Breaking Down the Cortical Representations of Speech in LFP and MUA

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What's LFP?

Extracellularly recorded neuronal activity can be divided into two components. The high frequency component, multi-unit activity (MUA), contains spiking activity. The low frequency component, local field potential (LFP), is related to dendritic activity but its physiological origins are still unclear. The low frequency component can be recored using not only penetrating electrodes but also electrocorticography (ECoG), electroencephalography (EEG) and magnetoencephalography (MEG). Here, the response properties of LFP and MUA are characterized using speech stimuli. We investigate the functional dissociations of different components of LFP and how they may be related to the signal obtained from other recording methods.

Stimuli & Data Analysis

Stimuli: 30 three-second duration sentences from the TIMIT database, presented contralaterally to the recording site.

Electrophysiological activity was recorded from primary auditory cortex (AI) of awake, passively listening, adult female ferrets (11 animals, 477 recording sites) using high-impedance tungsten electrodes (1.0 MΩ).

The spectro-temporal receptive fields (**STRF**), were estimated by boosting (David et al. 2007) based on the MUA and LFP responses to speech.

Phase-locked Response: the LFP response (< 600 Hz) averaged over trials.

Non-phase-locked Response: the single-trial LFP response, after the phase-locked response is removed. The **power of non-phase-locked response** is extracted after the response is filtered into narrow frequency bands.

MUA: the power of neural recording filtered between 600 and 3000 Hz.

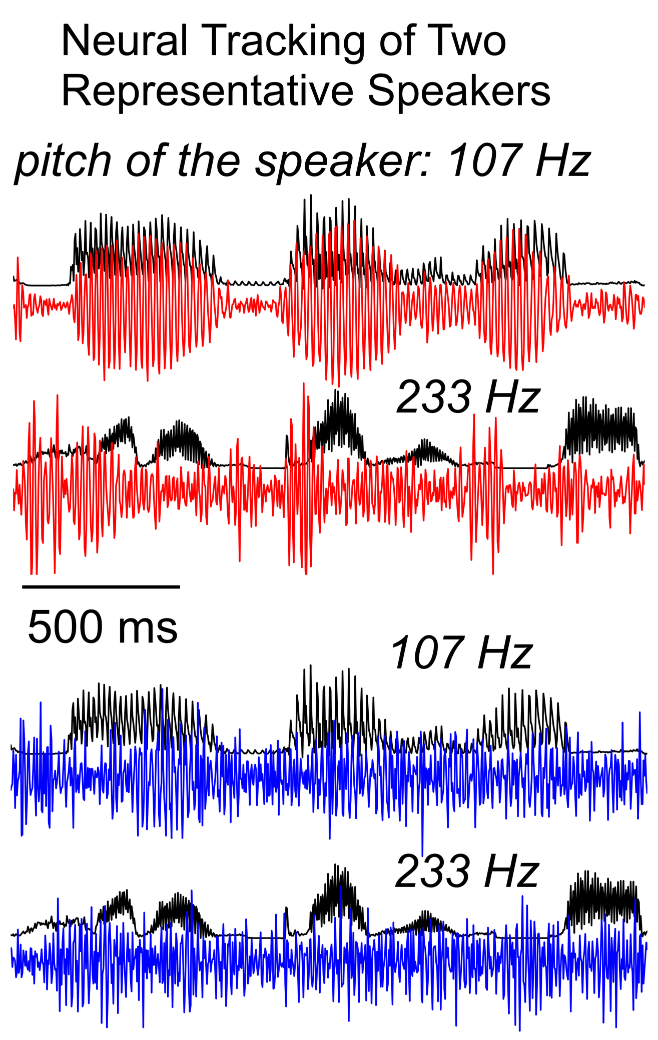
A comprehensive model for phase-locked LFP

$LFP(t) = STRF(t) * Stimulus(t) + H_1(t) * MUA(t) + H_2(t) * LFP(t-1) + e(t)$.

The model has 3 components: 1) stimulus (sub-cortical input), 2) interactions between LFP and MUA, and 3) properties of recurrent cortical networks.

Phase-Locked LFP (Fast or Slow?)

