Breaking Down the Cortical Representations of Speech in LFP and MUA

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How are auditory stimuli represented in LFP and MUA?

Local field potential (LFP), the low frequency component of extracellular recordings, is closely related to neural measures commonly available for human subjects, such as EEG and MEG. Therefore, the LFP provides a valuable bridge between single-unit animal and non-invasive human neurophysiology.

Here, we characterize the spectro-temporal tuning of LFP and multi-unit activity (MUA) recorded from ferret primary auditory cortex (A1) using natural stimuli and compare in particular their spontaneous versus stimulus-evoked dynamics.

Stimuli, Neural Recording, and Terminology

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

Electrophysiological activity was recorded from primary auditory cortex (A1) of awake, passively listening, adult ferrets (11 animals, 477 recording sites) using high-impedance tungsten electrodes (1-4 MΩ). MUA was defined as the time-varying power of neural recording between 600 and 3000 Hz, and LFP was analyzed in several bands below 300 Hz. Spectro-temporal receptive fields (STRFs) were estimated from the speech response by boosting (David et al, 2007).

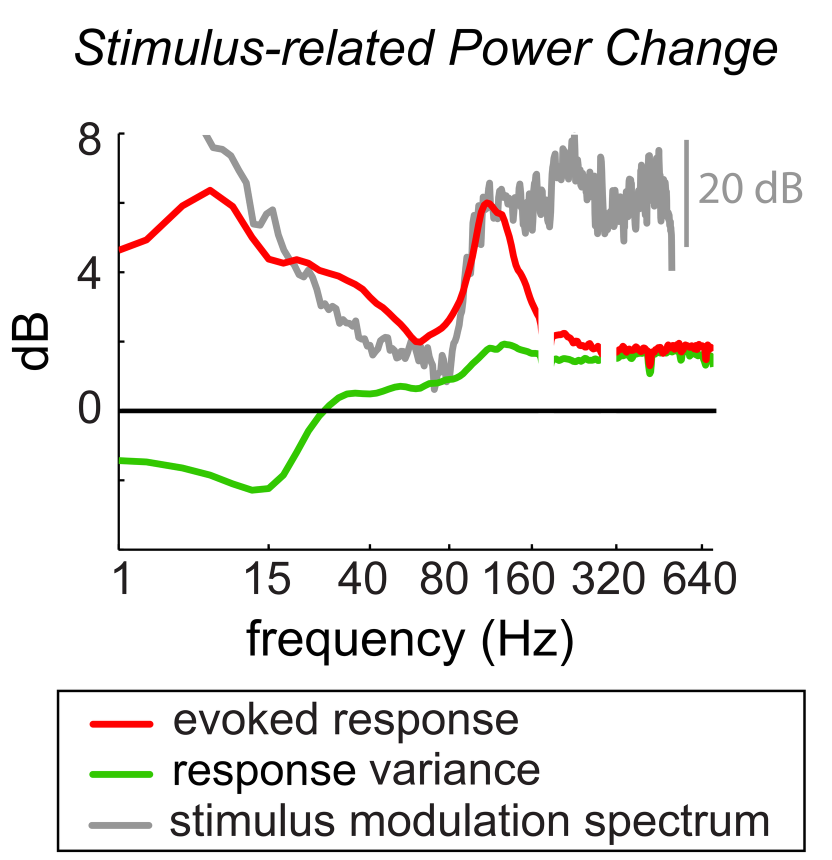
The evoked response is the neural activity over trials (i.e. presentations of the same stimulus). **The response variance** is its variance over trials. The response variance is also called the ***induced power***, i.e. the power of induced activity, which is the difference between the response in single trials and the evoked response.

