

Evaluating Feature Importance in the Context of Simulation-Based Inference for Cortical Circuit Parameter Estimation

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Abstract. Extracellular electrophysiology recordings capturing the activity of neuronal populations, e.g., Local Field Potentials (LFPs), have offered important insights into cortical dynamics. Yet there is still a lack of clarity about how features and characteristics of these extracellular potentials relate to the properties and function of the underlying neural populations. Mechanistic models combined with simulation-based inference (SBI) algorithms have emerged as an effective strategy for developing predictive tools that fit well with available empirical data and can be used to predict key parameters that describe neural activity. Numerous SBI techniques rely on summary statistics or interpretable features to approximate the likelihood or posterior. However, at present, a significant challenge is assessing how each feature impacts the SBI model’s predictions. Here, we developed an approach to determine feature importance in the context of cortical circuit parameter inference. We first created a dataset that includes a million distinct simulations from a spiking cortical microcircuit model of recurrently connected excitatory and inhibitory populations. Biophysics-based causal filters were coupled with spikes to generate realistic LFP data. We then extracted a set of meaningful features from simulated LFP data that were used to train an SBI algorithm. To evaluate feature importance, we employed SHAP values,

a prominent tool in machine learning for interpreting the contribution of each feature to the prediction outcomes. Our findings demonstrate the effectiveness of our approach in pinpointing the most critical features for inferring parameters of a recurrent cortical circuit model based on electrophysiological data.

Keywords: Spiking Neural Network Model · Machine Learning · Simulation Based Inference (SBI) · Feature Importance · SHAP · Local Field Potential (LFP).

1 Introduction

Mechanistic models of neural networks offer a principled means to bridge between observations made at different levels of investigation. In neuroscience, they can be used to explain the data collected at a coarser level of investigation in terms of microscopic interactions between neurons. Examples of these include using network models to understand what changes in extracellular field potentials, measured either intracranially, such as in Local Field Potential (LFP), or non-invasively, such as in electroencephalography (EEG), imply in terms of changes in the microscopic parameters of neural activity. [4, 25, 23, 39, 29, 35, 9, 26, 27]. However, given that extracellular potential data are high-dimensional, encompassing a wide spectrum of different relevant types of features, and because credible biophysical models are complex and have multiple parameters, it is difficult to identify relevant parameter regimes consistent with empirical data. A range of approaches has been developed in neuroscience to identify the optimal parameters for individual neuron models or neuronal network models that best fit empirical neural dynamics [41, 30, 22, 40, 31, 8, 10]. Simulation-based inference (SBI) techniques have recently been introduced [7] and applied across various neural models [38, 5, 13]. By leveraging simulation capabilities, these Bayesian optimization methods derive estimates of the likelihood or posterior from simulated data. The advantages of SBI methods, such as SNPE (Sequential Neural Posterior Estimation) [13], include their capacity to determine all parameter configurations that produce simulations compatible with observed data, providing, as well, information about parameter interactions, and their amortizable nature, meaning they do not necessitate additional simulations or retraining for each new dataset.

Scientists extract essential features or summary statistics from the model’s simulations to condense the high-dimensional output into a more manageable form, thus decreasing both problem complexity and computational costs. Moreover, integrating features that are directly related to underlying scientific mechanisms is crucial for ensuring that predictive models are both interpretable and reliable from a research standpoint. For example, when linking cortical circuit parameters to circuit-level aggregate measures of neural activity, features such as the aperiodic component of the power spectrum and neuronal oscillations have been described as robust proxies for measurements of changes in the excitation/inhibition (E/I) balance [4, 25, 1, 39, 12, 34]. Besides, to interpret prediction

results in a scientific context, it’s important to identify which features or feature combinations have the greatest influence on the prediction outcomes and which parameters they specifically impact. In the context of SBI, the Feature Selection Through Likelihood Marginalization (FSLM) method was introduced [3], which efficiently compares the posterior uncertainty estimated with and without including a specific feature in the SBI method. FSLM was used to study how the removal of individual features increased the uncertainty of the posterior. However, FSLM does not explicitly rank features and needs to be coupled with a greedy feature selection algorithm to identify useful features from a predefined set.

SHAP (SHapley Additive exPlanations) is a unified way to understand the output of any machine learning model. Using the coalitional game’s best Shapley values, SHAP provides a detailed view of how each feature contributes to the prediction for individual instances as well as across the entire dataset. SHAP has become widely used in machine learning because it excels in providing detailed, consistent, and interpretable insights into feature importance and interactions, making it valuable for understanding and explaining model predictions [2, 20, 18]. In this study, we focused on determining feature significance in SBI-based predictions by utilizing SHAP values to interpret and explain model outcomes. We examined the effectiveness of this approach in the context of predicting the parameters of a spiking cortical circuit model based on simulated LFP data. Our findings demonstrate the significance of our method for selecting optimal features from electrophysiological data that are instrumental in predicting key parameters of cortical circuit activity.

