Comparative Auditory Neurophysiology of the Inferior Colliculus of Two Molossid Bats, *Molossus ater* and *Molossus molossus*

II. Single Unit Responses to Frequency-Modulated Signals and Signal and Noise Combinations

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**Summary.**

1. Recordings were made from single inferior colliculus neurons of *Molossus ater* and *Molossus molossus* (Molossidae) to pure tone pulses and FM-pulses with different modulation heights, durations (20 ms, 2 ms) and directions (upward, downward sweeps).

2. Minimum thresholds to pure tone pulses at best frequency and FM-pulses centered at best frequency of equal duration were compared. Using stimuli of 20 ms duration, 58% of the neurons in *M. ater* (49% in *M. molossus*) had equal threshold values within ±5 dB, 28% in *M. ater* (37% in *M. molossus*) responded with more than 5 dB higher thresholds to FM-stimuli. With stimulus durations of 2 ms, the distribution changed: 27% of the neurons in *M. ater* (41% in *M. molossus*) responded 5 to 60 dB more sensitively to the FM-stimulus that mimics the FM-component of the orientation call, only 17% in *M. ater* (26% in *M. molossus*) responded more sensitively to pure tone stimuli. Comparison of thresholds to FM-stimuli of different sweep rates also revealed a population of neurons more sensitive to the fast sweep rate (22% *M. ater*, 29% *M. molossus*).

3. Specialized neurons were found that did not respond to a particular stimulus configuration (e.g. neurons not responding to upward sweeping FM-stimuli, neurons not responding to slowly sweeping FM-stimuli, etc.).

4. Response patterns of single neurons were found to depend on the frequency-time-course of the stimulus. Especially with slowly sweeping FM-signals, neuronal response activity (measured in number of spikes per stimulus) could be greater than to any other stimulus configuration employed. A stabilization of initial latency was frequently observed with fast sweeping FM-stimuli.

5. Threshold Signal/Noise-ratios were measured by masking the neuron's response to the signal (pure tone or FM) by bandpassed pseudorandom noise. The threshold Signal/Noise-ratios where either equal or lower for FM-stimuli than for pure tone stimuli of equal duration, i.e. more noise intensity is needed to mask the response to FM.

**Introduction**

The orientation calls of the South American bats, *Molossus ater* (*M. ater*) and *Molossus molossus* (*M. molossus*) contain a strong frequency-modulation (FM) following the short constant-frequency (CF) component. Frequency sweeps downward approximately one octave from the CF-frequency, which is about 42 kHz in *M. ater* and 52 kHz in *M. molossus*. The second harmonic of the FM is more pronounced than that of the CF, therefore increasing the bandwidth of the calls considerably. Duration of the CF is about 1–3 ms, the FM is about 1–2 ms long (Beuter, K., pers. comm.).

In order to get information, how the auditory system processes the species specific orientation call and to find adaptations of the sender-receiver system, one cannot rely solely on CF-stimulation but has to test FM-stimuli as well.

Depending on the question one poses on the system, there are at least two ways possible in designing the FM-stimuli. The first is to use FM-stimuli mim-
icking as closely as possible the FM-component of the orientation call in frequency range and sweep-rate. The responses of single neurons can then be most readily interpreted as the system's performance under natural conditions (Pollak et al., 1978). However, with this procedure a bias is introduced in favour of those neurons with best frequencies (BF) in that particular frequency range. The second possibility avoids this by centering the sweeps around the neurons' BFs. Analysis of the single neuron responses to FM-pulses of different durations, modulation heights and directions, as done by Suga (1969), can lead to an understanding of the neuronal mechanisms responsible for extraction of a particular stimulus “feature” and can give information about the degree of specialization of the auditory system to the species specific echolocation call.