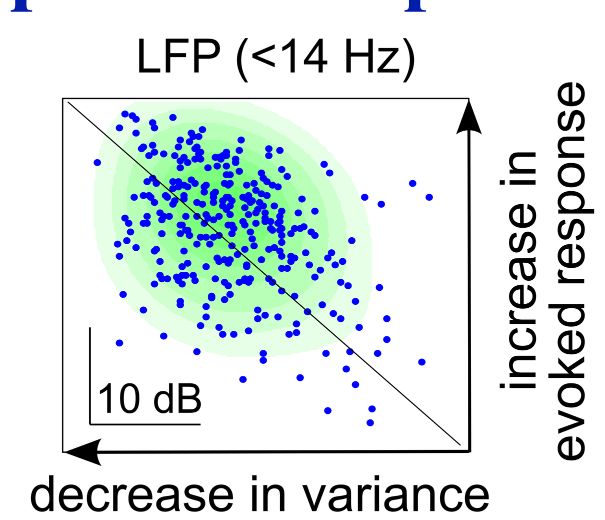
Mathematically, for a neural response $X(t)$, the *evoked response* is $E(X(t))$ and the *induced response* is $X(t) - E(X(t))$, where E() denotes the expectation or mean operation. The variance of $X(t)$ is exactly the power of the induced response, i.e. $Var(X(t)) = E([X(t) - E(X(t))]^2)$.

possible patterns of stimulus-related changes in response variance

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

LFP Response to Speech: Spectral Properties





The low-frequency LFP (<14 Hz) in 79% of the recording sites shows a stimulus-related decrease in response variance. For these sites, the amount of decrease in response variance is correlated with the strength of the evoked response ($R = 0.45$).

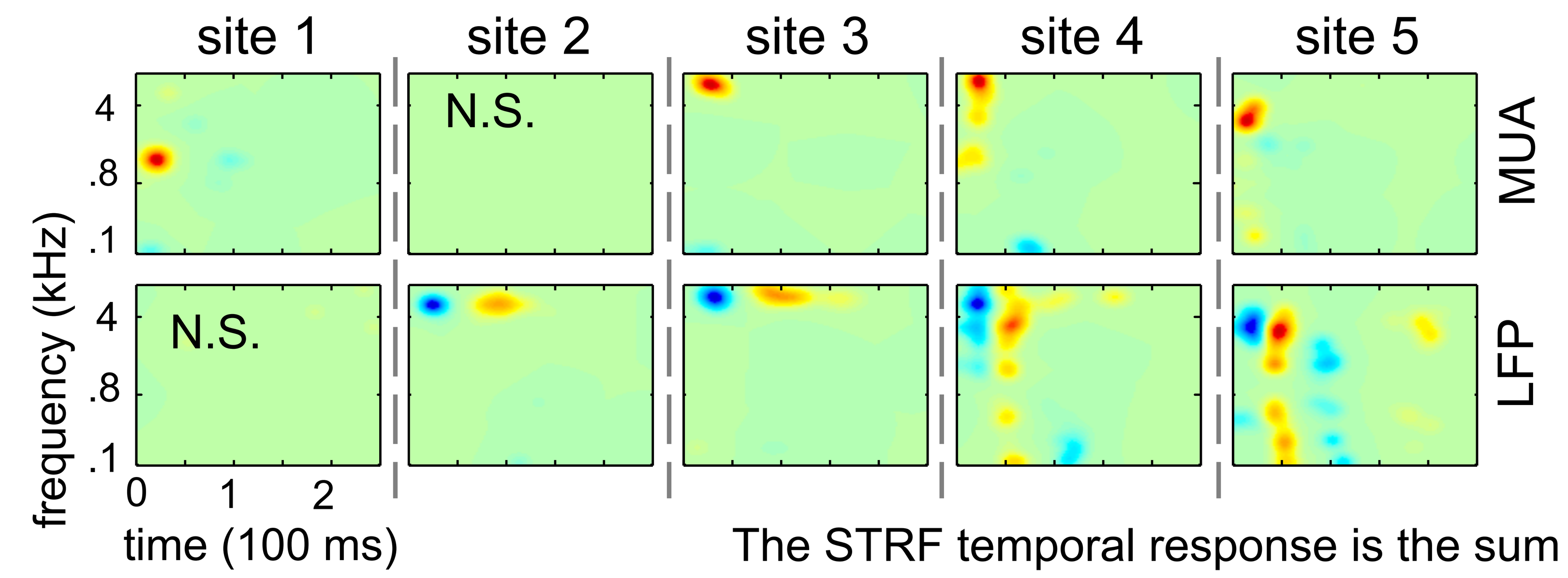
The stimulus reduces the inter-trial variance of low-frequency LFP (<15 Hz) but increases the inter-trial variance of high-frequency LFP (> 40 Hz).