2 Methods

2.1 Spiking point-neuron network simulations and biophysics-based forward modelling of the LFP

Spiking neuron network models describe neural phenomena at micro- and mesoscopic scales [42, 21, 27, 6]. This positions them at an exceptional intermediate level of biophysical detail to interpret the relationship between neuronal and synaptic changes mediated by molecular and cellular mechanisms with properties of large-scale brain dynamics [24, 23, 9]. Here we simulated a generic recurrent network model of interacting excitatory (E) and inhibitory (I) integrate-and-fire neuronal populations (8192 and 1024 neurons, respectively) driven by external fixed-rate Poisson processes. Network parameters correspond to the best-fit parameters employed in the reference publication [14], except for J_{EE} , J_{EI} , J_{IE} and J_{II} (being J_{YX} the synaptic weights between presynaptic population X and postsynaptic population Y), τ_{synE} and τ_{synI} (synaptic time constants of excitatory and inhibitory synapses) and J_{ext} (weight of extrinsic synapses), which were systematically varied to yield a million distinct parameter configurations. These parameters fully characterize how synaptic mechanisms of the model contribute to cortical circuit activity and, ultimately, the resulting macroscopic brain signals. Considering that synaptic alterations are significant factors in the context

of neurodegenerative diseases [19, 15] and neurodevelopmental disorders [4, 39, 36, 16, 28], we opted for focusing on studying this type of parameters and leaving the other parameters unchanged. Biophysics-based forward calculations of extracellular signals and the LFP arising from simulated synaptic activity were performed using the *LFPy* kernels package [14]. To obtain the current dipole moment (which was used as a proxy of the LFP), we convolved the population spike rates by spatiotemporal filter kernels that accounted for the biophysics of neurons, spatial distributions of cells and synapses and network connectivity from network-equivalent populations of conductance-based multicompartment neurons. For the sake of simplicity, we used the reference network of ball-and-sticks neurons for the multicompartment neuron network [14].

2.2 Feature extraction

We utilized the *catch22* library [17] to perform feature extraction on simulated LFP data. The *catch22* library, which constitutes a reduced subset of 22 features from the *hctsa* toolbox [11], provides an effective data-driven summary of temporal, spectral and statistical properties frequently observed in time-series data-mining tasks. The collection of features includes properties of the distribution of values in the time series, its linear and non-linear autocorrelation, measures derived from power spectral densities, temporal statistics, scaling of fluctuations, and others [17]. By computing the *catch22* features, we can leverage well-established time-series methods to uncover and interpret a wide range of significant trends and dynamics observed within the neural data.

2.3 SBI tools for prediction of cortical circuit model’s parameters

A SNPE model from the *sbi* library [37] was trained (default settings of SNPE) with the *catch22* features (predictors) and circuit parameters (dependent variables) obtained from the simulation dataset. Rather than training the SNPE model with the four parameters that define the recurrent synaptic connectivity (i.e., J_{EE} , J_{EI} , J_{IE} and J_{II}), we used the metric $[E/I]_{net} = (J_{EE}/J_{EI})/(J_{IE}/J_{II})$, which is the ratio between predicted E/I of excitatory and inhibitory populations, respectively. This summary measure quantifies the net effect of excitatory and inhibitory processes in the circuit model and may be seen as a global E/I ratio from model simulations. Thus, the neural network was finally trained using the parameters $[E/I]_{net}$, τ_{synE} , τ_{synI} and J_{ext} .

To ensure robustness and generalizability of the inference results, we trained the SNPE algorithm using 9 folds for training, leaving the remaining fold for testing and computing the SHAP values in each iteration of a 10-fold cross-validation. Given that dense sampling of the posterior in the SBI algorithm is computationally demanding, we randomly drew 500 samples from the test fold instead of using all available samples. These 500 samples were then used to compute the posterior estimates and to calculate the SHAP values. After computing the SHAP values for all iterations, we averaged them to obtain the final SHAP values.

2.4 Metrics to quantify the dependency between parameters and features

We used SHAP values [18] to explain the contribution of each feature to the predictions made by SBI methods. To characterize the posterior distribution estimated by SBI tools, we computed two specific metrics from it: the mean and the interquartile range (IQR) of the posterior distribution. The mean identifies how the central, high-probability value of the parameter shifts in response to changes in the features, offering insight into the general direction and magnitude of the parameter’s response. The IQR, on the other hand, focuses on the variability or variance within the parameter’s distribution, revealing how the spread of the parameter values changes with different feature values. SHAP values were calculated to explain how features affect these two metrics. By employing both metrics, we gain a comprehensive understanding of how features influence the distribution of parameter predictions, considering both central tendency and distribution variability.

