http://github.com/mschachter/cosyne2014_poster

Characterizing Local Field Potential Synchrony in the Avian Auditory System

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*Designed and performed the experiments

Introduction

Abstract

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.

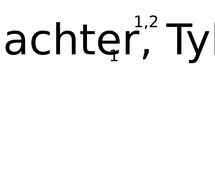
Electrophysiology and Stimuli

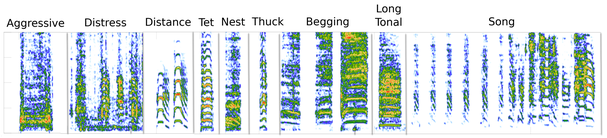
*Experiments were designed and executed by **Julie Elie**.*

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 over sites determined histologically to include Field L, NCM and CM, both primary and secondary auditory areas.

The electrodes are shown in a schematic to the bottom right. Rows were spaced apart 250 microns, while columns were 500 microns apart.

Under urethane anaestesia, sounds from the entire vocal repertoire of the Zebra FInch were randomly interleaved and played, with 10 repeats per sound.





Methods

Sound Amplitude Envelope Construction
For each sound, we extracted the stimulus amplitude envelope from the sound pressure waveform. This was accomplished by full-wave rectification of the sound pressure waveform, followed by low-pass filtering the rectified signal with a cutoff frequency of 200Hz. Then a logarithm transform was applied to the envelope, converting it into units of decibels.

LFP Preprocessing
As noted in the previous section, the LFPs had a sample rate of 381Hz. The LFP was z-scored; the mean across time was computed, subtracted off, and then the waveform was divided by the standard deviation computed over time. We computed spectrograms using a sliding Gaussian window with a width of 150ms. For visualization, a logarithm transform was applied to the spectrum, and values less than the 10th percentile of the overall power distribution across the entire spectrogram were eliminated.

Stimulus Encoder
Within an electrode, the LFP was averaged across presentations. We only used song stimuli. We built a linear filter model that mapped the temporal history of stimulus log amplitude envelope to the LFP. We allowed for a total filter length of 500ms, and used an implementation of LASSO linear model fitting implemented in the SPAMS toolbox.

To prevent overfitting, we used 5-fold cross validation, which means that we partitioned the data into 5 roughly equal folds, and fit 5 different models, each trained on a different 4/5 of the data. The filters illustrated in the next section are averaged across folds, and the correlation coefficient was computed on the held-out data for each fold, then averaged to produce the performance noted in the next section.

Coherence
The coherence is a symmetric measure of correlation between two time series that is a function of frequency. We computed the coherence between all pairs of electrodes for a given site. For each pair, we first computed the complex spectrogram of each LFP. For each frequency band, we computed the coherence at that frequency band, for each time point, as the weighted mean of the normalized cross-spectrum:

$$\gamma^2(t,\omega) = \frac{|\sum_{k=-\Delta t}^{k+\Delta t} h(k) S_1(k,\omega) S_2^*(k,\omega)|}{\sum_{k=-\Delta t}^{k+\Delta t} S_1(k) S_1^*(k) \sum_{k=-\Delta t}^{k+\Delta t} S_2(k) S_2^*(k)}$$

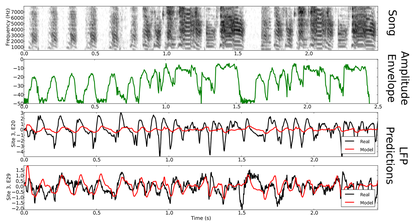
To remove the effects of spurious coherence due to auto-correlations, we computed a coherence "floor" by shuffling indices in one signal and recomputing the coherence. We then repeated this process with the other signal, and averaged the coherence. This process was repeated 150 times, and produced an estimate of the mean and standard deviation of the coherence floor. The mean floor was subtracted from the coherence, and any values below two standard deviations were zeroed out.

To summarize the coherence between an electrode pair, we integrated over frequency at each time point to produce a quantity called the Normal Mutual Information (NMI):

$$NMI(t) = \int_0^{\omega_{max}} 1 - log_2(\gamma^2(t,\omega)) d\omega$$

Analysis and Results

Regional Variability in Stimulus Encoding



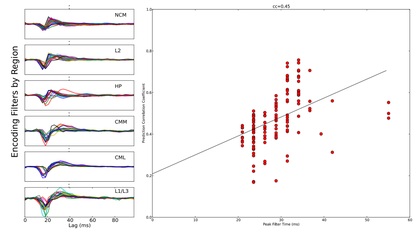
LFP is Strongly Correlated to Sound Amplitude Envelope
We fit linear models that predicted each trial-averaged LFP from the stimulus amplitude envelope.

The top subplot shows a spectrogram for a Zebra Finch song used as a stimulus. The green trace is the log amplitude envelope of the song.