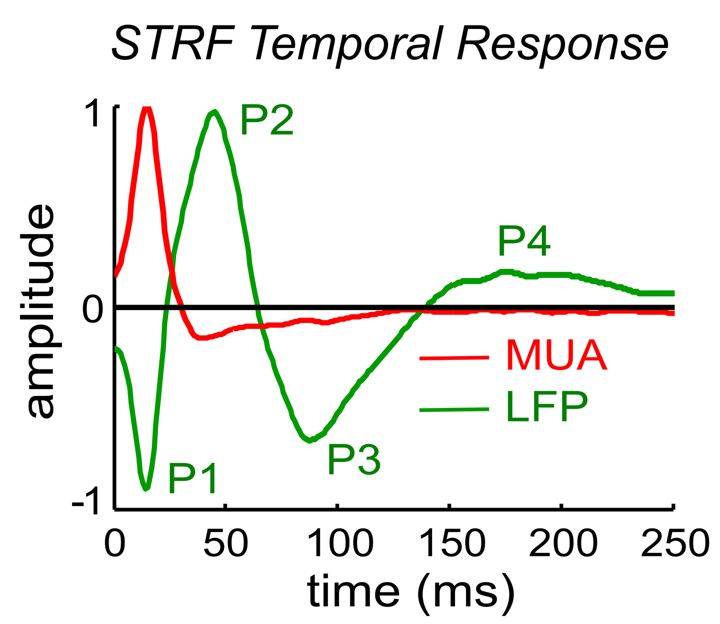
The anti-correlated increase in evoked response and reduction of response variance observed in low-frequency LFP channels is evidence in support of a phase resetting theory: the stimulus-driven LFP response is at least partly converted from ongoing spontaneous LFP.

Auditory stimuli do not only evoke phase-locked LFP responses but also reduce the variance of ongoing low-frequency LFP activity.

STRFs for MUA and Evoked LFP

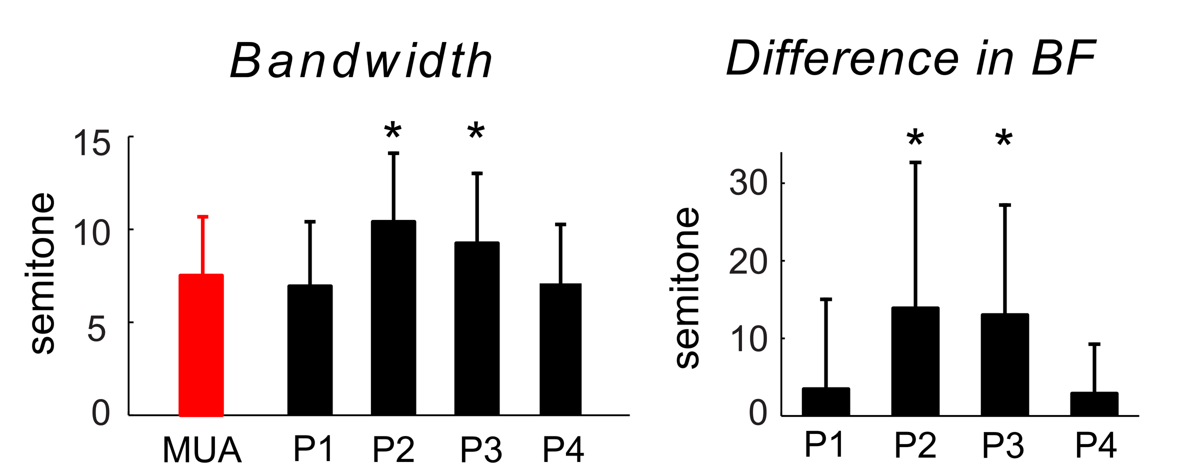
Examples of STRFs for MUA (upper) and evoked LFP (lower).





