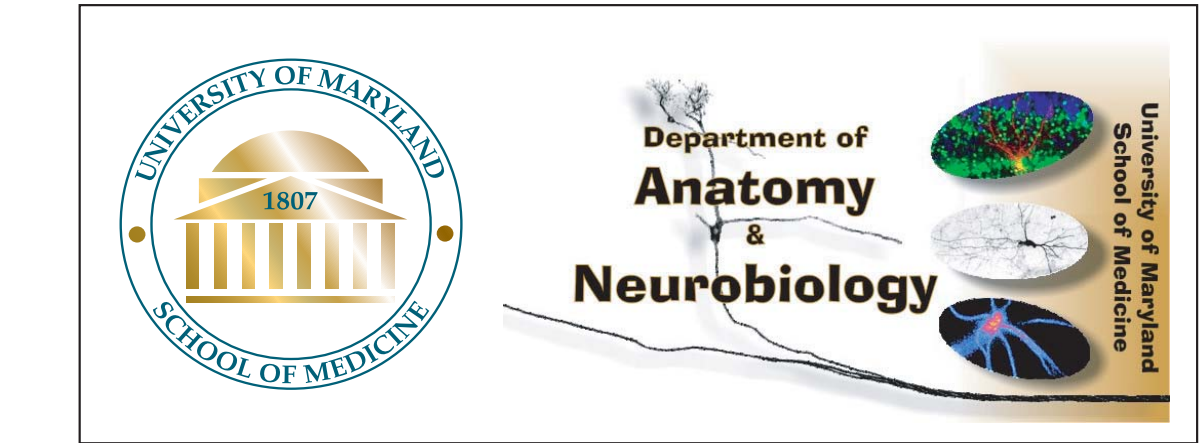


A Simple Extension To The STRF That Accounts For Rate-Level Non-Linearities

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Abstract

The spectrotemporal receptive field (STRF) has been used as a linear characterization of auditory neuronal responses. It is often derived from spike rates as a function of complex sounds or dynamic moving ripple (or auditory grating) stimuli with modulation depths greater than the neuron's dynamic range. Classic STRF computation assumes a completely linear relationship between deviations of the stimuli from a mean level and a unit's response. Real-world neurons, however, often show dramatically non-linear rate-level functions (e.g., saturation or contrast-selectivity), that disrupts the classic STRF's linearity assumption. We propose a simple extension to the STRF that additionally models level-specific characterizations of neural responses. This new STRF allows for richer neural characterization and prediction (e.g., to stimuli of different contrasts). We apply this new STRF to example cells from inferior colliculus and auditory cortex recorded in awake ferret (*Mustela putorius*).

Introduction

In the standard linear STRF model, neurons in the auditory pathway are modeled as sets of linear filters. Although a simple model, it has proved to be remarkably effective in a variety of applications -- capturing as much as 85-90% of a cell's response. However, there are times when this linear model fails, sometimes dramatically.

The linear STRF model predicts a constant scaling of any input. In particular, an arbitrarily high input results in an arbitrarily large response. Similarly, for arbitrarily small inputs, there is no lower bound on firing rate. However, real-world neurons have a maximum firing rate, and they can not fire at negative rates. One possible non-linearity is a neuron's rate-level function.

We propose two extensions to the linear STRF model that introduce non-linear functions. Using data obtained from recordings in inferior colliculus and auditory cortex of the awake ferret, we compare the power of the validation and predictions made by the three models.

Neurophysiology

Ferrets were surgically implanted with chronic multi-electrode microdrives, with electrodes positioned in the central nucleus of inferior colliculus (ICC) or in primary auditory cortex (AI). Electrodes were tungsten (1-6 MOhms, Microprobe). After recovery, animals were tested approximately daily.

During recordings, ferrets were awake and restrained. Alertness was monitored and treats provided between stimulus sessions to sustain wakefulness. Sessions ended when animal became too restless or when isolated units were lost. Typical recording sessions lasted 1-3 hours.

Extracellular activity was digitized on all electrode channels. Possible spikes for each channel were identified initially with peak threshold criteria, then sorted off-line (MClust and Klustakwik). For the purposes of this analysis, spike sorting was done conservatively.

Stimuli

Neurons were probed with dynamic ripples or TORCs (Temporally Orthogonal Ripple Combinations) to estimate STRFs as described previously by Klein et al. (2000). Densities ranged between -2 and 2 cycles/octave for both ICC and AI. Velocities ranged from 8 to 48 Hz for ICC, and 4 to 32 Hz for AI. Mean levels were generally around 50 dB SPL. Except for the final prediction trials, contrasts (modulation depths) were 60 dB on a log intensity scale for ICC recordings using single ripples (corresponding to 99.8%), or 90% linear modulation for TORCs in either ICC or AI.

Waveforms were generated through Matlab and a Tucker Davis Technologies RX6 DSP processor. Stimuli were presented from an overhead speaker (Manger Transducers), about 1 meter at zenith from the animal's head. SPL calibrations were made with a microphone placed approximately where the animals' heads would be.

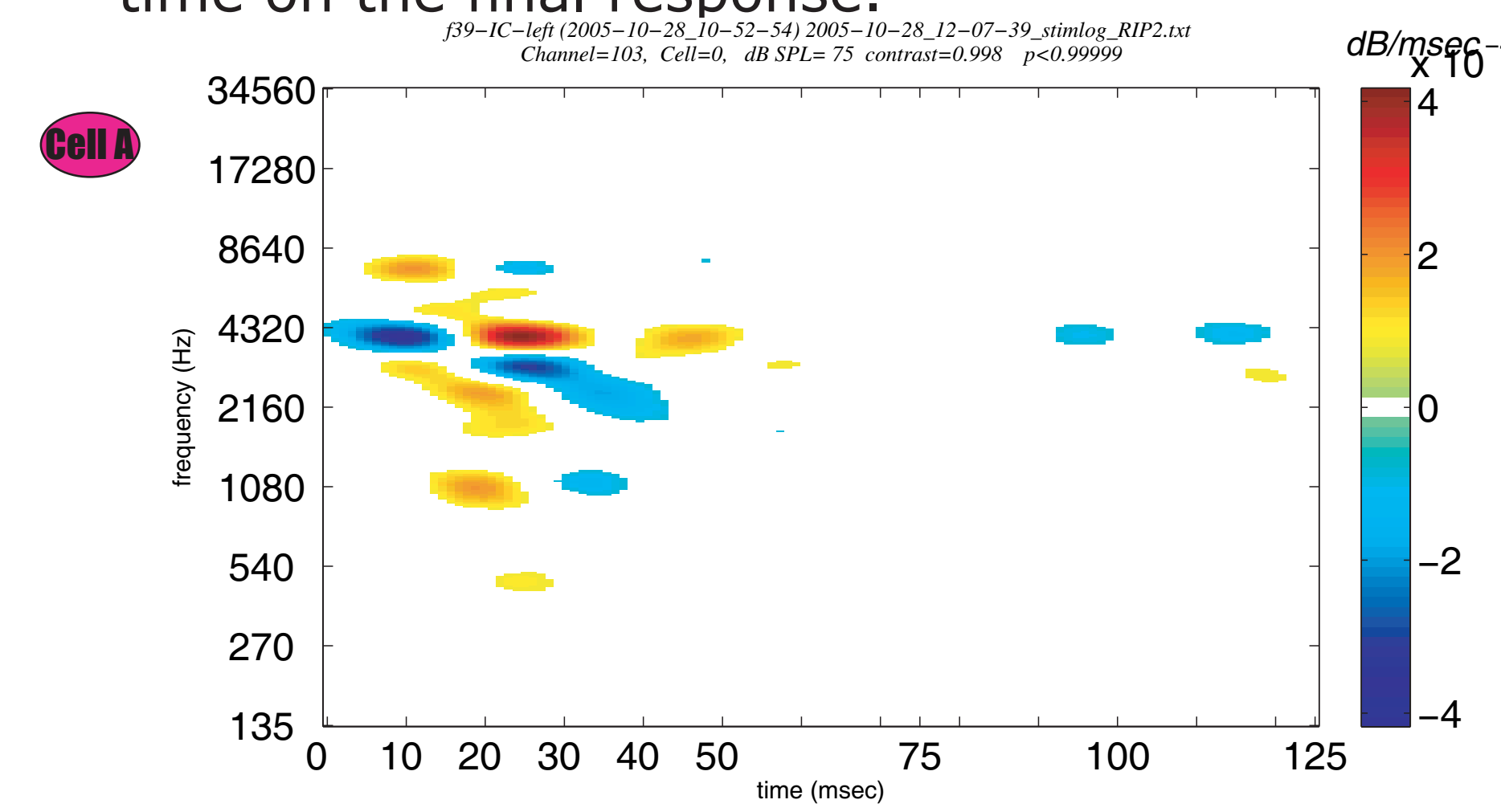
Analysis and Modeling

All analyses and modeling were performed in MATLAB. STRFs were computed with 1 msec bins of spike times. Model predictions of spike rates were made either with 1msec bins -- "Fine" -- or low-passed at the highest ripple velocity presented (typically 48 Hz) -- "Low-passed." Model validations and predictions are therefore presented with both "Fine" and "Low-passed" results.

