

Spectrotemporal Integration and Response Variability in the Inferior Colliculus, Auditory Thalamus, and Auditory Cortex

Monty A. Escabi^{1,2}, Heather .L. Read², Lee .M. Miller² and Christoph E. Schreiner²

¹Department of Electrical and Computer Engineering and Biomedical Engineering Program, University of Connecticut, Storrs, CT 06269

²W.M. Keck Center for Integrative Neuroscience and UCSF/UCB Joint Bioengineering Graduate Group, University of California, San Francisco, CA 94143

The overall goal of our research is to understand how complex sounds are encoded by single neuron activity in the central auditory system, how the activity of single neurons gives rise to spatially distributed representations or "sensory maps" for acoustic signal attributes, and how these representations are transformed from one auditory station to the other. I will present recent work from our laboratory describing how spectral and temporal sound features are jointly represented in the central nucleus of the inferior colliculus (ICC), the auditory thalamus (MGBv), and the primary auditory cortex (AI).

Spectro-Temporal Integration

It is well known that central auditory neurons selectively process temporal and spectral sound information. In the auditory midbrain and cortex, for example, neurons can respond selectively to a restricted range of temporal modulations (much like a temporal bandpass filter). Furthermore, these same neurons selectively respond to a restricted range of frequencies and therefore perform spectral filtering. Although these basic acoustic transformations are well described for simple acoustic stimuli (e.g. pure tones and modulated tones) much less is known about how complex and dynamic stimulus attributes are encoded. It is the goal of our work to understand how both of these acoustics dimensions (spectral and temporal) are jointly processed by the brain.

We use complex time-varying signals with a dynamic spectrum (Fig. 1 A and B) to study the spectro-temporal processing capabilities of single neurons in the ICC, MGBv, and AI of cats. As a first order measure, we use the spectro-temporal receptive field method in order to estimate the feature processing abilities of neurons within these three stations (Fig. 3 A for description of methods; Fig. 1 C-H for examples). Neurons within these three stations are categorized using various

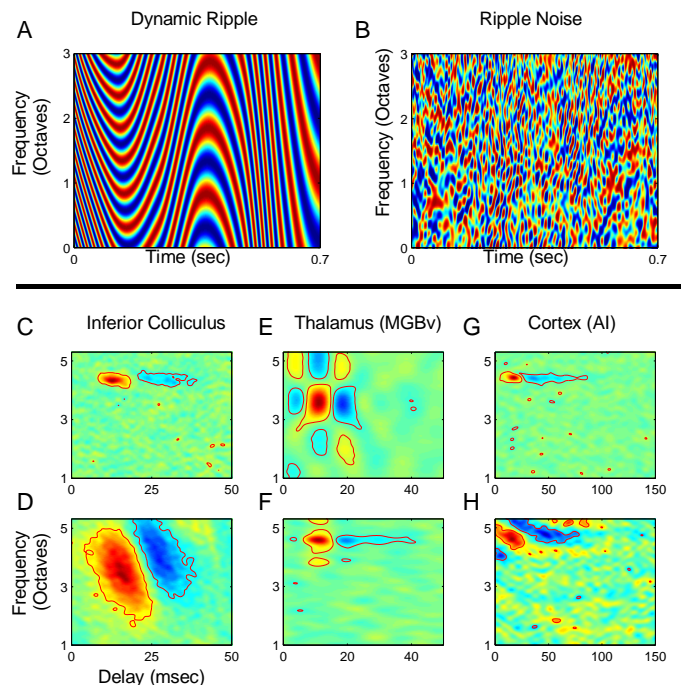


Figure 1: Dynamic ripple and ripple noise stimulus used to study the spectral and temporal preferences of auditory neurons (A and B). Example spectro-temporal receptive fields (STRF) from the inferior colliculus (C and D), auditory thalamus (E and F), and auditory cortex (G and H). Note the general "slowing" observed between ICC and AI. Red contours designate statistically significant boundaries ($p < 0.002$).

physiologic and theoretically defined criteria. These include the neuron’s ability to 1) phase-lock to spectro-temporal sound patterns, 2) respond selectively to the dynamic ripple versus the ripple noise stimuli, and 3) their degree of response variability (see below).

In the ICC, a small subset of neurons (~15%) is observed which show selective enhancement in their response patterns to the structured dynamic ripple sound. This subset of neurons generally has low spike rates, do not response to the ripple noise stimulus, and have low variability. By comparison most neurons in the ICC (~60%) do not show this selective enhancement and appear to function roughly as linear integrators. Based on the ability to phase-lock to the stimulus spectro-temporal envelope, we also observe an additional subset (~25%) of neurons that do not phase-lock (and therefore do not produce STRFs) but yet respond selectively to spectro-temporal sound patterns. While neurons in the ICC can be subdivided into three distinct physiologically defined categories, we currently find no evidence for similar categories in the MGBv and AI.