We also assessed the dependency between parameters and features by computing the mutual information (MI) [32, 33] using the *mutual_info_regression* function provided by the *scikit-learn* library (which treats model parameters as continuous target variables in a regression context). This analytical approach served as an initial evaluation of the simulated data, aimed at examining how features relate to the underlying circuit parameters. However, it is important to note that this technique does not incorporate SBI predictions.

2.5 Computational resources

Simulations, training of the SBI algorithm, and computation of SHAP values were parallelized on: (1) a high-performance computing server equipped with a 64-core CPU and 256 GB of RAM, (2) a high-performance cluster consisting of 6 nodes, with each node equipped with 24 cores and 64 GB of RAM, and (3) the supercomputer *Albaicin* (*Huawei FusionServer Pro series*) of University of Granada.

3 Results

3.1 Relationship between parameters of a cortical model and LFP features

Our study began by generating a simulation dataset, including parameters that describe the synaptic connections of a spiking circuit model and the resulting LFP time-series data from simulated neural activity. Next, we utilized the *catch22* library to extract relevant features from the simulated LFP data and subsequently integrated these features into our dataset. Before exploring the influence of features on SBI prediction model results, we focused on studying the relationships between cortical model parameters and LFP-derived features. To

reveal potential associations between model parameters and features, we measured the mutual information between the *catch22* features and each parameter of the model, i.e., $[E/I]_{net}$, τ_{synE} , τ_{synI} and J_{ext} (Fig. 1). This initial mutual information analysis helped in identifying and quantifying the relevance and potential predictive power of features in the context of a machine learning regression framework.

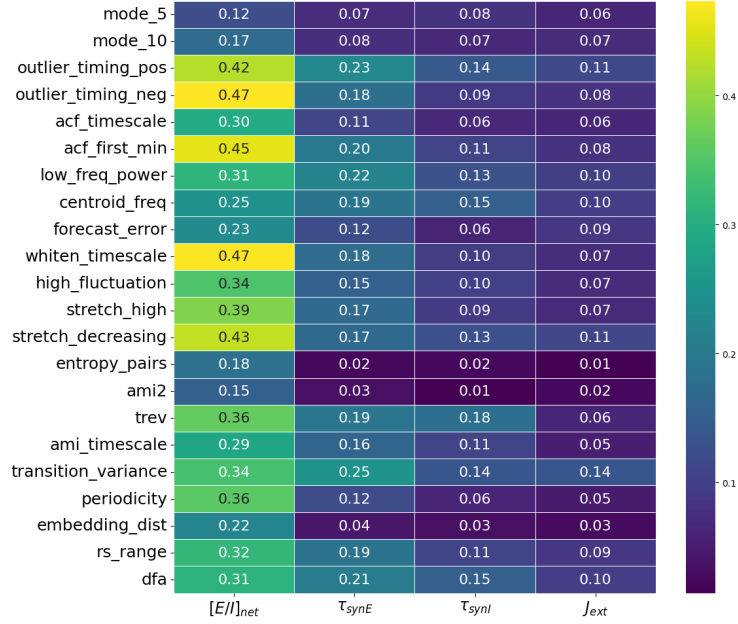


Fig. 1: Mutual information between parameters of the cortical circuit model and *catch22* features computed using all samples of the dataset.

Among the parameters, $[E/I]_{net}$ had the highest MI scores with most of the features (Fig. 1), though features such as *mode_5*, *mode_10*, *entropy_pairs* and *ami2* appeared to be less informative, indicating a weaker relationship with $[E/I]_{net}$. Indeed, these features were associated with some of the lowest values among all the parameters analyzed. On the other end of the spectrum, J_{ext} showed low MI values across the majority of features (with a few exceptions such as *transition_variance*). Interestingly, certain features exhibited high MI values overall across all parameters (e.g., *outlier_timing_pos*, *low_freq_power*, *transition_variance* and *dfa*), reflecting their significant and strong relationship with all parameters. In summary, the mutual information analysis demonstrated that certain features provide more insight into specific parameters, while others are highly informative across all parameters.

3.2 Analysis of feature importance in SBI prediction models through SHAP values

Our next step was to evaluate the significance of features within the framework of SBI predictions. We leveraged SHAP values to provide insights into how each feature affects the predictions made by SBI methods. To describe the posterior distribution estimated by SBI tools, we calculated its mean and IQR. SHAP values were employed to explain how features affect these two metrics for all four parameters of the cortical model (Figs. 2, 3, 4 and 5). These bar plots of mean SHAP values show the average impact of each feature on the SBI model’s predictions. Features with higher mean SHAP values are more important, meaning they have a greater impact on the model’s output.

