronotus parnellii*, there is an overrepresentation of neurons tuned to frequencies of the CF component of the second harmonic of the Doppler shifted echoes (Suga and Jen, 1976). The neurons that encode for this component of the biosonar signal are clustered together in an area defined as the Doppler-shift constant frequency (DSCF) area. Similarly, in most species of FM bats (i.e. those broadcasted only frequency modulated signals), even if the functional specialization of the AC is often not so clearly apparent, neurons processing frequencies of their echolocation signals are more abundant (Esser and Eiermann, 1999; Hoffman et al., 2008; Macías et al., 2009). Temporal features of the biosonar signal are also well represented in the cortex of bats. In the auditory cortex of CF-FM bats and the FM bats *Carollia perspicillata* and *Pteronotus quadridens* there are large regions packed with delay tuned neurons that encode echo-delay and hence target-distance (Suga and O'Neill, 1979; Hagemann et al., 2010, 2011; Hechavarría et al., 2013).

Abbreviations: AI, Primary auditory cortex; AC, Auditory cortex; CF, constant frequency; FM, frequency modulated; DSCF, Doppler-shifted CF processing area; FRA, frequency response area; ChF, characteristic frequency; BF, best frequency; MT, minimum threshold; BL, best level; α , angular direction; Lz , vector magnitude

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Unlike frequency and temporal properties of the biosonar signals, the representation of sound amplitude in the cortex of bats has been less studied. Sound-level tuning (also known as amplitude tuning and intensity tuning) appears in the form of non-monotonic response-level functions that depict the response of a neuron to changing sound levels. Neurons with non-monotonic response-level functions respond more robustly to a particular sound pressure level (defined as best level), and their response drops down at both higher and lower sound levels (Heil et al., 1994; Watkins and Barbour, 2008). In bats, amplitude tuning was described in detail in the DSCF area of the mustached bat (Suga, 1977). The DSCF area occupies at least 30% of the AI of the mustached bat and within this area; neurons with different best levels are organized forming an “amplitopic” map (Suga, 1977; Suga and Manabe, 1982). This “amplitopic” representation is orthogonal to the well-known cochleotopic organization of neurons according to their preferred frequencies. It has been hypothesized that having cochleotopic and amplitopic maps in the cortex allow bats to represent sounds in the cortical lamina according to their frequency and intensity (Suga, 1977).

Among bats, amplitopic maps have been found only in *P. parnellii*. It is still unknown if they are a generalized feature of the bat auditory cortex, as it is the cochleotopic organization of neurons. The main goal of the present study is to look for amplitude tuning and amplitopic maps in the cortex of bat species that use FM-echolocation (that is more general than CF-FM echolocation). We studied the auditory cortex of the aerial-hawking bat *Molossus molossus* and the gleaning bat *Macrotus waterhousii*. In a previous report we have shown that the auditory cortex of *M. molossus* contains a disproportionately large region dedicated to the processing of frequencies between 30 and 40-kHz, frequencies that are characteristic of the search signals of this species (Macías et al., 2009). The auditory cortex of *M. waterhousii* was not studied before. It is expected to find a larger representation of low frequency sounds such as those generated by prey, similar to the auditory system of other gleaning bat species (Neuweiler, 1990; Rübsamen et al., 1988).

2. Methods

2.1. Animals

The study was conducted on the AC of eight adult *M. waterhousii* (4 males and 4 females) and four *M. molossus* (3 males and 1 female). The animals were captured at the entrance of their diurnal refuge during their evening exodus and kept in captivity in a room with temperature, humidity, and photoperiod conditions similar to those of the bats' natural environments. The animal use in this study was authorized by the Centre for the Inspection and Control of the Environment, Ministry of Science, Technology, and Environment, Cuba.

