Temporal encoding of auditory objects in rostral superior temporal cortex of behaving macaques

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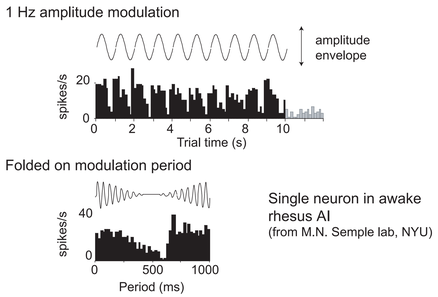
Introduction

Unlike objects in static visual scenes, auditory objects unfold in time. At the level of primary auditory cortex, the firing rate of a neuron may track periodic features of the sound envelope (e.g. amplitude or frequency modulation), but such tracking is not apparent in neurons rostral to the core auditory fields. Here we quantify temporal modulations in the spike trains of single units in the rostral superior temporal gyrus (rSTG) and assess whether these discharge patterns carry stimulus-specific information.



Recording Sites

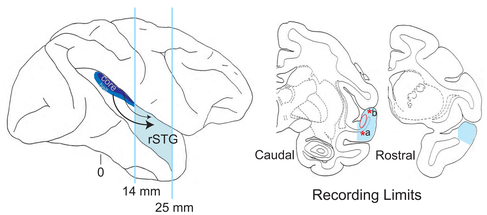
Rostral superior temporal gyrus (rSTG)
Anterior to the core and belt fields
(some recordings may include RT)

Left and right hemispheres of 2 rhesus

Single units analyzed: 47

Mean onset latency: 52 ms

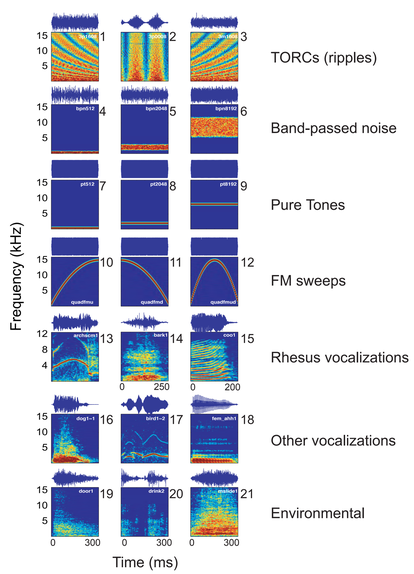
Task:
Auditory delayed-match-to-sample, sample presentation of all trials analyzed



Stimuli

The stimulus set consisted of 21 sounds, each ~300 ms in length, including synthesized sounds (rippled noise, band-pass noise, tones, frequency sweeps), animal vocalizations (rhesus monkeys and other species), and environmental sounds.

Median of 480 trials per neuron, or 480/21=23 presentations per stimulus



Analysis

Individual spike trains were:

1) binned at 1 ms resolution, 0-300 ms from sound onset
2) smoothed with a Gaussian spike-density function, σ = 10 ms
3) downsampled at 5 ms intervals to yield 300/5=60 values per response

The covariance matrix of the set of responses was decomposed by Principle Components Analysis (PCA). Each response waveform was then described by a set of coefficients in the PCA basis set.

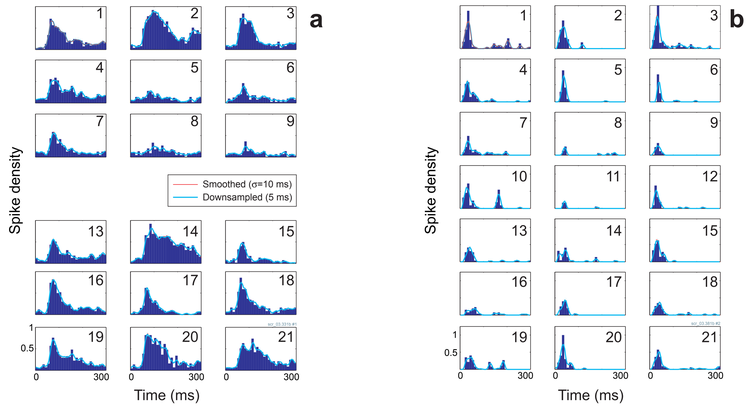
(c.f. Richmond and Optican 1987 in inferotemporal (IT) visual cortex)

Simple classifier to build confusion matrices and measure lower bound of mutual information between spike waveforms (or counts) and stimulus identity:

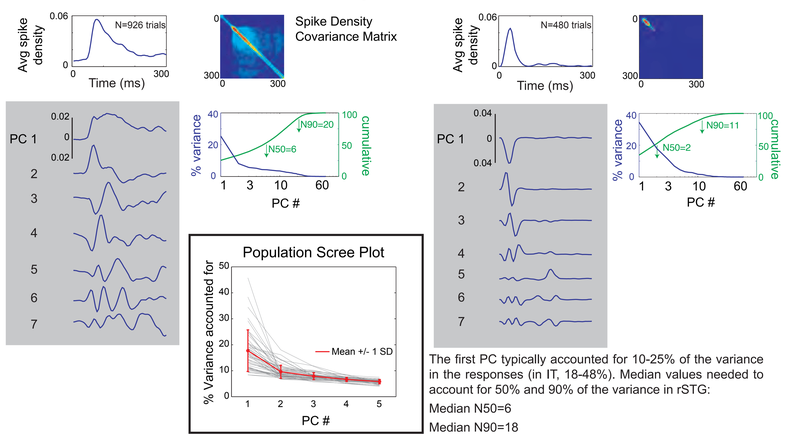
Matlab statistics toolbox "classify", linear discriminant
(c.f. Schnupp *et al.* 2006, ferret AI)
Leave-one-out cross-validation
Bias estimated by bootstrap of random class assignments