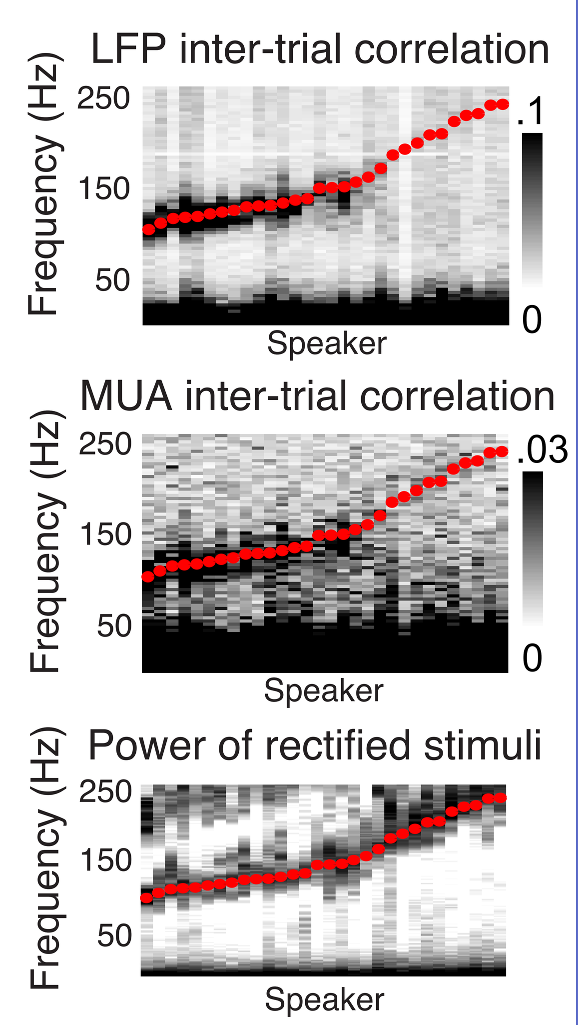
The neural phase locking to amplitude modulated (AM) sound breaks down below 30 Hz for single unit activity but remains at ~100 Hz for ECoG and MEG. Here, we examine this discrepancy by comparing MUA and LFP recorded from the same electrode.



Left: Examples of LFP and MUA responses to two speakers.
Red: LFP
Blue: MUA
Black: envelope of stimulus speech

Right: The peak response frequency matches the mean pitch of each speaker (red dots).

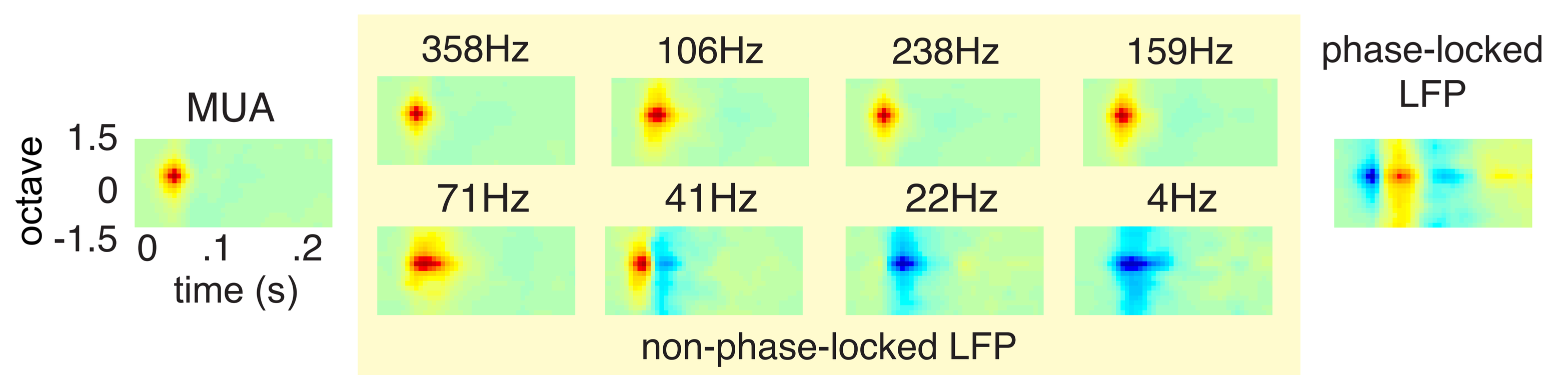
LFP but not MUA can phase lock to fast modulations near 100 Hz. The LFP phase locking breaks down at ~150 Hz.



The fast phase-locked component of LFP (70-150 Hz) may reflect thalamic input and is not well preserved in spiking activity in AI.