2.2. Surgical preparation

The bats were anaesthetized with a subcutaneous injection of pentobarbital ($0.05 \text{ mg g}^{-1} \text{ b.w.}$) and placed in a Styrofoam sandwich. Surgery and experiments were carried out in a sound-attenuated chamber kept at a temperature of $32\text{--}37^\circ\text{C}$. The skull was exposed and a head bolt fixed with dental cement and secured to a metal frame. The temporal musculature was partly removed and retracted to expose the temporal skull. Using a scalpel the skull was incised carefully such that several pieces of bone could be easily removed one by one during the experiment to enlarge the cortical area for mapping as necessary. In most experiments, the dura mater was left intact. If the electrode did not penetrate through the dura mater easily, the dura dorsal and ventral to a large

characteristic blood vessel in the dura was carefully removed. Anaesthesia was maintained with supplemental pentobarbital (10–40% of the initial dose, s.c.).

2.3. Acoustic stimulation and neuronal recording

Mapping was done by recording single- and multiunit responses at recording sites across the cortex. The distance between recording sites was between 200 and 250 μm . Blood vessels were avoided. During mapping, recording sites were marked on a detailed drawing of the cortical vasculature. Marks at the skull and prominent crossings or branching points of blood vessels served as reference points for the reconstruction of the cortical map according to the outline of the skull (see below). Carbon electrodes (Carbostar 0.4–0.8MO; Kation Scientific, Minneapolis, Minnesota, USA) were inserted perpendicular to the cortical surface using a piezo-microdrive (PM10-1, Science Products, Hofheim, Germany) and units were recorded in a depth of 100–500 μm corresponding to cortical layers II to V as defined from Nissl-staining. After the first penetrations, the angle of the electrode was not changed and only moved in rostrocaudal and dorsoventral direction using a micropositioning system.

After amplification (Differential amplifier EX1, Dagan) and band-pass filtering between 200 Hz and 5 kHz, the neuronal signal was digitized by a Microstar DAP board (sampling rate 33 kHz), processed by the computer program, and stored for further analysis. Analysis of the measured electrophysiological data was performed with MatLab R2009b custom-written script (Mathworks). The recorded multiunit activity was amplitude filtered so that for the subsequent analysis we selected only those spikes whose amplitude was at least three standard deviations above the recording baseline.

Once a neuronal response was found, the unit's frequency response area (FRA) was determined with randomly presented pure-tone bursts (10-ms duration with 0.5-ms rise/fall time presented at a repetition period of 250 ms) with variable frequency and level combinations. As a rule, five averages were sufficient to obtain an accurate estimate of the units FRA. FRAs were visualized as filled contour plots (contourc function, Matlab). Threshold curves were calculated as 25% of the maximum response. For each unit the following parameters were calculated: minimum threshold (MT) and characteristic frequency (ChF) (i.e. the frequency and level at the lowest tip of the threshold curve); best frequency (BF) and best level (BL) (i.e. the delay and echo-level that evoked the unit's maximum response).

2.4. Construction of cortical maps

For each bat, coordinates of the recording sites in relation to a branch of the median cerebral artery were estimated using the ocular scale of the surgical microscope (20 μm resolution at $50\times$ magnification, Carl Zeiss Stemi, 2000c). In each species, cortices showed the same pattern of vessels ramification. This was used to determine the orientation of the ordinate axis of the bidimensional Cartesian space of analysis.

A gradient analysis was conducted to determine the spatial orientation of maps. The gradient of a function of two variables (i.e. $F(x, y)$, where F is the response property of interest (i.e. the BF) and x and y indicate coordinates of each recording site) is expressed as a collection of vectors pointing in the direction of increasing values of F . Gradients vectors were calculated in each individual animal and their angular orientation was accumulated and plotted in the form of circular scatter plots. Two parameters were used for characterization of circular scatter plots, i.e. the mean angular direction (α) and mean vector magnitude (L_α). The value of α indicates the angular orientation of a particular circular distribution. L_α is a measure of the distribution variance (V), it is calculated by the

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