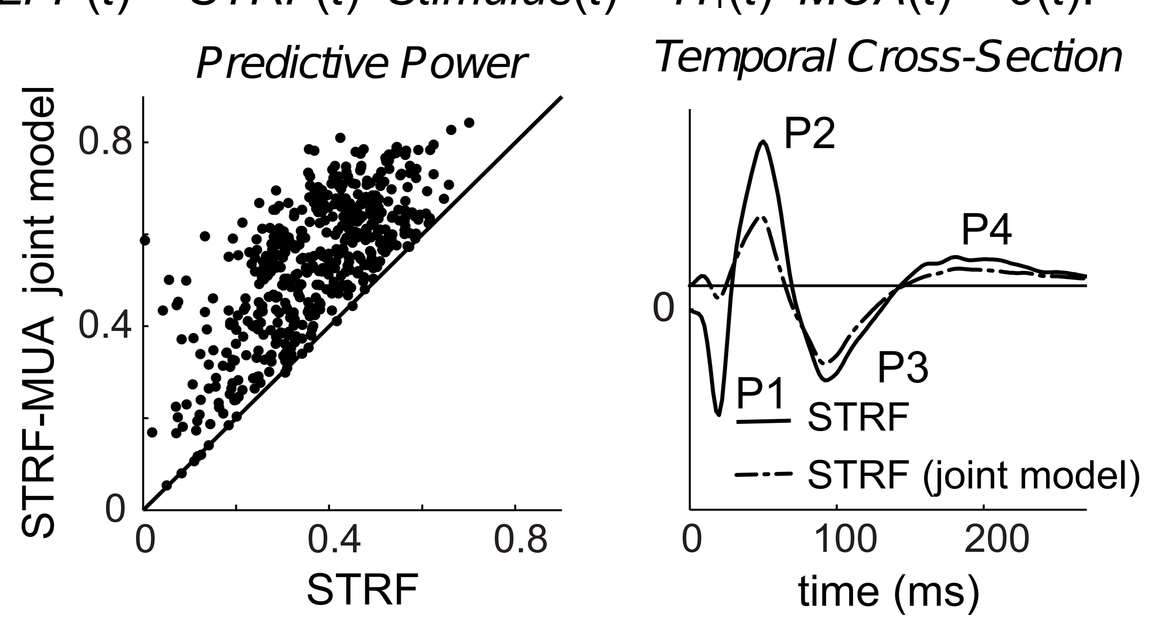
The STRF temporal response is the sum of the STRF over frequency. The averaged MUA temporal response is dominated by a single excitatory peak, while that of the evoked LFP oscillates through four peaks (P1-P4) and lasts for more than 200 ms. The first peak of LFP STRF has a BF and bandwidth similar to the MUA STRF.

The **predictive power** is the correlation between STRF predicted response and actual response, calculated using cross-validation. The predictive power of MUA and LFP STRFs is moderately correlated across recording sites ($R = 0.43$).



The STRF for evoked LFP shows tends to have multiple peaks over time, with only the first peak similar to that of the MUA STRF.

The STRF model explains the LFP response using only the stimulus. Here, we also consider a model that explains the LFP response using both the stimulus and MUA from the same site. This joint model can be expressed as $LFP(t) = STRF(t)*Stimulus(t) + H_1(t)*MUA(t) + e(t)$.



