**Title**: Population coding of complex sounds in the Avian Auditory System

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**Summary**: Auditory neuroscientists have yet to describe how complex sounds are represented in the ensemble response. More generally, the role of correlations, synchrony, oscillations, traveling waves or other properties of population activity in sensory coding remain an open question. Here we attempted to characterize how populations of neurons throughout the Zebra Finch auditory system interact to process behaviorally relevant communication signals by investigating the pairwise coupling structure amongst local field potentials recorded simultaneously from multiple brain regions. We probed the avian auditory system with acoustic stimuli that span the entire vocalization repertoire of the zebra finch (alarm calls, distance calls, distress call, songs, etc) and also include synthetic noise-like stimuli. To study the population activity, we then developed a novel analysis that involves the estimation of a time varying pair-wise coherence across all simultaneously recorded sites. This approach allows us to investigate both average correlations as well as transient correlations, including those produced by waves of activities or elicited by specific stimuli. On average, we found that, as expected, the pairwise coherence declined quickly as a function of recording distance. We have, however, observed transient stimulus-driven long-range coherences including inter-hemispheric coupling. We also observed particular sites that appear to be sources and sinks of waves of correlated activity. Finally, we have quantified stimulus-dependent deviations from the average coupling, and showed that it depends on the class of vocalization used. These analyses are not only revealing to understand the functional connectivity of the system but also demonstrate the important role that a population code plays in the representation of sensory information.

## Additional Details

We recorded extracellular potentials from the auditory forebrain of the zebra finch using two 16-channel multi-electrode arrays placed one in each hemisphere. The arrays were positioned to cover much of the auditory forebrain, and electrode recording sites were determined histologically to include Field L, the avian analogue of primary auditory cortex, as well as NCM and CM, both secondary auditory areas. From each electrode we extracted local field potentials from the recordings by low-pass filtering with a cutoff frequency of 381 Hz and used this signal for all subsequent analyses.

To quantify the time-varying synchrony of the multi-electrode LFP, we computed the multi-taper coherence between all pairs of electrodes using a 167ms sliding window. The coherence represents the degree to which two signals are linearly related as a function of frequency. It is superior to a more commonly used measure such as the correlation coefficient; it is insensitive to phase shifts and does not require signals to be smoothed as a preprocessing step.

We reduced the coherence at each time point to a scalar by computing the Normal Mutual Information (NMI). If $\gamma_{ij}(t,f)$ is the coherence between electrodes i and j at time t and frequency f, the NMI is computed as:

$$N_{ij}(t) = \int log2(1-\gamma_{ij}(t,f))\,df$$

The NMI is equal to the mutual information between two signals when they are stationary, linearly related, and noise is Gaussian; it remains a useful measure even when those assumptions are violated.

After integrating across the frequency axis to compute the NMI, we are left with the time-varying symmetric 32x32 matrix indexed by $N_{ij}(t)$. A video illustrating transient long range coherence and spatially propagating waves can be viewed at:

http://www.youtube.com/watch?v=9EL-33kjNH8

The video demonstrates many properties of note, including transient long range coherence and spatially propagating waves of synchronous activity.