Spectro-temporal Tuning of for MUA, Phase-Locked and Non-Phase-Locked LFP

Spectro-temporal Receptive Fields (STRF) are estimated from MUA, phase-locked LFP (mean over trials), and the non-phase-locked power of LFP in several frequency bands (inter-trial variance in narrow frequency bands).



The figure above shows the STRF averaged over recording sites, where the best frequency (BF) of each STRF is aligned before averaging.

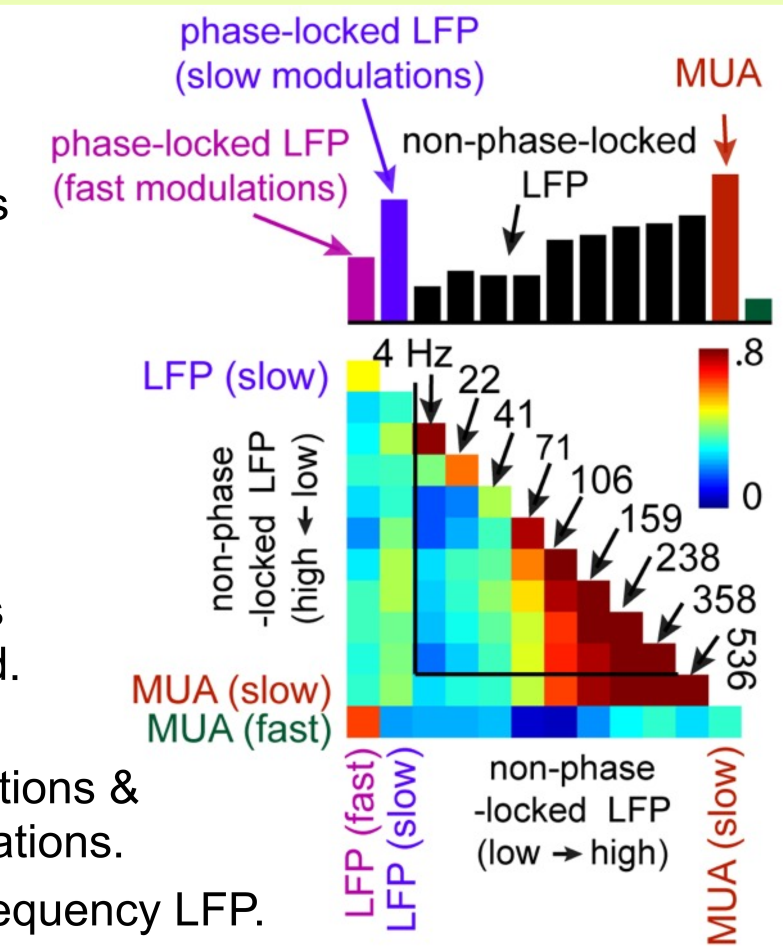
Frequency-specific stimulus features **enhance** MUA and non-phase-locked power of high frequency LFP (> 70 Hz) but **suppress** non-phase-locked power of low frequency LFP (<20 Hz). The phase-locked LFP lasts long and oscillates.

MUA and non-phase-locked fast LFP have a excitatory average STRF. Non-phase-locked slow LFP have a inhibitory average STRF. Phase-locked LFP shows an oscillatory STRF.

The *predictive power* is the correlation between the STRF prediction and actual neural response. It reflects how well the neural response encodes stimulus features (in a linear way).

The bar graph shows the mean predictive power of STRFs derived from different neural measures.

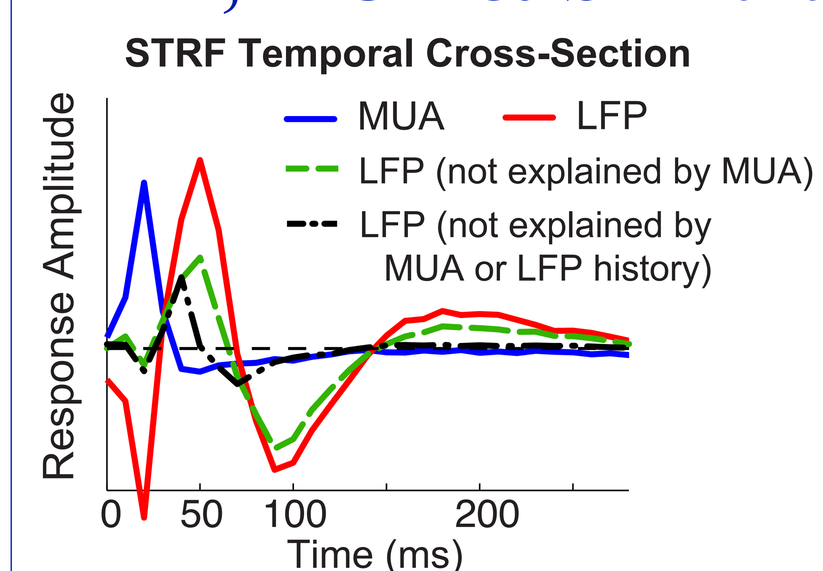
The matrix shows the cross-correlation of the predictive power of different STRFs. The encoding of fast and slow modulations in LFP and MUA are separately considered.