The generalized measure of validation and prediction is the Pearson correlation coefficient ("rho"). The summary rho for a cell and stimulus set, reported here, is the mean correlation coefficient of the individual rhos for each response/prediction pair for all stimuli.

Linear STRF

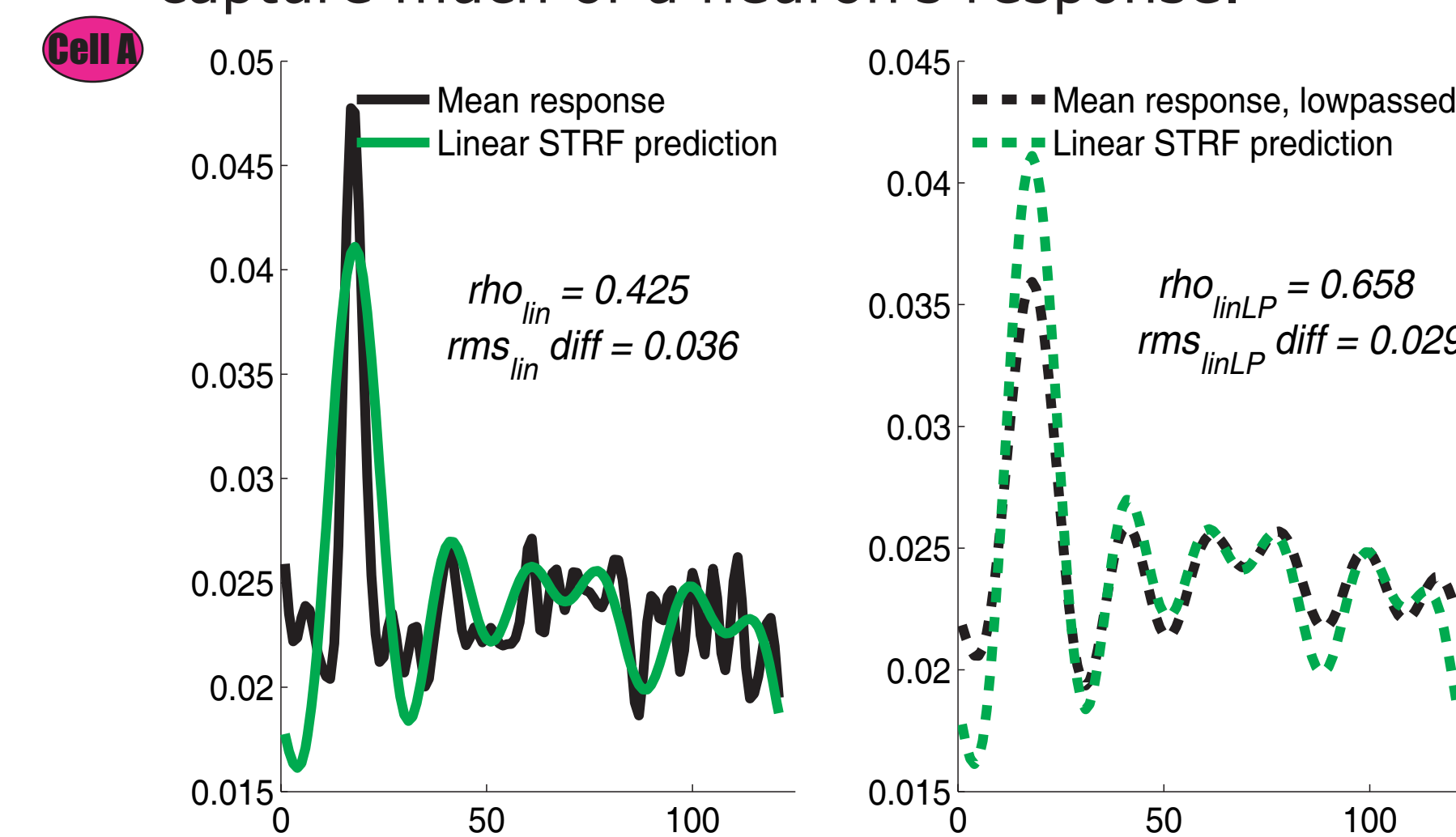
The STRF is the joint time and frequency representation of a cell's receptive field, estimated by a reverse correlation of spikes with the test stimuli. Each point in the STRF thus represents the linear influence of a stimulus frequency at a point in time on the final response.



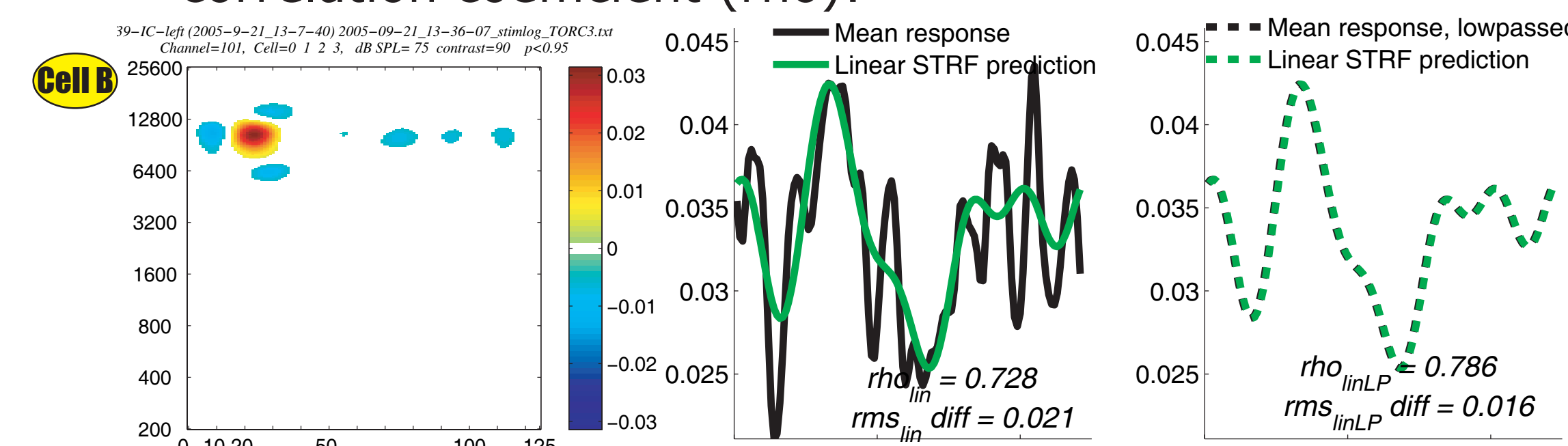
The deterministic prediction of a neuron's response to a stimulus is therefore the convolution of the STRF with the spectrogram of that stimulus:

$$resp_{pred}(t) = \iint STRF(\tau, f) \cdot S(t - \tau, f) d\tau df$$

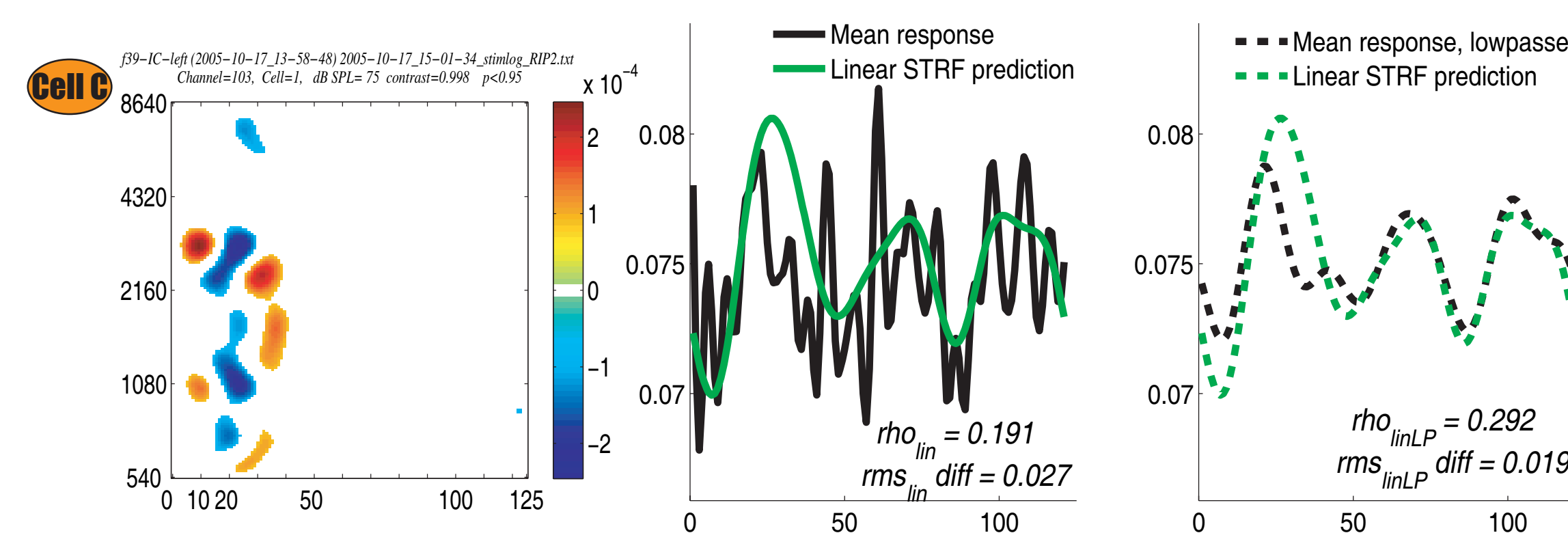
Validating the predictions with the original test stimuli shows that the simple linear model can capture much of a neuron's response.