For each functionally defined category and for each of the three auditory stations, we determined the population transfer function in order to estimate the processing capabilities of each. This was done by averaging the ripple transfer function (RTF) of each neuron. The RTF describes the neurons response as a function of two parameters: the temporal modulation rate, F_m (units of Hz) and the ripple frequency (i.e. the number of spectral resonances per octave). In the ICC, a clear segregation is observed between phase-locking and non phase-locking neurons (Fig. 2 A and B). While the range of preferred ripple frequencies are similar for ICC, thalamic, and cortical neurons, it was not surprising that thalamic and cortical neurons where significantly slower (responded best to low modulation rates; Fig. 2A, C, and D). Furthermore, spectral envelope selectivity appear to be lowpass in nature for all stations, whereas temporal selectivities have a bandpass character.

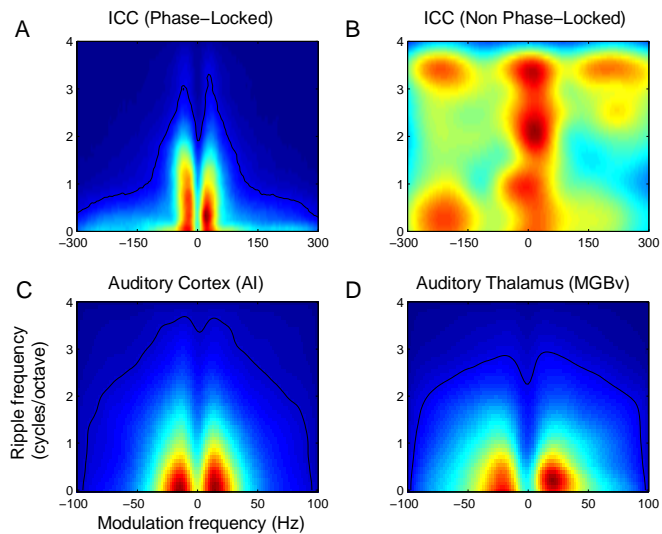


Figure 2: Population Ripple Transfer Functions (pRTF) for the ICC (A and B) , MGBv (C), and AI (D). ICC phase-locking neurons respond to a restricted range of spectral and temporal frequencies. Neurons that respond to fast modulation rates respond only to broad spectral envelopes (low ripple frequencies) whereas slow neurons respond to both narrow and broad spectral envelopes. Non phase-locking neurons respond to a wide range of spectral and temporal preferences. Cortical and thalamic neurons respond in a similar manner as for (A), however, the range of temporal modulation rates is significantly reduced. Contours designate the isomagnitude border that accounts for 95% of the pRTF energy.

Response Variability

Although the STRF description is suitable for estimating various response attributes, such as best modulation rate and best spectral envelope, it is not suitable by itself for estimating other aspects of the neuronal response. One such aspect of interest is the variability of the neuronal response. In order to quantify the variability of an individual neuron’s response to complex stimuli, we perform a second-order analysis. The first order analysis (i.e computing the STRF) is analogous to computing the mean value of a signal, whereas the second-order analysis is analogous to computing its variance.

From its definition the STRF gives us the average sound pattern that tended to evoke

action potentials. It does not tell us anything about the individual patterns of sound activity that independently activated each action potential. One possibility is that the constituent sound patterns are highly stereotyped from one action potential to another (low variability), much like the expected response pattern for a hypothetical "feature detector". An alternate possibility, is that central auditory neurons perform linear filtering on the incoming sound patterns, in which case, the spike to spike variability would be significantly higher. Although it is clear that sensory neurons won't fall explicitly at either of these two categories, it is useful to know where they lie along this continuum (from linear to feature selective).

To measure the response variability of single neurons, we perform a second-order analysis with respect to the STRF and the stimulus spectro-temporal envelope (see Fig. 3B). This is done by performing a second pass through the data in which the STRF is compared to each of the spectro-temporal sound patterns that evokes an action potential (the *pre-event sound pattern*). We ask, how similar is the STRF to each of the constituent pre-event sound patterns? To quantitatively access this, we compare the STRF and the pre-event sound pattern with the correlation coefficient or similarity index:

$$SI_k = \frac{\langle STRF, S_k \rangle}{\|STRF\| \|S_k\|}$$

where SI_k similarity index measurement for the k^{th} action potential, S_k is the pre-event stimulus envelope for the k^{th} action potential, \langle, \rangle is the dot product operator, and $\|STRF\|$ and $\|S_k\|$ are the STRF and pre-event stimulus norms respectively (i.e. their energies). This measurement provides a number from -1 to 1 for each spike. In the case that 1 is produced the STRF and pre-event sound pattern share a large degree of resemblance indicative of low variability. By comparison, a value of 0 indicates that the pre-event sound pattern and the STRF have nothing in common (high variability). By averaging over the similarity index of all spikes we can define the feature selectivity index (FSI). Theoretically we expect a value of $FSI=1$ for a hypothetical "feature detector" and $FSI=0$ for a linear integrating neuron. Thus if a value of $FSI=1$ is produced, the sound patterns that are averaged to produce the neuron's STRF are identical for each spike (low variability). Otherwise, a value of zero indicates that the pre-event sound patterns that make up the STRF are distinctly different for each spike (high variability).

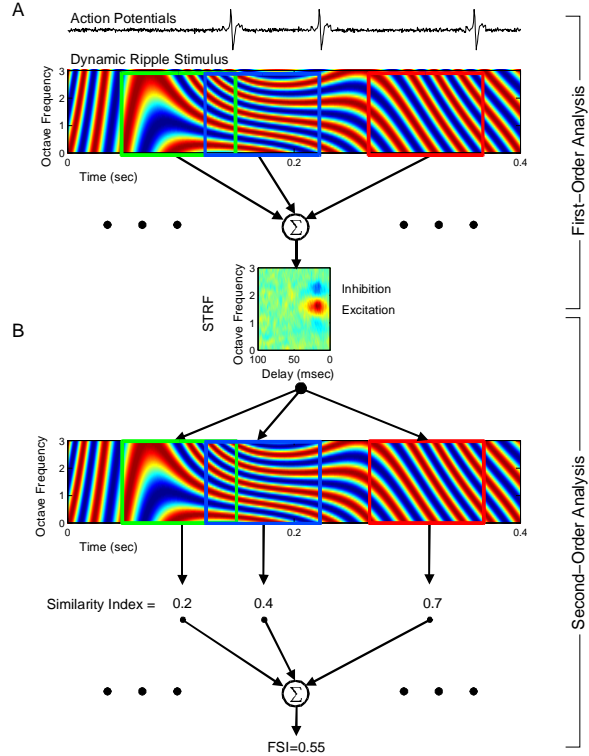


Figure 3: The spectro-temporal receptive field is obtained by averaging all sound patterns that preceded a neuronal response. These sound patterns are depicted by red, green, and blue contours for three distinct action potentials. This descriptor gives a picture of the "best" sound pattern, described along time and frequency, that tended to evoke an action potential. In order to estimate the variability of the neuron's response to a diverse repertoire of sound inputs, we perform a second-order analysis in which we compare the neuron's STRF (the average pattern) to each of the spectro-temporal sound patterns that make up the STRF (those highlighted by the colored contours). For each action potential, this comparison is performed by computing a similarity index. This measurement gives a number between -1 and $+1$, where $+1$ indicates high similarity between the STRF and the reference sound. The overall variability of the neuron is obtained by taking the average of all SIs (Low variability: $FSI=0$; High variability: $FSI=1$).

Measurements from the ICC, MGBv, and AI reveals an overall degradation in feature specificity between the inferior colliculus and auditory cortex. In the ICC two subsets of neurons are observed, one with high variability (mean population FSI=0.18) and the other with low variability (mean population FSI=0.56). The latter subset of neurons coincides precisely with those neurons that show selective enhancement for the dynamic ripple sound. This observation is consistent with the idea that these neurons are more feature selective for sound patterns that closely resemble their STRFs; whereas the first subset appears to integrate a wide range of spectro-temporal sound envelopes as expected for a linear integrator. Thalamic neurons by comparison show low and intermediate levels of response variability. Cortical neurons, surprisingly, are the most variable.

We are currently testing various models in order to explain observed response differences in the ICC, MGBv, and AI. A simple linear spectro-temporal integration model combined with a Hodgkin-Huxley spike generator accounts for several of the observed nonlinear effects. Results from our model supports our hypothesis that the selective enhancement of ICC neuron's response to the dynamic ripple sound and their low variability is attributed to the relative level of the neuron's intracellular threshold. This finding suggest that response variability is inversely proportional to the neuron's response threshold. Therefore, high thresholds are accompanied by low spectro-temporal variability whereas low thresholds are accompanied by high variability.

Conclusion

In addition to a well described reduction in following rates between ICC and AI, the presented findings further suggest that: 1) distinct neural codes are employed for acoustic feature decomposition (spectro-temporal) in the ICC, 2) these acoustic representations are not fully present in the MGBv and AI and that 3) the response variability of single neurons progressively increases from ICC to AI.