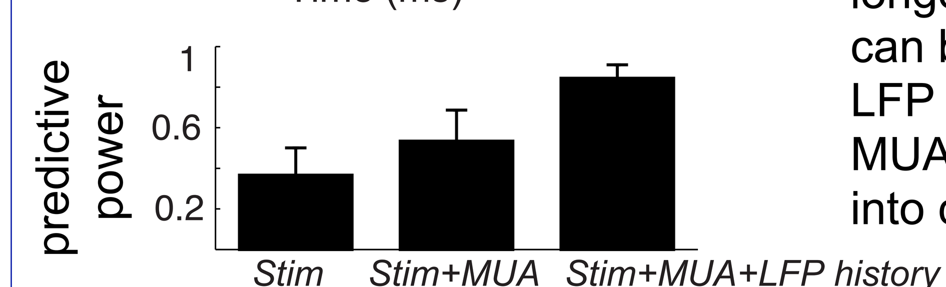


Highly correlated neural measures:
LFP phase-locked to fast temporal modulations & MUA phase-locked to fast temporal modulations.

MUA & non-phase-locked power of high frequency LFP.

LFP, MUA & Stimulus Encoding





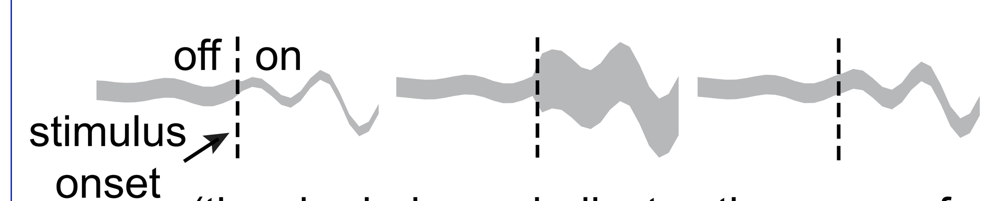
STRFs are derived for the LFP and MUA response to slow temporal modulations (<50 Hz). The temporal cross-section of STRF (STRF summed over frequency), averaged over sites, shows that the MUA response ceases in 50 ms but LFP response lasts ~200 ms.

The short latency (~20 ms) component of LFP can be explained by MUA. The longer latency (~100 ms) component can be explained by the history of LFP. LFP signal is better explained when MUA and the history of LFP are taken into consideration.

In contrast to the phasic MUA activity, the LFP in AI lasts more than 200 ms, which may reflect properties of recurrent cortical networks.

Stimulus-Related Change in LFP Power

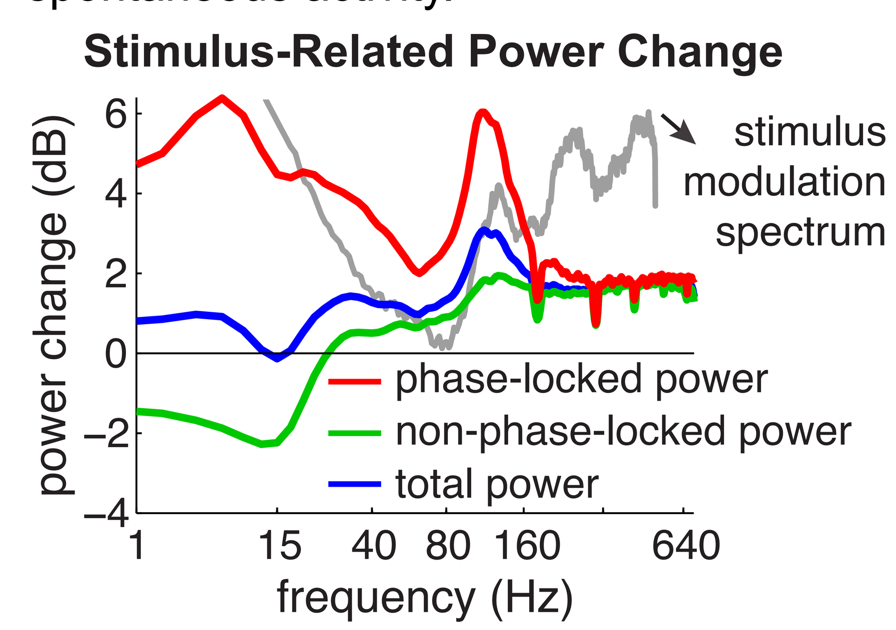
The power of neural activity can be divided into a phase-locked component (the power of the response averaged over trials) and a non-phase-locked component (variance over trials), i.e. $E(X^2) = E(X)^2 + Var(X)$.