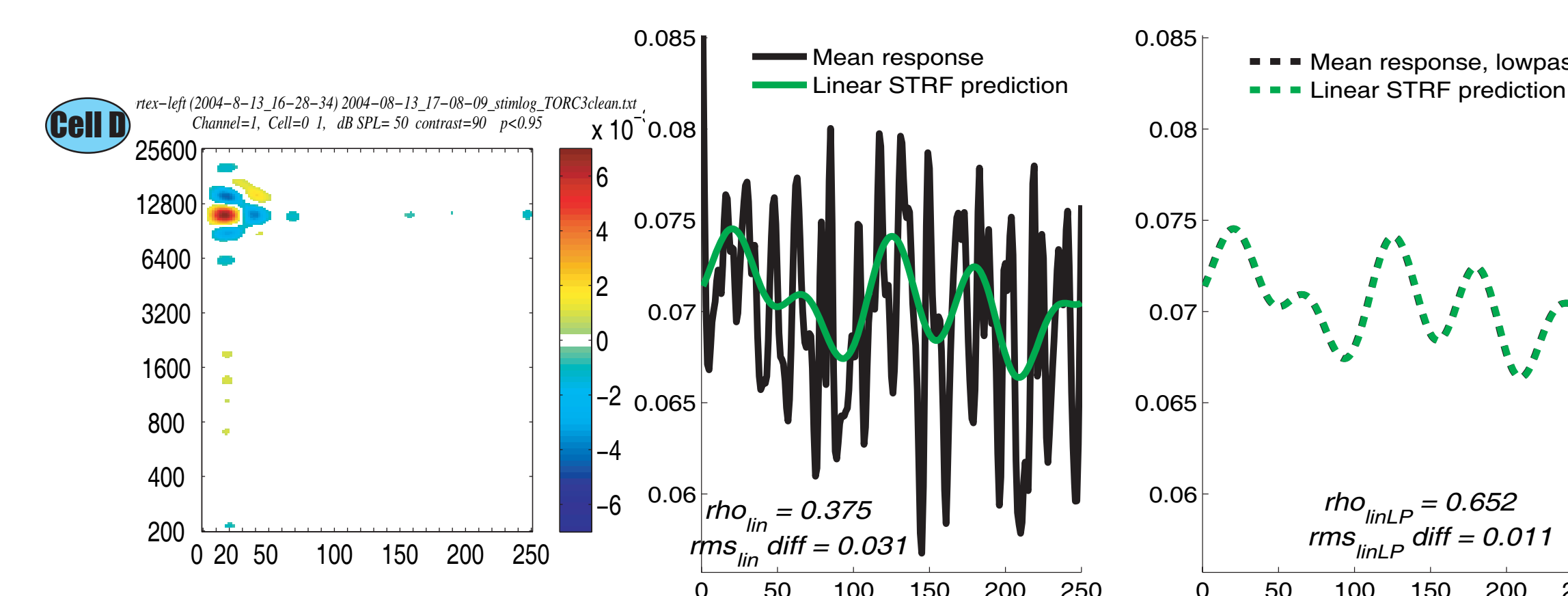
Validation of the linear STRF ranges from a high correlation coefficient (rho):



to a low correlation coefficient:

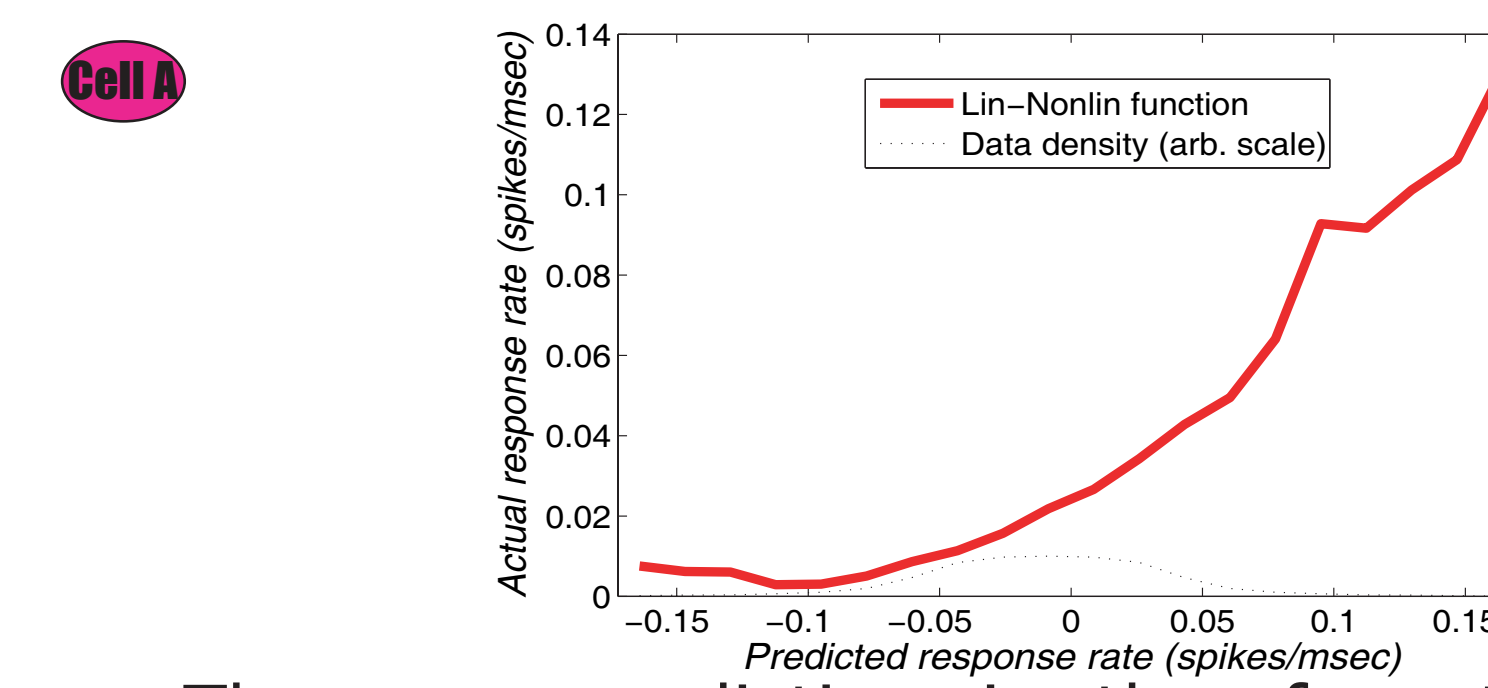


Auditory cortex displays similar ranges:



Linear STRF + Non-Linear Rate Transform

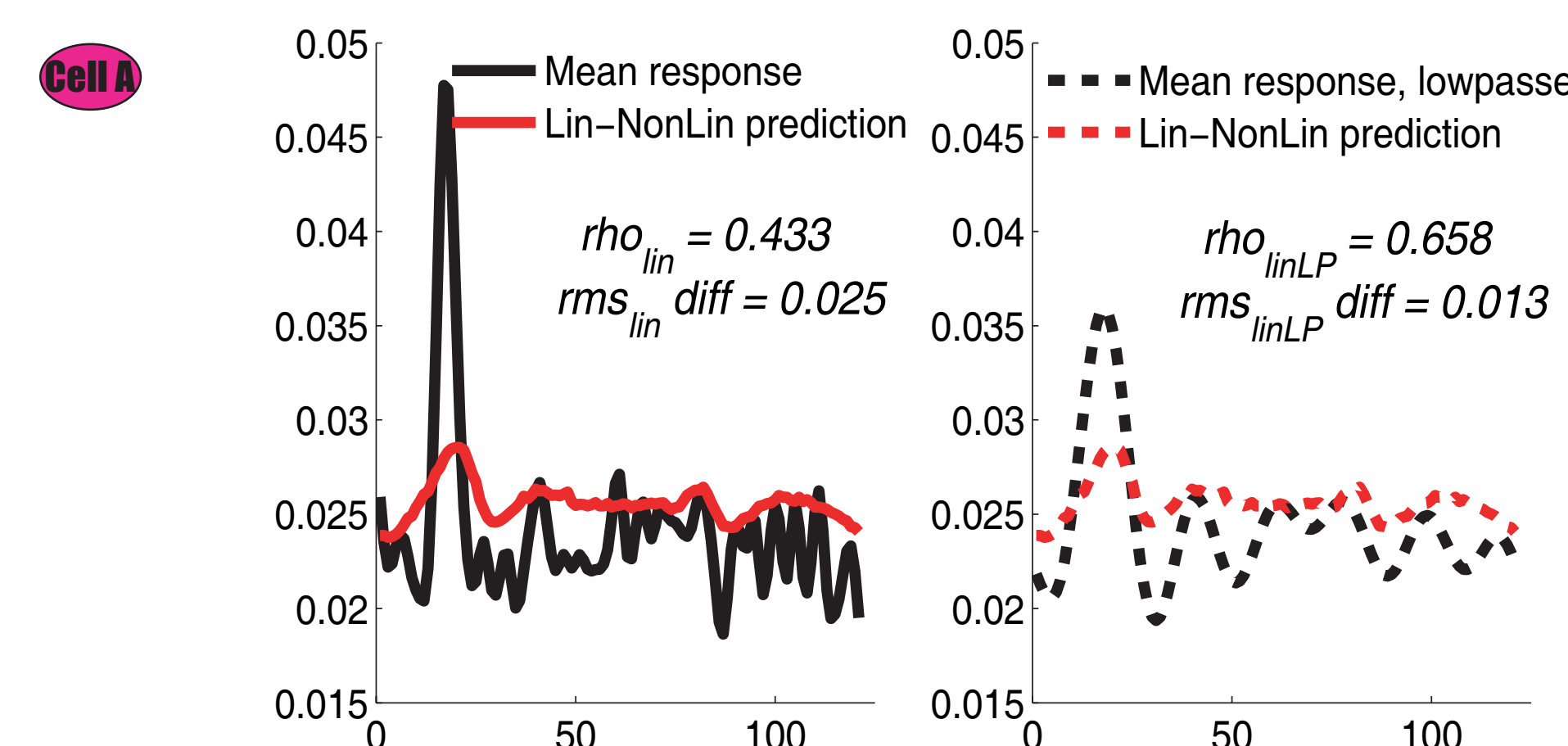
For this model, each point in the linear STRF still represents the stimulus' spectro-temporal influence on the neuron's response. In addition, a subsequent instantaneous non-linearity is computed as a function of the linear STRF- predicted spike rate and actual spike rate (from the probe stimuli). This non-linear function thus transforms the STRF output into the final predicted neuron response, acting as a rate mapper and limiter.



The new prediction is therefore the non-linear mapping function applied to the linear STRF prediction:

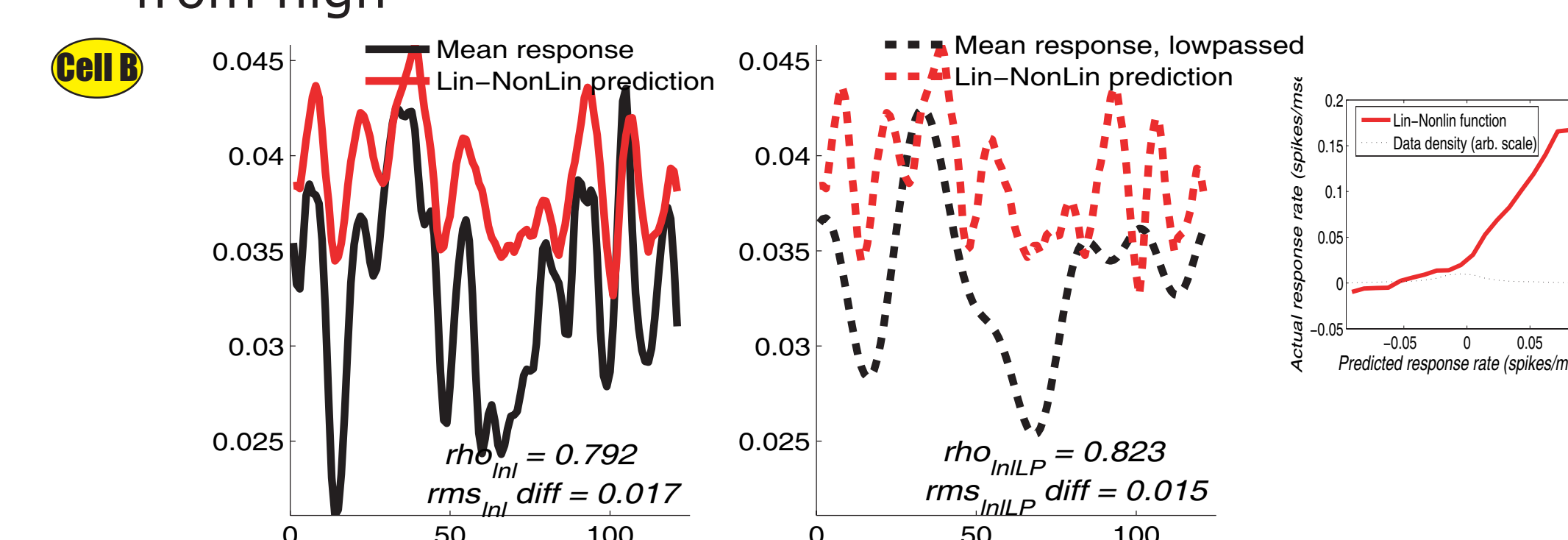
$$resp_{pred}(t) = NL(\iint STRF(\tau, f) \cdot S(t - \tau, f) d\tau df)$$

This additional term can improve response predictions.

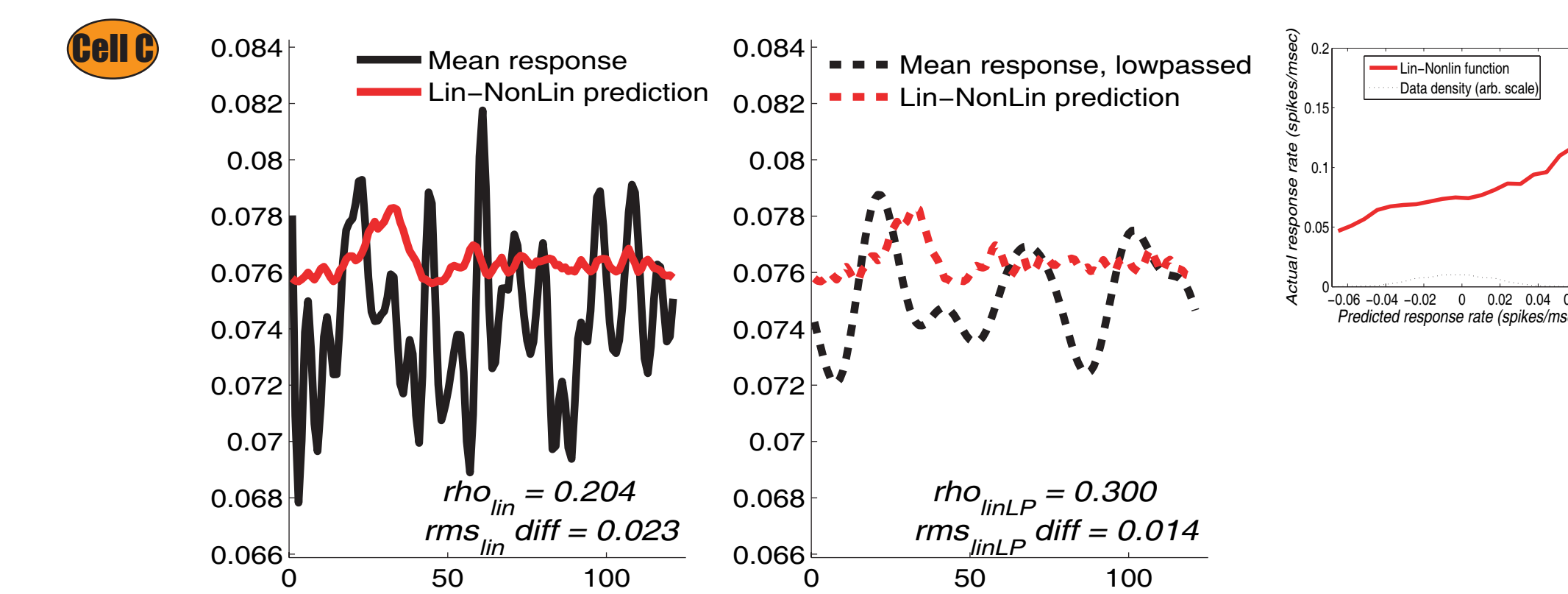


However, the "matching function" is difficult to interpret and still leaves room for improvement:

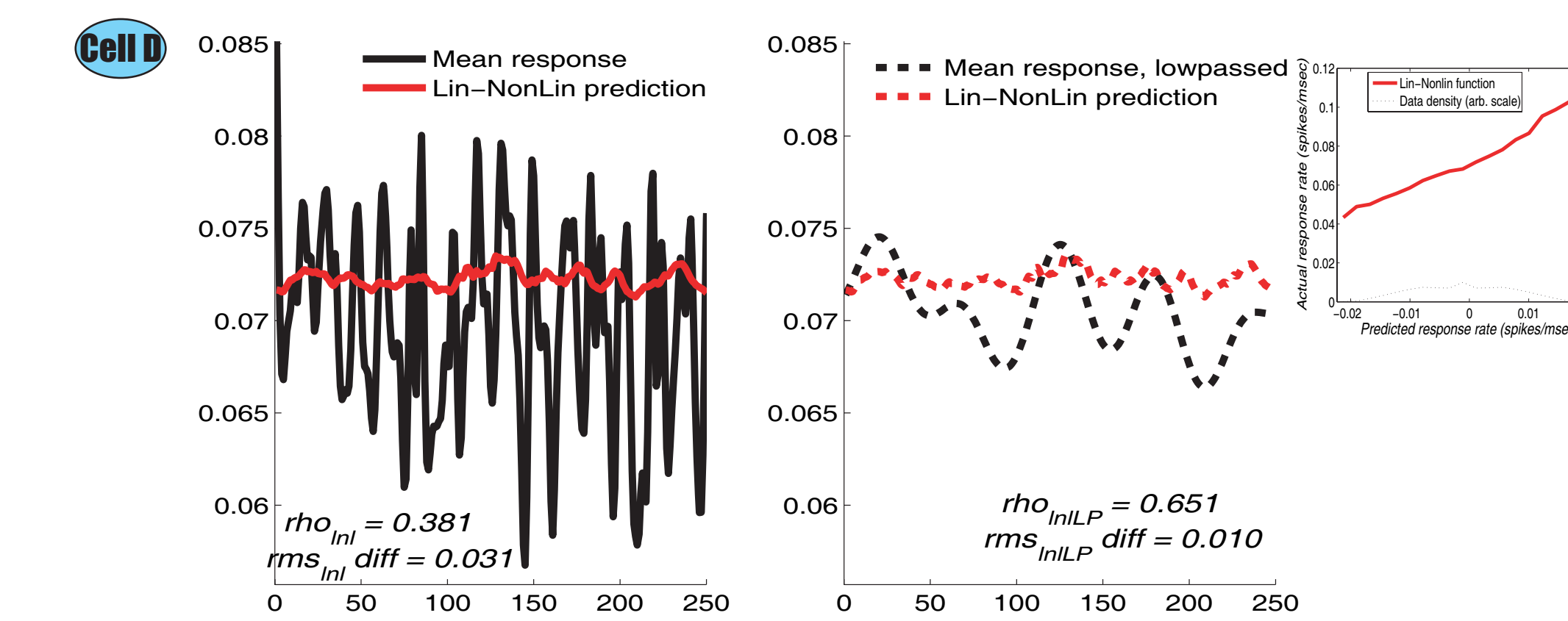
Validation of the Non-linear Rate Transform ranges from high



to not so high:

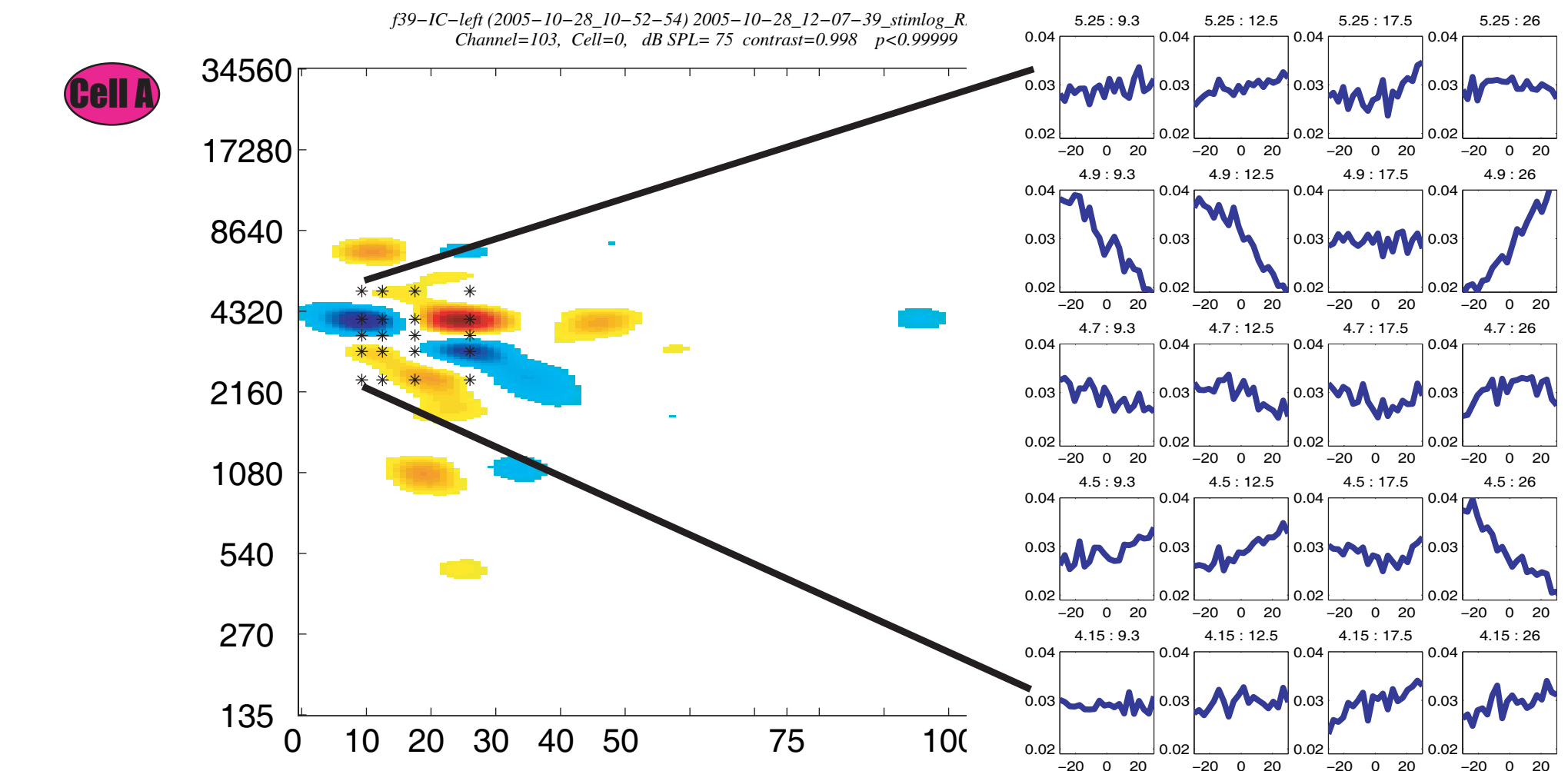


Auditory cortex is similar:



STRF + Non-Linear Rate-Level Function

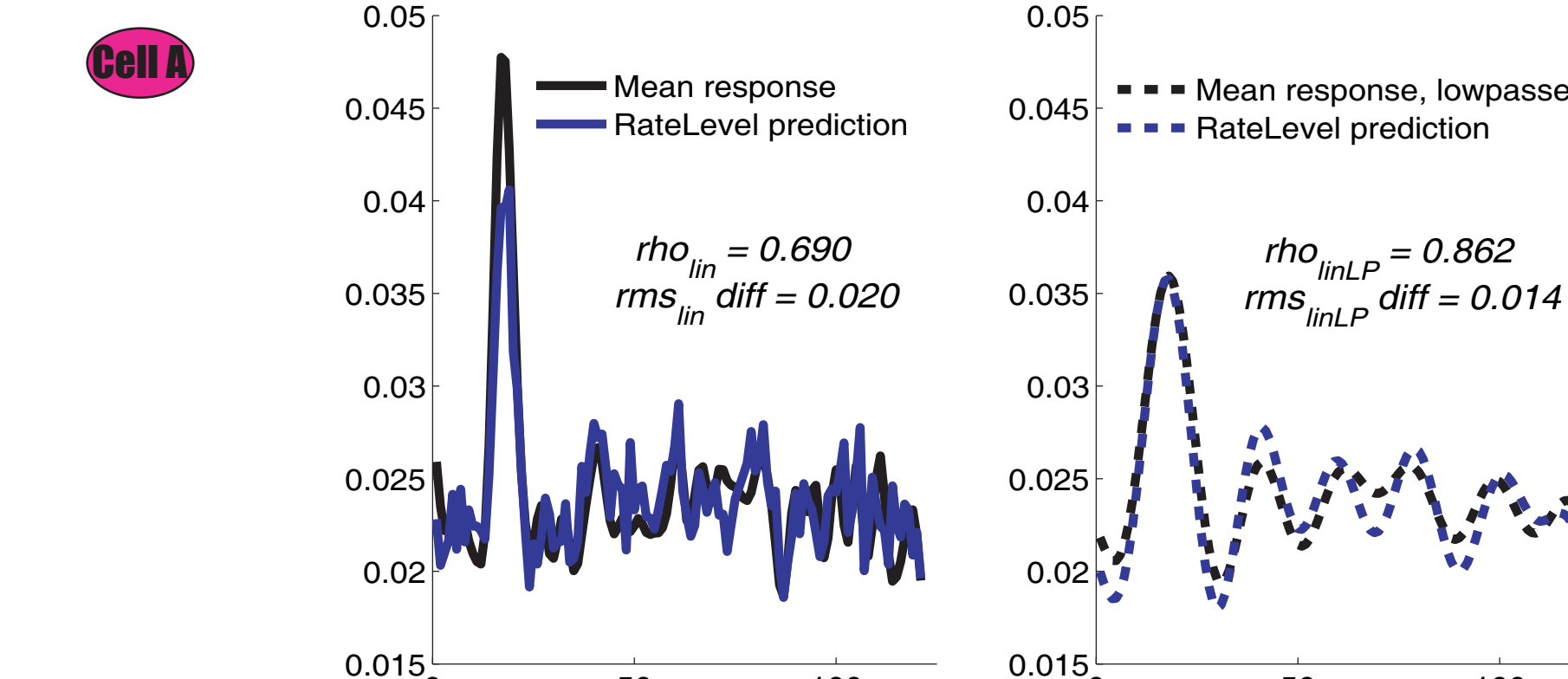
For this model, each point in the STRF still represents the stimulus' spectro-temporal influence on the neuron's response, but as a function of an underlying full rate-level function. The rate-level functions are computed by reverse correlation with the probe stimuli. Equivalently, each point of this STRF is simply a rate-level function, with the axis representing level scaled by the point's value.



Thus, this model's prediction of a neuron's response is:

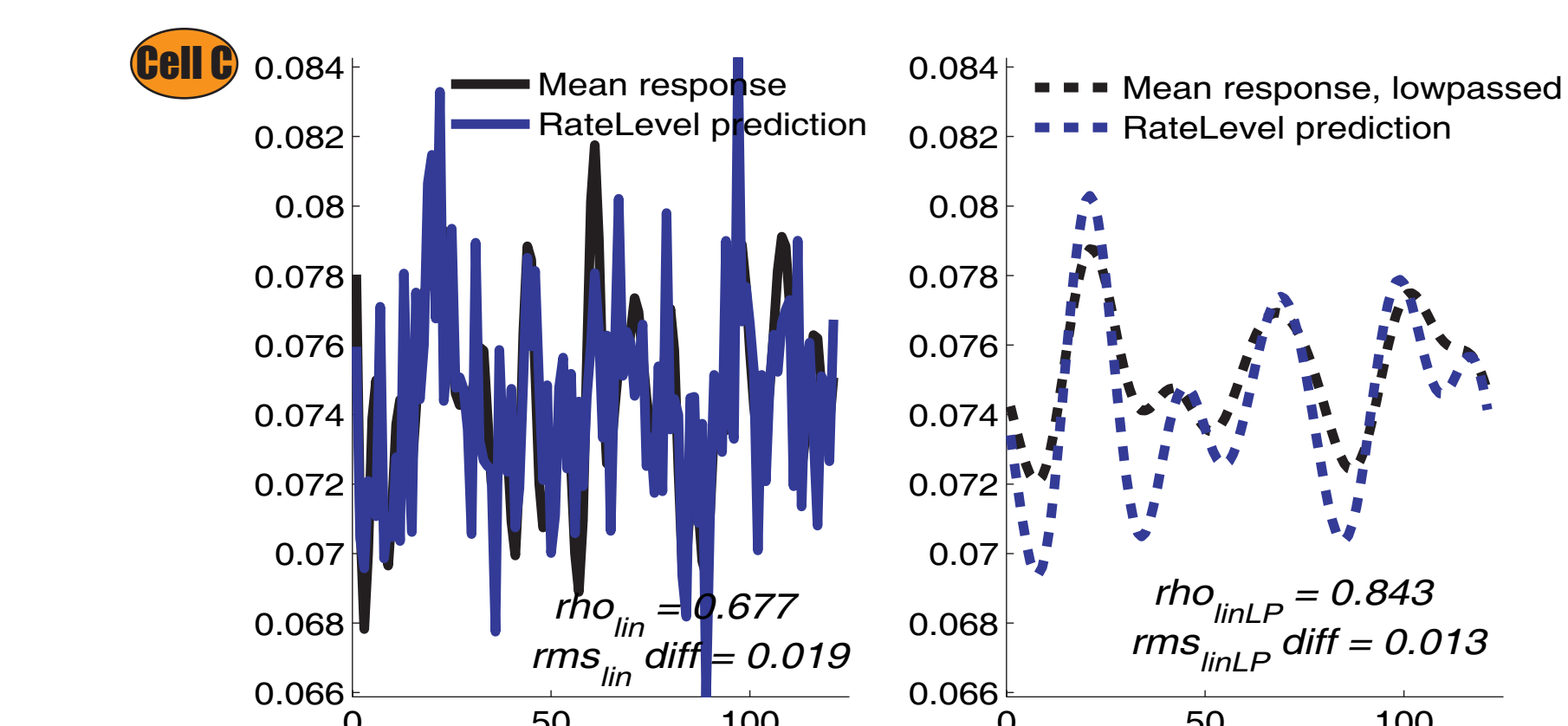
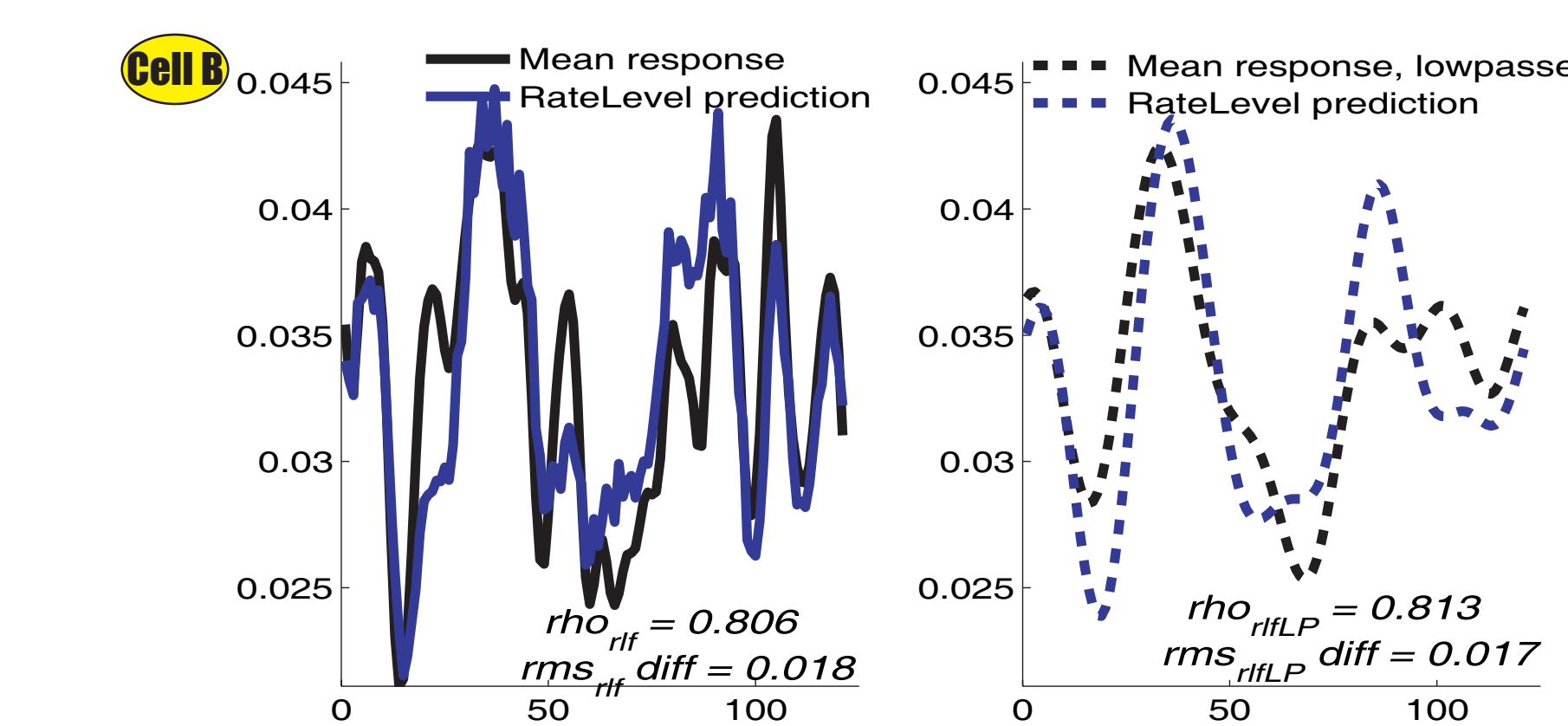
$$resp_{pred}(t) = \iint RLF(\tau, f) \cdot S(t - \tau, f) d\tau df$$

This model can improve the predictive power.