$$\mathrm{MI} = \sum_{x,y} p(x,y) \bullet \log_2\left(\frac{p(x,y)}{p(x) \bullet p(y)}\right) - \mathrm{Bias}$$

Example Responses



Principle Components Analysis



The first PC typically accounted for 10-25% of the variance in the responses (in IT, 18-48%). Median values needed to account for 50% and 90% of the variance in rSTG:

Median N50=6

Median N90=18

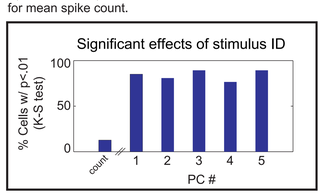
Effects of Stimulus Identity

For each of the 21 stimuli, PC coefficients were averaged across repeated presentations to determine if temporal characteristics of the response were consistent within stimuli.

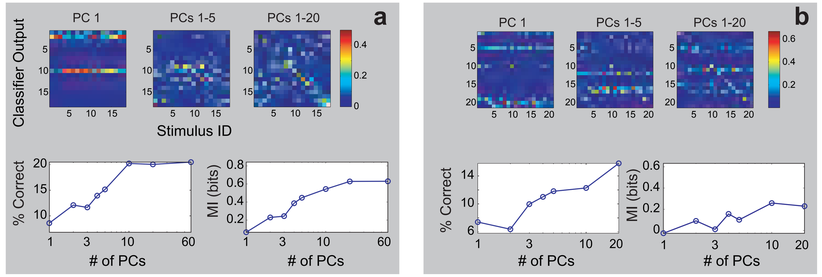
Correlation of the mean first PC with spike count was typically weak, unlike the correlation in the visual responses of IT neurons.

- Neuron **a** (above, left): PCs correlated strongly with mean spike counts
- Neuron **b** (above, right): Weak or nonexistent correlation
- Population: Among the 1st 5 PCs, ~20% correlated with spike count (p<.01)
- In IT, all neurons showed a strong correlation between 1st PC coefficient and spike count

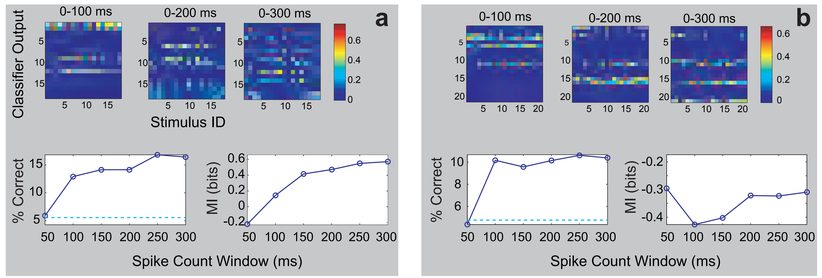
Compared to randomly drawn bootstrap samples, the first PC (and in most cases >5 PCs) of >80% of neurons showed a significant effect of stimulus identity. By contrast, only 15% of units showed a similar effect for mean spike count.

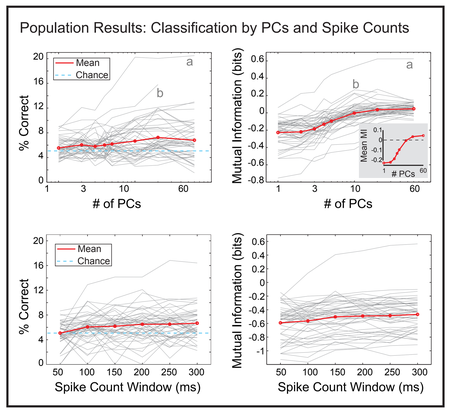


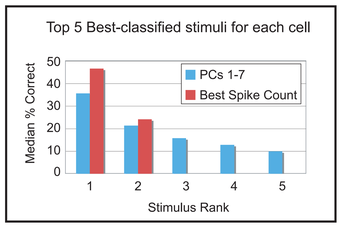
Mutual Information from Principle Components



Mutual Information from Spike Counts







Conclusions

Mutual information was higher when classifying based on (multi-dimensional) principle components, compared to spike counts.

Overall percent correct was often near chance, though individual stimuli could be reliably classified (possibly implying sparse coding).

Temporal characteristics of spike trains appear more informative, and less dependent on spike count, in rSTG than in IT neurons. This may reflect the temporal fluctuation present in auditory stimuli, and/or a difference in processing strategy between object-selective higher sensory cortices.

References:
Richmond and Optican (1987). *J. Neurophysiol.* **57**: 147.
Schnupp et al. (2006). *J. Neurosci.* **26**: 4785.

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