Efficient coding of sounds in the auditory midbrain

An original research paper by
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Research interests:
1. Processing of complex sounds in mice
2. Processing of species-specific vocalizations in the auditory midbrain of mustached bats
3. Effects of age-related hearing loss on encoding of complex sounds
4. Behavioral analyses of acoustic communication

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Efficient Coding of Ultrasound in Mice

Mice produce ultrasonic vocalizations (>30 kHz)
Pups: isolation calls when cold, isolated (Haack B et al, 1983)
Males: generate songs in presence of females or odor of female urine (Holy, T. E. and Guo, Z., 2005).
Q? Do mice encode ultrasonic vocalizations “efficiently”

- **efficient coding**
  - = heterogeneous encoding

  Many cells, but only a few respond to “complex stimulus.”
  - Spiking cells are rare.
  - Many combination-sensitive cells.

- **inefficient’ coding**
  - “redundant” coding in the paper.
  - Distributed representation of complex stimulus.
  - Many cells active at once.

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Note repetition, then changing pattern of syllables

Example of a phrase repeated three times without interruption in the original song.
The three repeats are shown one above the other, aligned on the start time for the phrase.

- pitch shifted x 16
- Long time scale changes in syllable type.
  - Syllable type is categorized by whether low jumps are present (LJ+) or absent (LJ−).
  - Shown is the number of syllables without low jumps, out of the most recent 20 syllables.

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2% female CBA/Cj mice. Top panel: Isoflurane anesthesia for surgery.
Restraint, craniotomy over one IC; hollow rod glued to skull for stability.
Recovery from anesthesia for 1 hr, acepromazine sedative.
Tungsten ground electrode, sharp glass electrode for electrophysiology.
Multi-day experiments.

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### Auditory pathways

- **dorsal view mammalian brain**

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- **auditory cortex**
- **medial geniculate**
- **inferior colliculus**
- **superior olive complex**
- **cochlear nucleus**

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24 female CBA/Cj mice. 5% females.
Restraint, craniotomy over one IC; hollow rod glued to skull for stability.
Recovery from anesthesia for 1 hr, acepromazine sedative.
Tungsten ground electrode, sharp glass electrode for electrophysiology.
Multi-day experiments.
Acoustic Analysis and Synthesis

Original (noisy) vocalizations analyzed for Frequency, amplitude and phase, as a function of time, both for fundamental and harmonics.

“State-space statistical model” and “Kalman Smoothing” used to track frequency, amplitude and phase.

Synthesized sounds are free from noise, echo, etc. Can be modified parametrically for playback.

Electrophysiology Methods

Single unit recording. Glass pipette, central nucleus of IC.
CF determined (characteristic or best frequency)
Present all vocal variants (library)

SPIKE TRAIN METRICS: for comparing spike train A and B
1) spike timing similarity within a given stimulus.
2) spike timing similarity between different stimuli.
3) firing rate similarity – overall firing rate, independent of time

In this study, IC units are mostly tuned to low-frequency sounds (below 20 kHz)

Responses of 6 neurons suggests heterogeneous responses

Fig. 5 Spectral and temporal responses of one cell in IC

Response of the IC unit to simple sinusoidal tones of differing frequency (x axis) and amplitude (y axis) in spikes per tone (color). Cell is tuned to 10-30 kHz.
Spectral-temporal response field (STRF) of same cell. Average frequency and time of sound that triggered a spike at time zero.

Three vocalizations. The response to the vocalizations, and the model-predicted responses based on the STRF. C and D: response fits model well. E: does not fit model.

A, B, and C are FRA for three cells with different tuning. The calls given do not overlap the frequency of the FRA. Altering the spectral/temporal features of a natural call sometimes improves responses from a given cell.

Effect of vocalization duration on the responses of IC neurons.

removal of AM or FM can cause the unit to increase or decrease firing.
"Efficiency of vocalization discrimination in the IC
A primary motivation behind this study was to objectively test whether the IC encodes information more efficiently than lower auditory nuclei by increasing the heterogeneity of the neural responses to complex vocalization stimuli. This hypothesis is based on evidence that the IC is the first site in the ascending auditory system that shows selectivity to complex features found in vocalizations (Klug et al., 2002) and that increasing the heterogeneity of neural responses results in a theoretical increase in information throughput (Gawne and Richmond, 1993; Bell and Sejnowski, 1995; Shamir and Sompinsky, 2006; Chelaru and Dragoi, 2008).

For each neuron in the study, the information transfer \( H \) was calculated to quantify how efficiently the neuron could discriminate among the variants of each natural vocalization (e.g., 30kHz harmonic). If a particular neuron had weak or correlated responses to each variant of a vocalization, then it was difficult to classify what vocalization was responsible for a particular response and \( H \) was low. If the responses were highly heterogeneous, then classification was possible and \( H \) was increased."

Heterogeneity of responses across the neural population
Although the previous efficiency measure was focused on the heterogeneity of responses from a single neuron to a suite of vocalization stimuli, another efficiency measure is based on the heterogeneity of responses across the neural population to individual vocalizations.

For each vocalization variant in the study, the information transfer \( H \) was calculated to quantify how heterogeneous the responses were across the whole neural population. If each neuron in the study had weak or correlated responses to a particular vocalization variant, then it would be difficult to classify which neuron a given response could be attributed to and \( H \) would be low for the vocalization variant. If the responses were highly heterogeneous, then classification was possible and \( H \) was high.

"It has been shown that the pure tone response characteristics of neurons from lower auditory nuclei are sufficient to estimate their responses to complex vocalization stimuli (Bauer et al., 2002; Pollak et al., 2003). To approximate how the neurons in our study of the IC would respond if they had been in a lower auditory nucleus, we used a pure tone spectrotemporal modeling methodology (see Materials and Methods) to predict their responses to our vocalization stimuli. The output of the model was an estimated PSTH with a bin width of 2ms (chosen to approximate the refractory period of the neuron). We were then able to generate simulated spike trains for each neuron and vocalization by interpreting these modeled PSTHs as the probability of finding a spike within each 2 ms window. Using this method, we generated a set of simulated spike trains of equal number to the recorded data (20 spike trains per stimulus) and performed an identical assessment of the information transfer, \( H \), of each neuron for each vocalization class. This enabled us to directly compare the discrimination efficiency of neurons in the IC with the discrimination efficiency of neurons from lower auditory nuclei. Figure 12 summarizes the results of this analysis."

PREDICTION:
IF EFFICIENT: \( H \) will be HIGHER THAN for Neurons than PREDICTED BASED ON MODEL from lower auditory responses.
Summary

1) Mice produce ultrasonic vocalizations (tones, FM sweeps)
2) A new method for analysis of vocalizations permitted synthesis with modification of harmonic frequencies, timing, duration.
3) Vocalizations played to single neurons in IC.
4) Spike rate compared to model, based on responses to simple sine waves.
5) IC units respond to complex characteristics, not simply sinusoidal frequency.
6) Efficient code (combinations of inputs from lower auditory centers).

BACKGROUND REFERENCES