A stimulus may decrease, increase or not change the variance of neural activity.

(the shaded area indicates the range of responses measured over trials.)

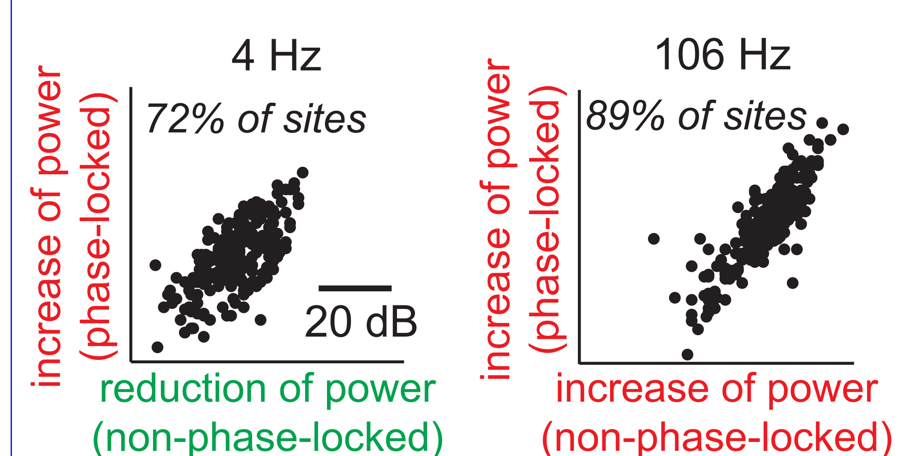
The non-phase-locked power, i.e. variance, of LFP, should
1) *not change*, if the stimulus evokes a perfectly phase-locked response independently of spontaneous activity;
2) *increase*, if the stimulus evokes a loosely phase-locked activity;
3) *decrease*, if phase-locked activity is generated by resetting the phase of spontaneous activity.



The *stimulus-related power change* is the difference between the long-term power before and after the stimulus starts.

The LFP response to speech has distinct phase-locking properties in low (<40 Hz), middle (100-150 Hz), and high (>160 Hz) frequency regions.

Phenomenologically, activity in the 3 frequency regions shows phase-resetting, loose phase locking, and no phase locking.



Scatter plots of stimulus-related changes in phase-locked and non-phase-locked power for recording sites showing a decrease (increase) in the non-phase-locked power of low (high) frequency LFP. The changes in phase-locked and non-phase-locked power are correlated.

Conclusions:

Based on the similarities between spectro-temporal response properties, neural signals recorded from AI can be divided into at least four components, some of which may relate to other recording modalities.

1st: LFP phase-locked to fast temporal modulations (70-100 Hz) thalamic input *(ECoG, MEG, EEG)*

2nd: The earliest component of the LFP response to slow temporal modulations (<50 Hz) thalamic input?
MUA AI spiking
Non-phase-locked power of LFP above 100 Hz same as MUA? *(ECoG)*

3rd: Long latency phase-locked LFP feedback? oscillations? *(ECoG, M/EEG)*

4th: Non-phase-locked power of LFP below 70 Hz not spikes

The phase-locked LFP is better modeled by not only considering the stimulus but also the MUA from the same site and the history of LFP, which suggests nonlinearities in neural encoding and the influence of network dynamics.

References: David, Mesgarani & Shamma, Network: Comput. Neural Syst. 2007
David, Mesgarani, Fritz & Shamma, J. Neurosci. 2009

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