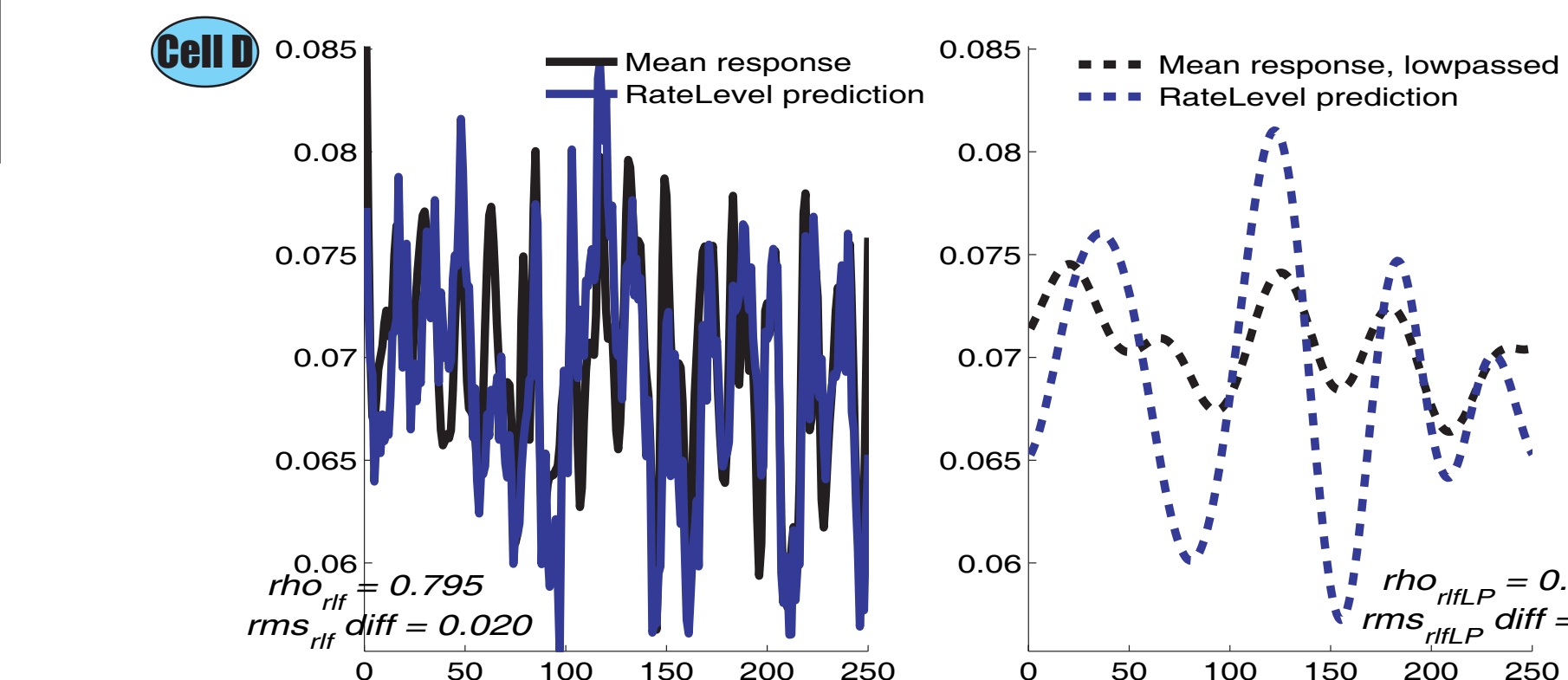


In general, this model gives the best predictions, though at the cost of computational time and complexity.

Validation of the Rate-Level STRF show great improvements:

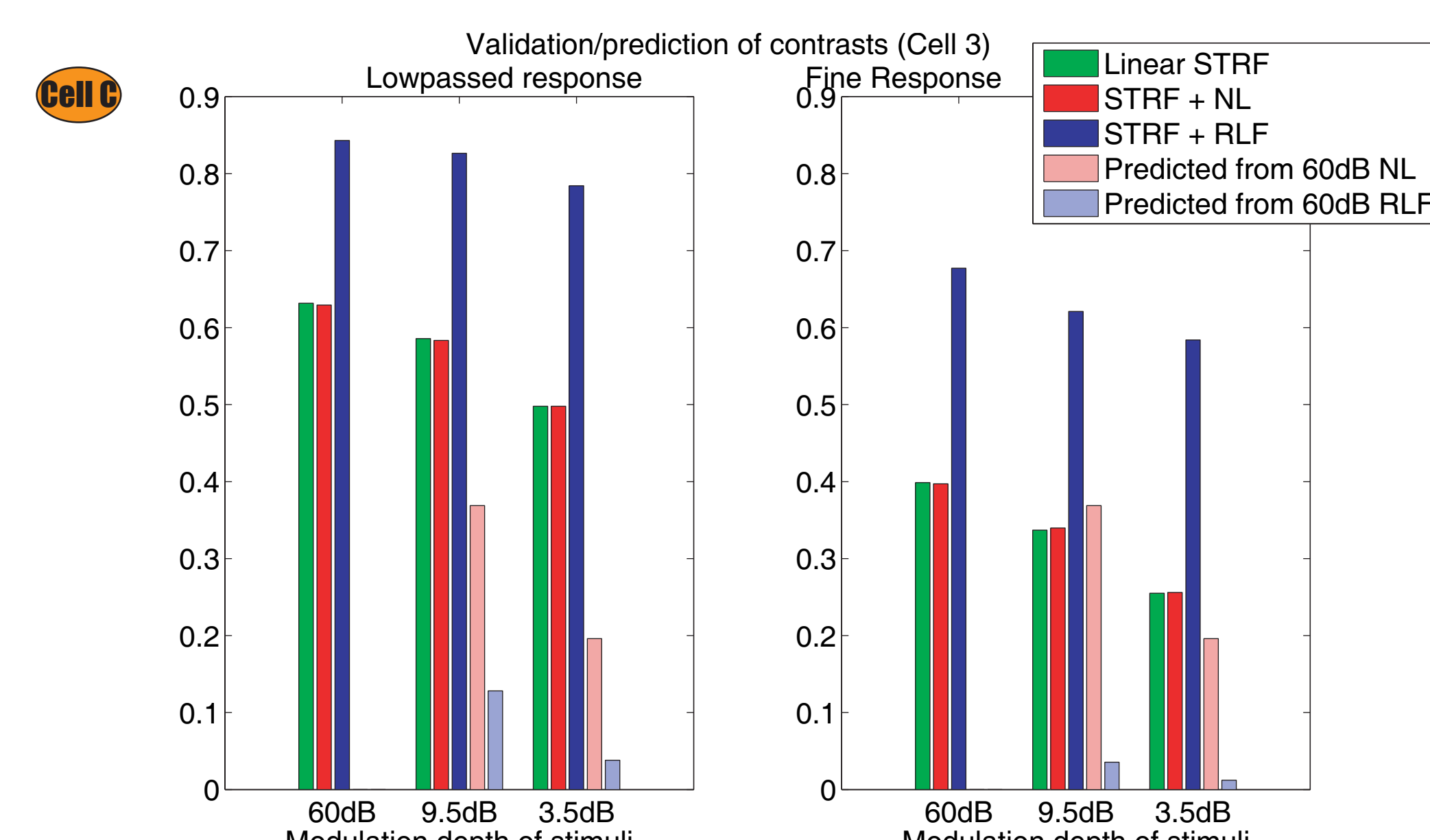
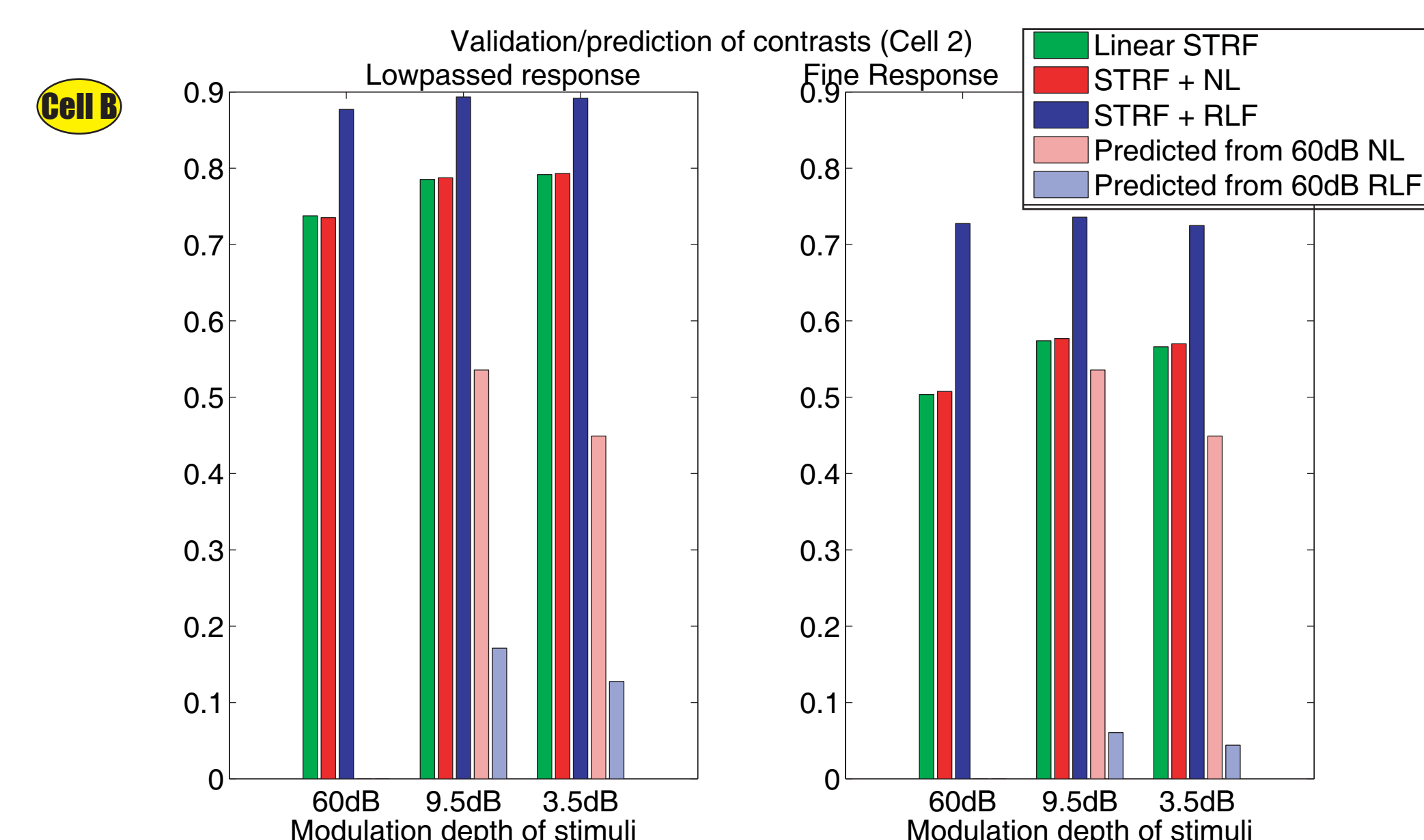
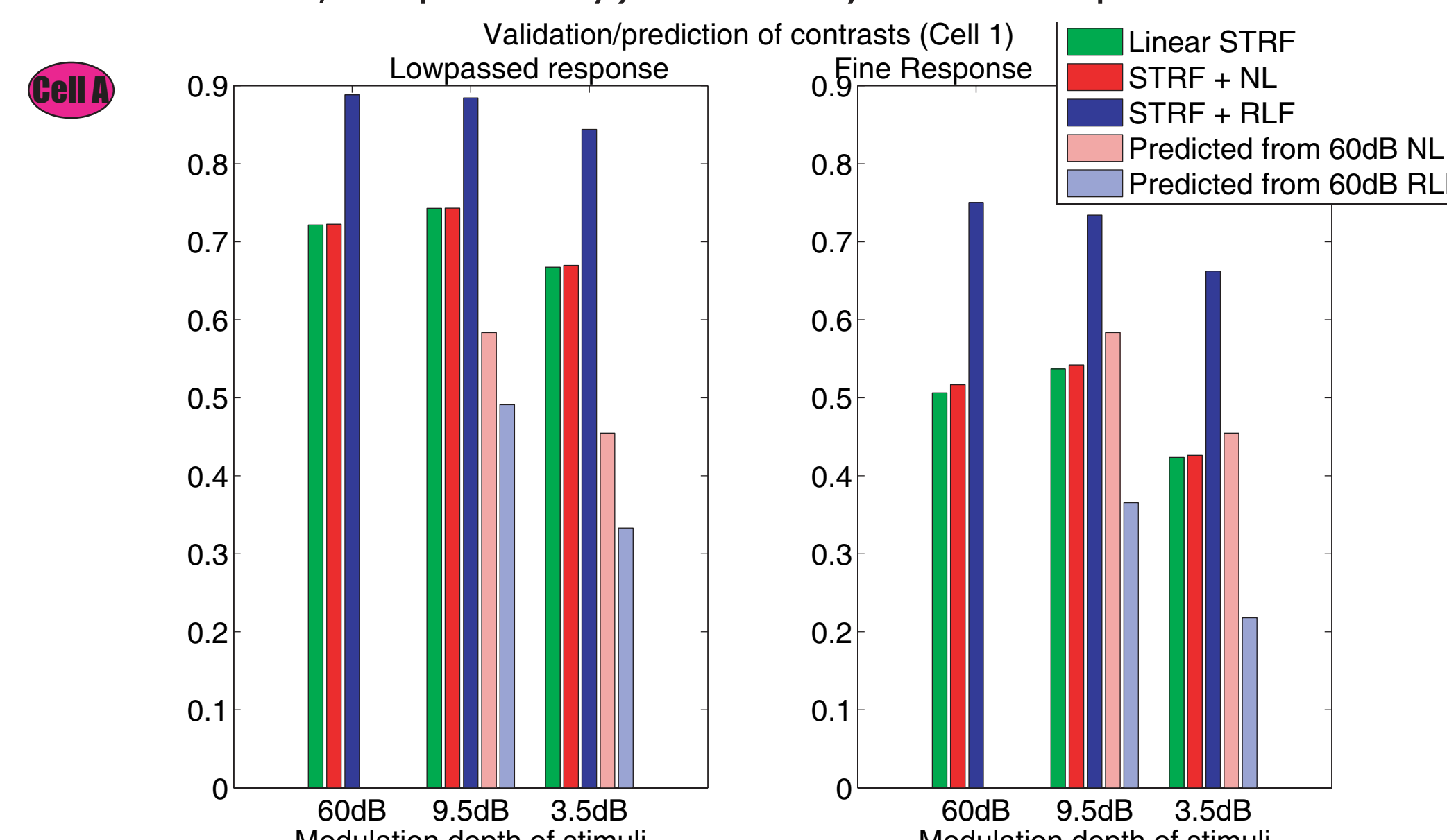


And also in auditory cortex:



Validating and Predicting Contrasts

Can these models be used for lower contrasts? Responses were recorded to same cells illustrated to the left to stimuli at 9.5 dB and 3.5 dB contrast (equivalent to 50% and 20% modulation, respectively). Summary rhos are presented:



The three models do well at different contrasts, with the STRF+rate-level producing the best validation. Predicting lower contrast responses from the 60 dB modulation stimuli does not do as well.

Conclusion

These simple extensions hold great promise in improving the STRF model without undue complexity. In particular, the non-linear rate-level function STRF has the consistently highest validation, especially to the fine structure of original response. The consistent validation trend across the models demonstrates the qualitative value of the extensions.

Using the STRF models derived from a high contrast stimulus to predict responses to lower contrast stimuli seems less successful and is a subject for further investigation. In particular, some implementation parameters of the model may not be optimal.

Selected References

Anzai A., Ohzawa I., Freeman R.D. (1999). Neural mechanisms for processing binocular information I. Simple cells. *Journal of Neurophysiology* 82(2):891-908.
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 Klein, D. J., Depireux, D. A., Simon, J. Z., & Shamma, S. A. (2000). Robust spectrotemporal reverse correlation for the auditory system: optimizing stimulus design. *Journal of Computational Neuroscience*, 9(1), 85-111.

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