

## Azimuthal Position Affects Analysis of Complex Sounds in the Mammalian Auditory System

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Recognition and localization of sounds are two essential tasks of the auditory system in all animals. Almost all sounds in the natural environment of animals, including communication sounds and returning echoes from echolocation calls, contain frequency and amplitude modulations. Analyzing their temporal pattern is essential for sound recognition. To date it remains unclear whether the mammalian auditory system performs this analysis of temporal patterns independently of the spatial context, that is, location of the sound source. Using sinusoidally frequency-modulated (SFM) sounds, we investigated the effect of the location of a sound source on neuronal response characteristics to various modulation frequencies of neurons in the inferior colliculus (IC) of the big brown bat. In this study, we found that approximately 75% of the tested neurons change their response to frequency-modulated sounds when the binaural input is altered by presenting the sound from different locations. Neurons alter either their filter properties for modulation frequency based on spike counts or their temporal firing pattern. Our results suggest that binaural, neuronal interaction affects the filter properties for temporal stimulus characteristic of IC neurons.

A major part of the information for sound recognition lies in the temporal structure of the sound pattern [1]. Auditory nerve fibers and most neurons in the lower nuclei of the auditory brainstem follow the temporal structure of a modulated sound, i.e., they respond to each modulation cycle in a phase-locked manner. Com-

pared to lower order auditory nuclei phase-locking of IC neurons declines, the optimal modulation frequency becomes lower, and the range of modulation frequencies neurons respond to becomes narrower. This change in filter characteristic at the level of the IC suggests active neuronal filtering of frequency and amplitude modulations (for review see [2]).

At the same time binaural integration, which is essential for sound localization, first occurs in the superior olivary complex. Further processing of binaural information takes place in the IC (for review see [3]).

In the IC projections from a number of monaural and binaural nuclei of the auditory brainstem converge (for review see [4]). This raises the question of whether there is functional interaction between the mechanisms underlying pattern recognition and sound localization in single neurons of the IC. We addressed this issue by investigating the effect of the position of a sound source on the SFM filter characteristics of single neurons in the IC of the big brown bat (*Eptesicus fuscus*). SFM sounds were used as an example for complex stimuli since a substantial proportion of neurons in the IC of this bat is highly selective for modulation frequency [5].

Action potentials were recorded from 38 neurons in the central nucleus of the IC that responded well to SFM signals. Extracellular recordings were made using glass pipettes filled with 3 M KCl. Surgical procedures were according to [6]. Stimuli were computer generated (Tucker Davis technology; custom designed software by H. Koenig) and presented via a free-field

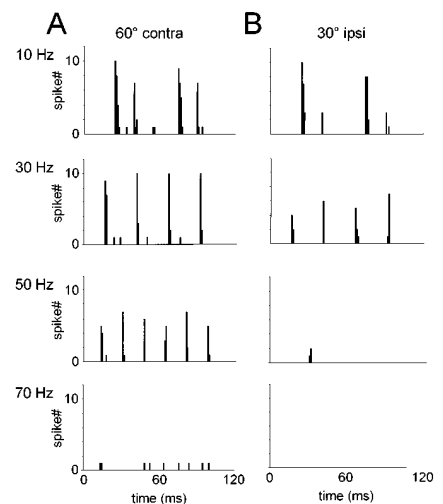


Fig. 1. Poststimulus time histograms of one IC neuron. The stimulus was an SFM tone that started at 0 ms with a duration of 100 ms. The signal was modulated at four different modulation frequencies (10, 30, 50, 70 Hz) and presented from two different loudspeaker positions (A: 60° contralateral, B: 30° ipsilateral). Each bar, number of spikes per time bin (bin width: 1 ms) summed over all trials (ten trials per stimulus). The neuron's response was phase-locked with one or two discharges to each modulation cycle. At a modulation frequency of 10 Hz the neuron responded equally well at both loudspeaker positions. However, when the sound was presented from 60° contralateral (A) the neuron still responded to a 50-Hz frequency modulated sound. Almost no discharge could be evoked at 50 Hz when the sound was presented from 30° ipsilateral (B)

loudspeaker to the animal. The loudspeaker could be rotated horizontally at a fixed distance around the bat's head. Sound pressure level was usually set 20 dB above each neuron's individual threshold measured at the optimal speaker position. The signal was a tone of 100 ms duration that was sinusoidally frequency modulated around the neuron's characteristic frequency and with the optimal modulation depth ( $\pm 5$ –20 kHz). All neurons tested responded to a SFM stimulus either with a phase-locked response, a sustained discharge, or a phasic on-response.

A range of modulation frequencies (10–1000 Hz) was presented from several azimuthal positions in the frontal hemifield of the animal (usually from 90° contralateral to 60° ipsilateral to the midline).