This approach might not seem as comprehensive as the above cited, but one has to keep in mind that the acoustic environment of bats is far more complicated than it appears at first glance. The vocalization repertoire of bats not only consists of various types of echolocation calls (Griffin, 1958; Simmons et al., 1975; Habersetzer, 1978; and see below), but also contains complexly structured communication sounds (Brown, 1976; Fenton et al., 1976; Habersetzer, 1978). Bats can also rely on passive hearing (Fiedler, 1978; Habersetzer, 1978). Furthermore, to define a particular orientation sound structure as the “characteristic” orientation call of a species might be an oversimplification. At least in some bat species, the structure of the call can vary depending on the orientation situation. Tadarida brasiliensis, also a molossid bat, was found to emit CF, short CF-FM and multi-harmonic FM-calls (Simmons et al., 1978). These changes in structure are discussed to serve different purposes, e.g., long CF-signals are used in the searching phase while the bat is flying in open air, broadband FM-signals with one harmonic are emitted in the approach phase, and in the presence of clutter interference multi-harmonic FM-signals occur (Simmons et al., 1978).

In our study, both of the above cited approaches in stimulus design were used with the objective of finding specializations of the auditory system to the echolocation call. Therefore, we compared the influence of stimulus structure (CF and various FM) on thresholds, response patterns and intensity coding of single inferior colliculus neurons of awake molossids. A more critical test for the adaptive properties of the auditory system is to look for its performance under non-ideal acoustic conditions. Therefore, “masked thresholds” of single neurons to the different stimuli were measured, using pseudorandom wide band noise as interference signal.

**Material and Methods**

Surgical procedure and recording system were the same as described in the companion paper (Vater et al., this volume).

CF- and FM-pulses were amplitude-shaped with 0.5 ms rise-fall times and delivered with a repetition rate of 4/s. Durations of both CF- and FM-signals were equal (2 ms and/or 20 ms). The linear FM-sweeps filled out the entire pulse duration, i.e. 2 ms or 20 ms, respectively. FM upward or downward sweeps were always centered around the neurons' BFs. Modulation heights were 40, 20, or 10 kHz (as a consequence of the constant pulse duration, changing modulation height also changes sweep rate, for the two pulse durations 20–5 kHz/ms and 2–0.5 kHz/ms, respectively). The orientation call of 2 ms CF-duration and 2 ms FM-duration with the downward modulation starting at the bat's CF-frequency was also simulated. Sounds containing a second harmonic have not been available in this study.

Excitatory tuning curves were measured with 20 ms CF-signals. Input-output functions (spike counts) were computed off-line from PST-histograms for all stimulus types employed.

To study threshold Signal/Noise ratios in single neurons, pseudorandom noise of 20 kHz bandwidth centered around a neuron's BF was added to the signals (CF of FM). The pseudorandom noise was generated by a Wavetek 132 VCG/Noise generator, low-pass filtered and multiplied with the pulsed carrier frequency. Duration of the noise-pulse was 80 ms, rise-fall time 1 ms, repetition rate 4/s. The tonal signals were delayed for 20 ms relative to noise onset (see also results on masked thresholds).

**Results**

**Comparison of Thresholds to Different Signal Types**

The thresholds of single neurons strongly depended on the different signal structures used. A comparison was made between single unit thresholds to CF-pulses at BF and downward frequency-modulations of 40, 20 and 10 kHz modulation height centered at BF. Modulation rate was changed by shortening the pulse duration from 20 ms to 2 ms keeping the modulation height constant.

In Fig. 1A threshold values to the 20 ms FM-pulse (ordinate) are plotted against thresholds to the 20 ms CF-pulse (abscissa). If the two values were equal, the points would fall on the 45° line. For all neurons, thresholds to these CF- and FM-signals were equal within ±5 dB (58% M. ater, 49% M. molossus). Only a minority showed lower thresholds to FM (14% M. ater, 14% M. molossus). By comparing thresholds to the short (2 ms) duration signals (Fig. 1B), the distribution changed: a large percentage (27% M. ater, 41% M. molossus) of the neurons showed up to 60 dB lower thresholds for the FM-pulse, few neurons (17% M. ater, 26% M. molossus) had more than 5 dB higher thresholds to FM than to CF.

Thus, a comparison of CF- and FM-signals revealed that in terms of thresholds, a large population