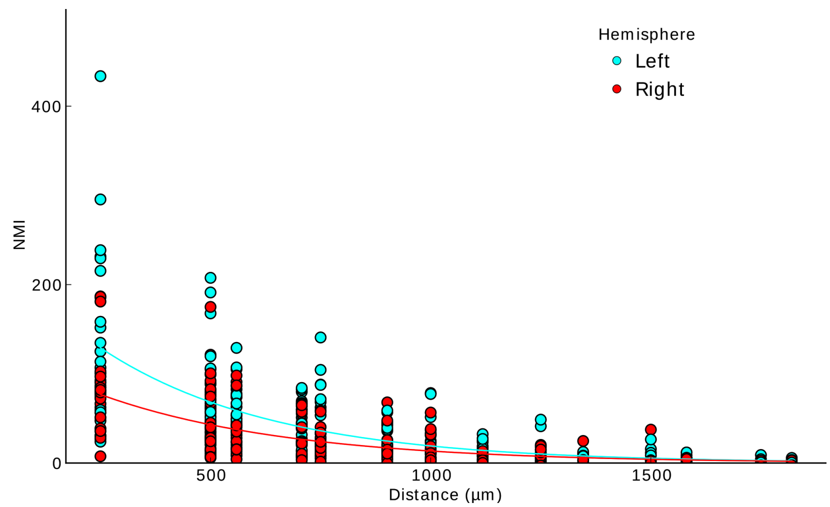


**Figure**: Within hemisphere, coherence falls quickly with distance. The x-axis labels the distance between two given electrode pairs, and the y-axis gives the overall mean NMI between the two. For this particular site, the left hemisphere decayed with a space constant of 430 $\mu m$, the right with 392 $\mu m$.

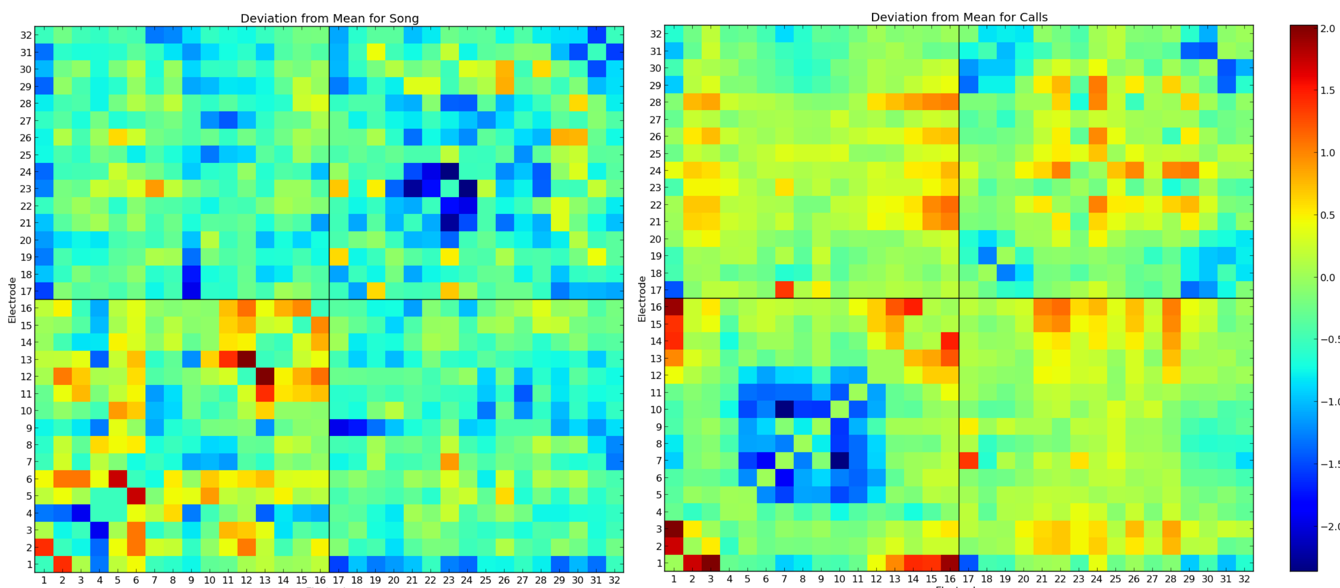


**Figure**: The stimulus-dependent coupling structure differs by call type. For each stimulus, we averaged the coupling structure across repeated trials, and then averaged over the peri-stimulus duration to compute an overall mean coupling matrix per stimulus. We then averaged mean coupling matrices across stimuli within vocalization type (“Song”, “Calls”). Finally, we subtracted off the grand mean NMI matrix across all time to produce the difference from the average coupling. In the plots above, element i,j of a matrix is the average change in pairwise coupling between electrode i and j due to presentation of a songs (left) or calls (right). Electrodes 1-16 are on the left hemisphere and electrodes 17-12 on the right hemisphere.  Color scale shows the difference from average mutual information in bits.