Compared with the pure STRF model, the STRF estimated from the joint model shows essentially no P1, a reduced P2, but almost the same P3 and P4.

The MUA can explain short-latency but not long-latency LFP responses to a sound stream.

References: David, Mesgarani & Shamma, Network: Comput. Neural Syst. 2007
David et al., J. Neurosci. 2009; Ding & Simon, J. Comp. Neurosci. 2012; Kayser, Neuron 2009

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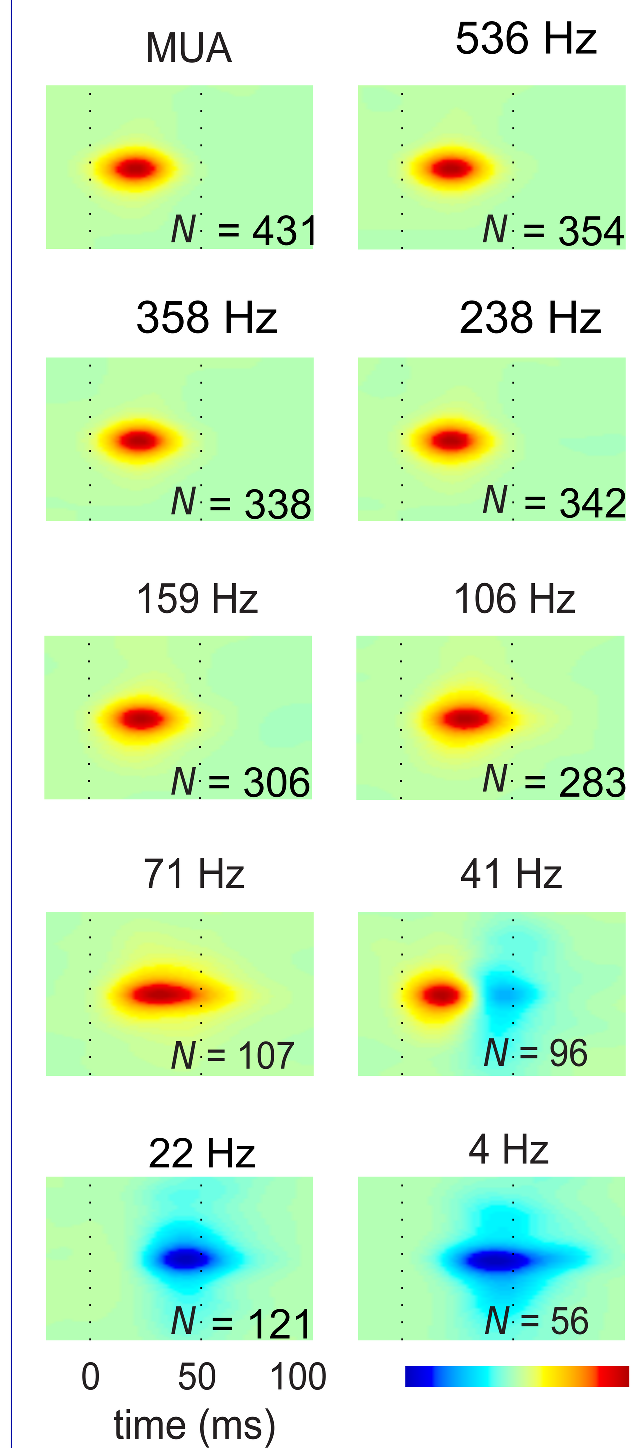
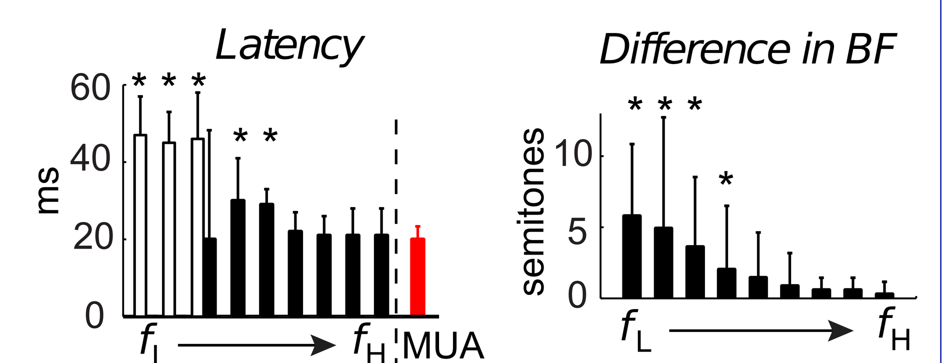
STRFs for LFP Response Variance