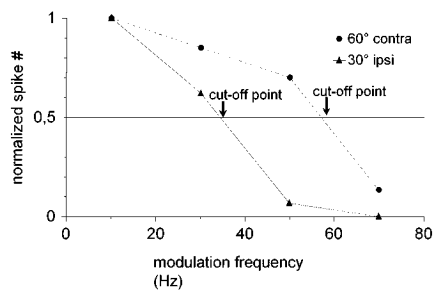


Fig. 2. MTF for the same neuron as shown in Fig. 1. Each point represents the normalized number of spikes averaged over all trials (1 is equal the maximal spike number for each loudspeaker position: 67 spikes for 60° contralateral, 45 spikes for 30° ipsilateral). Arrow, cutoff point where the number of spikes had dropped below 50% compared to the maximal spike count for each loudspeaker position. For this neuron the upper cutoff point shifted from 60 to 35 Hz when the sound direction was changed from 60° contralateral to 30° ipsilateral

We analyzed each neuron's response in two different ways: change in total number of spikes per stimulus and change in the degree of phase-locking to the stimulus envelope for various stimulus directions. Figure 1A shows a neuron's response to SFM stimuli modulated at various modulation frequencies presented from a source 60° from the midline in the contralateral hemifield. The neuron responded strongly to very slow modulation frequencies (10–50 Hz), with two discharges per modulation cycle at 10 Hz modulation frequency but only with one discharge to each cycle for higher modulation frequencies. The number of spikes decreased between 50 and 70 Hz. No response could be elicited from this neuron for modulation frequencies above 80 Hz.

This neuron changed its response properties, when the sound was presented from a different loudspeaker position (30° ipsilateral; Fig. 1B). At a modulation frequency of 10 Hz the neuron's response was equal to the response evoked when the sound was presented from 60° contralateral. Only the second discharge to each modulation cycle was slightly weaker. However, at a modulation frequency of 50 Hz the neuron no longer responded. In contrast, the neuron was still responding at 50 Hz, when the

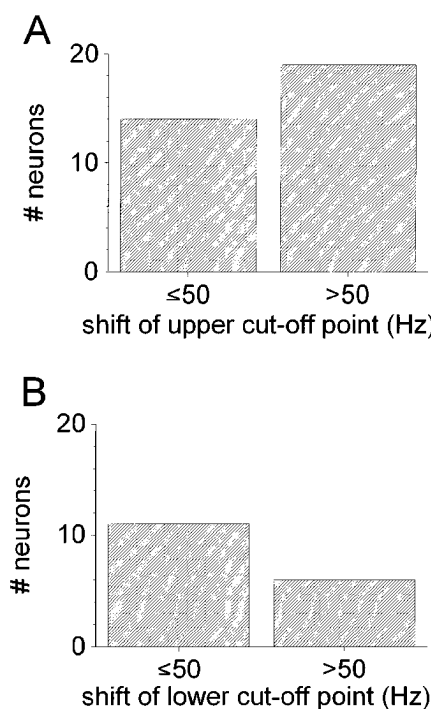


Fig. 3. Distribution of the shift of higher (A) and lower (B) cutoff points for the population of neurons tested. More than 50% of the neurons shifted their upper cutoff point more than 50 Hz when the sound was presented from a different direction. The lower cutoff point was changed more than 50 Hz by approximately 20% of the neurons when the sound direction was changed

signal was presented from 60° contralateral. Thus the SFM filter characteristic of this neuron is dependent on the position of the sound source.

For each sound direction the modulation transfer function (MTF) of a neuron was calculated based on spike counts (total number of spikes per stimulus to different modulation frequencies). For each MTF we determined the modulation frequency at which the response had dropped below 50% of the maximal response. These modulation frequencies were considered the upper and lower cutoff points.

For each neuron the general filter characteristic was determined at its optimal loudspeaker position (where the neuron discharged maximally). The neuron shown in Fig. 2 had an upper cutoff point at 60 Hz. No lower cutoff point existed; thus this neuron exhibited a low-pass filter characteris-

tic. Some 45% of the neurons showed such low-pass filter characteristics. About 40% of the neurons showed an upper and lower cutoff point, i.e., acted as a band-pass filter. For the remaining neurons the response never fell below 50% of the maximum for any of the tested modulation frequencies.

Changes in filter properties for modulation frequency were characterized by quantifying the shifts of upper and lower cutoff points. For the neuron in Fig. 2 the upper cutoff point shifted from 60 to 35 Hz when the speaker position was changed from 60° contralateral to 30° ipsilateral. The upper cutoff point was changed more than 50 Hz in 19 (out of 33) of the neurons tested when the signal was presented over a range of different azimuthal loudspeaker positions (Fig. 3A). The lower cutoff point was shifted more than 50 Hz in 6 (out of 17) of the neurons when presenting a signal at different loudspeaker positions (Fig. 3B). Across the population of neurons no systematic increase or decrease of upper or lower cutoff points were seen by changing the loudspeaker position from contra- to ipsilateral.