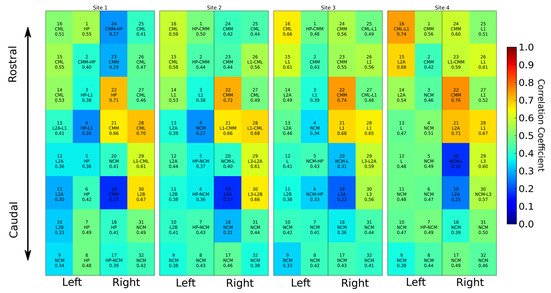
The black traces in the bottom two subplots are two trial-averaged LFPs from different electrodes. The red trace shows predictions of the encoder model.

Encoder Performance is Correlated with Filter Time-of-Peak
The first plot to the right shows the raw encoding filters grouped by region. The regions are ordered by mean time-of-peak, with NCM being having the shortest and L1/L3 having the longest.

The time-of-peak is strongly correlated with encoder model performance, as shown with second plot to the right.

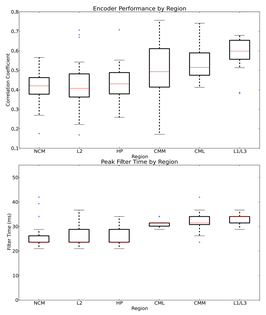


Encoder Performance by Site, Hemisphere and Anatomical Region



Encoder Performance and Time-of-Peak Varies with Region
The first upper subplot on the right is a box-and-whisker plot of encoder performance by region. NCM and L2 have the worst performance, while L1/L3 has the best.

The bottom subplot is a boxplot of filter time-of-peak by region. NCM has the shortest time-of-peak and L1/L3 the longest.

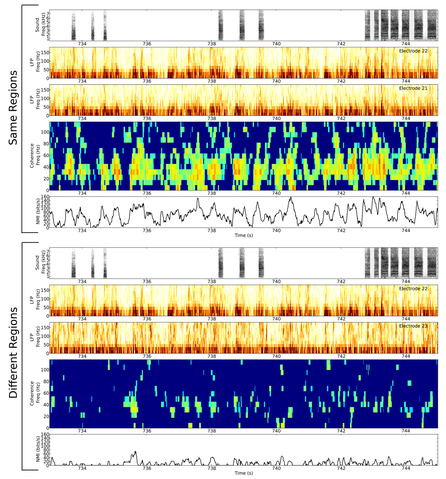


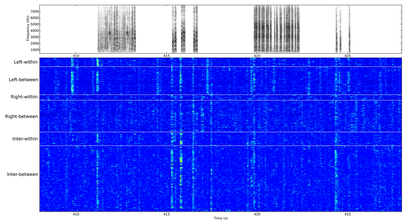
Global and Regional Synchrony

The Coherence was used to Measure Pairwise Synchrony
The plot to the right shows, from top to bottom, the stimulus spectrogram, the spectrogram of two LFPs, their coherence, and the normal mutual information, a summary quantity of the overall coherence across frequency.

The top pair illustrates strong coherence between adjacent electrodes in the same region.

The bottom pair illustrates much weaker coherence between adjacent electrodes in different regions.





Strong Global Coherence for Syllable Onsets
The color plot to the right illustrates the time-varying NMI for all electrode pairs. The pairs are separated by hemisphere and regional-connectivity; "within" sections indicate that the pairs are within-region, "between" indicates between regions.

There are strong stimulus-driven increases in coherence during the onset of song syllables. This may serve as a "phase-resetting" mechanism to ensure that the entire auditory network is phase-locked to an ongoing stimulus.

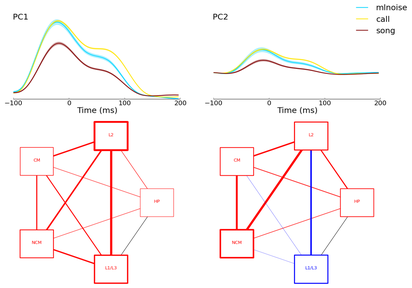
Inter-region Onset Synchrony Varies by Stimulus Class
To do this, we aggregated 32x32 time-varying electrode connectivity matrix to form a 5x5 time-varying regional connectivity matrix.

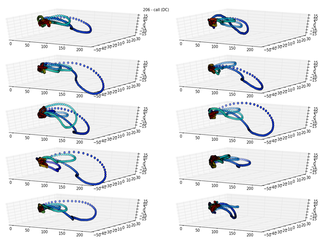
We then applied PCA to these regional connectivity matrices restricted to 100ms before and 200ms after the onset of each sound.

The top subplots show the PCA-projected time course of NMI for each of 3 stimulus classes. The bottom subplots show the PCs themselves.

PC1 shows an increase in coherence between regions, particularly L2, L1/L3 and NCM. The top subplot illustrates that this increase is greater for mlnoise and calls than for song.

PC2 shows a weaker module where coherence is lower in L1/L3. Song stimuli show much weaker changes in coherence than either calls or ml noise





Initial Exploration of Trial-by-trial Variation
We ran a different PCA on the 32x32 time varying NMI matrix and projected the onto the first 3 PCs for visualization.

The plot to the left shows 10 trials of a single distance call, and the PC-projected time-varying activity of the NMI. The color represents time, with blue being early in the stimulus, and red being late.

The onsets of each syllable in the distance call are evident as large deviant loops within a trial.