STRFs were also estimated based on the variance of the neural response in different frequency bands.



The STRFs averaged over all recording sites with predictive power >0.2 for each band are shown on the left (# of sites shown on each STRF). Each STRF was aligned based on its best frequency (BF) before averaging.



The variance based STRF is excitatory for LFP > 70 Hz, but inhibitory for LFP < 20 Hz.

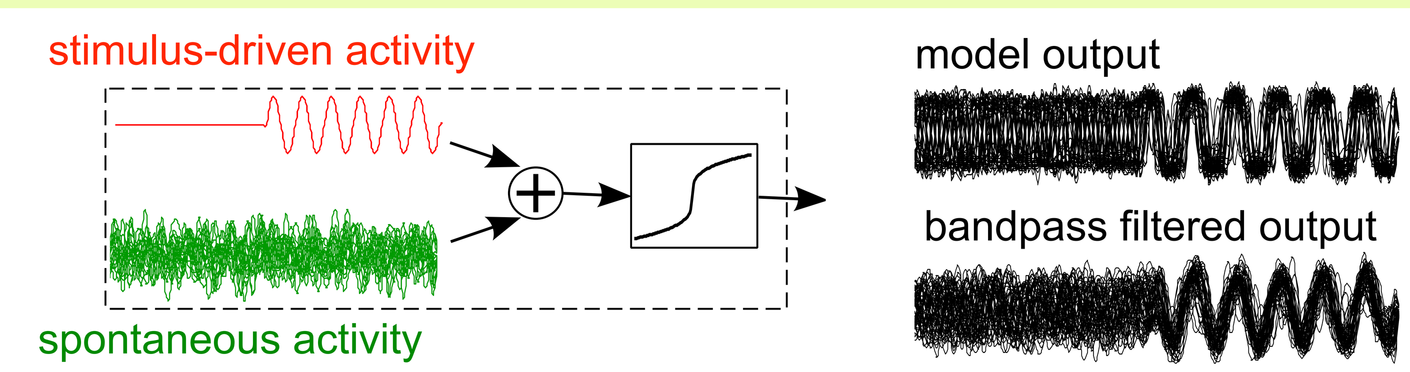
The latency of the MUA STRF is similar to the STRF latency for LFP > 150 Hz, but much shorter than the latency of the inhibitory STRF observed for LFP < 70 Hz.

The BF of the MUA STRF is also similar to the STRF BF for LFP > 150 Hz.

The spectro-temporal tuning of high-frequency LFP (>150 Hz) and MUA is similar. The decrease in variance for low frequency LFP (<40 Hz) reflects suppression with different tuning than the MUA.

A Schematic Model for "Phase Resetting"

The stimulus-related reduction of response variance is evidence for a phase resetting theory. In the following, however, we show that **phenomenological phase resetting may not indicate a direct relationship between stimulus-driven and spontaneous activity.**



In this model, the neural response is a linear summation of spontaneous activity and stimulus-driven activity, which are here independent of each other. However, due to the limited dynamic range of neuronal circuits, characterized by a static compressive nonlinearity, the summed response appears as what is predicted by the phase resetting theory.

Conclusions

MUA signals are strongly correlated with short-latency evoked LFP and high-frequency LFP response variance. The remaining components of the LFP must be explained by network dynamics other than local spiking.