The ability of a neuron to phase-lock to the envelope of the stimulus was analyzed by calculating the synchronization coefficient (SC) [7]. The SC was obtained for the neuron's response to each speaker position at the best modulation frequency (maximal discharge). The example in Fig. 4 illustrates that for this neuron the ability to phase-lock to the envelope of the stimulus was generally lower at 90° contralateral (Fig. 4A) than at 0° (Fig. 4B). At the best modulation frequency (200 Hz) the SC decreased from 0.55 to 0.17 when the loudspeaker was rotated from 0° to 90° contralateral. For approximately 50% of the tested neurons the ability to phase-lock to the stimulus envelope at best modulation frequency was significantly different for different loudspeaker positions ( $P=0.05$ ; Kruskal-Wallis  $H$  test).

The results of this experiment show that the majority of neurons in the mammalian IC change either their filter characteristic based on spike counts or their temporal spiking pat-

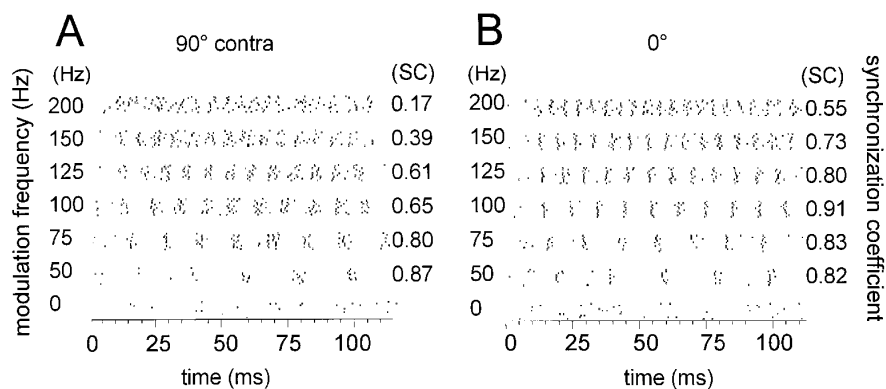


Fig. 4. Dot rasters of one individual neuron. *Each dot raster*, a neuron's response to ten repetitions of one stimulus presented with six different modulation frequencies. *Each dot*, the time when an action potential occurred. The stimulus was presented with the same modulation frequencies at two different loudspeaker positions. The precision of phase-locking increased when the loudspeaker position was changed from 90° (A) contralateral to 0° (B)

tern when a SFM sound is presented from different directions. This is coherent with a previous report showing that neurons in the IC of *E. fuscus* change their spatial receptive fields when different temporally and spectrally structured stimuli are presented [6]. A similar dependence of temporal spike patterns and sound location has recently been reported for the frog's auditory midbrain; there filter properties of neurons responding to amplitude modulated sounds are altered by the direction from which the sound is presented [8].

There are at least three mechanisms that might underlie changes in spike number and changes in temporal spike pattern. First, since pinna gain is dependent on frequency as well as on direction of the sound, monaural frequency channels converging at the IC could be weighted differently for stimuli containing different frequencies when sound direction is changed [9, 10]. Second, there is strong evidence that changing interaural intensity differences alters the relative timing of binaural inputs [11–13]. These changes in pattern of excitatory and inhibitory inputs may in turn influence the response characteristic of neurons to SFM sounds. Third, asym-

metries in frequency tuning of projections coming from the two ears could influence the effectiveness of different frequency bands of the stimulus depending on the position. Additionally, it cannot be excluded that overall changes in sound pressure level at the excitatory ear also contribute to changes in filter characteristics of the neurons. Future studies using independently controlled intensities at the two ears (earphones) should address this question.

The results of this study suggest that recognition and localization of sounds at the level of the IC are physiologically not processed independently from each other. Possible ways of neuronal coding for SFM signals include the number of spikes that a neuron fires and the temporal pattern of the spikes. Depending on the mechanism used by neurons at the next level of auditory signal processing (medial geniculate body or auditory cortex) changes in either discharge number or firing pattern influences a neuron's response differently. Neurons using coincidence detection are more sensible to inputs with changing temporal spike patterns whereas neurons using temporal integration of spikes are more affected when the total spike

number of the inputs changes. In most neurons both mechanisms are used but to different extents [14]. This raises the possibility that the temporal spike pattern contains additional information for localization to that mediated by discharge rate alone [15].

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