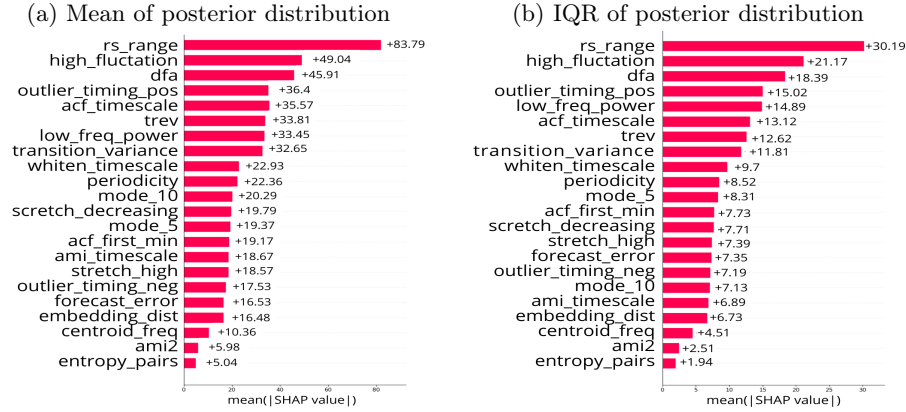


Fig. 2: Mean SHAP values for $[E/I]_{net}$ calculated with two different metrics: (a) mean and (b) IQR of the posterior distribution. The mean SHAP values were obtained by averaging all SHAP values across the 10 fold evaluations.

A key initial observation is that some features (e.g., *dfa*, *rs_range*, *low_freq_power* or *transition_variance*) were consistently top-ranked across all parameters, suggesting that these features are crucial and influential for predicting circuit parameters across the entire range of parameters analyzed. Notably, several of these features previously exhibited consistently high MI values across all parameters (see Fig. 1). In contrast, largely in agreement with our previous results from the MI analysis, features like *ami2* and *entropy_pairs* consistently received the lowest SHAP scores across all parameters. We also noted that, for each parameter, the ranking of features based on SHAP values remained largely consistent across the two metrics used (the mean and the IQR of the posterior distribution), which reinforces the robustness of the SHAP analysis across the different statistical measures computed for the posterior distribution. In summary, the

agreement between the mutual information analysis and SHAP values implies that the identified features are genuinely important for the model's predictions, and it strengthens the overall confidence in the model's interpretability and the validity of the analysis.

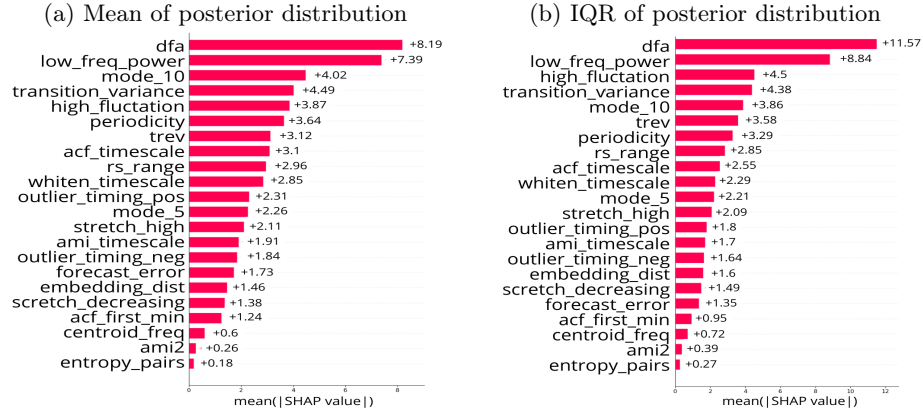


Fig. 3: Mean SHAP values for τ_{synE} .

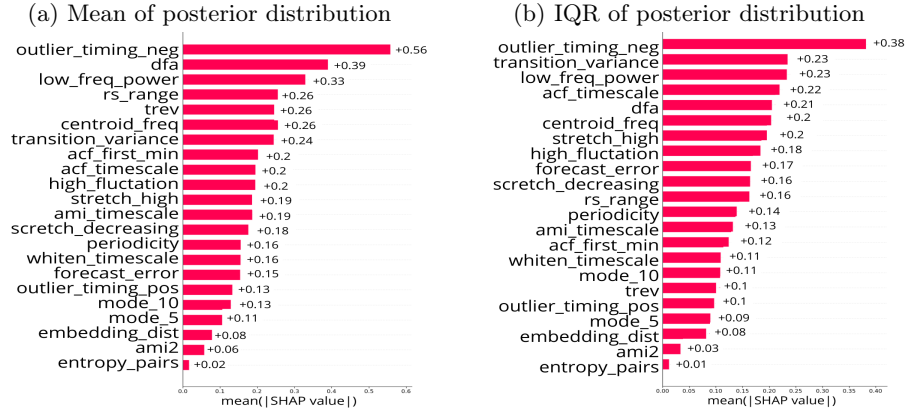
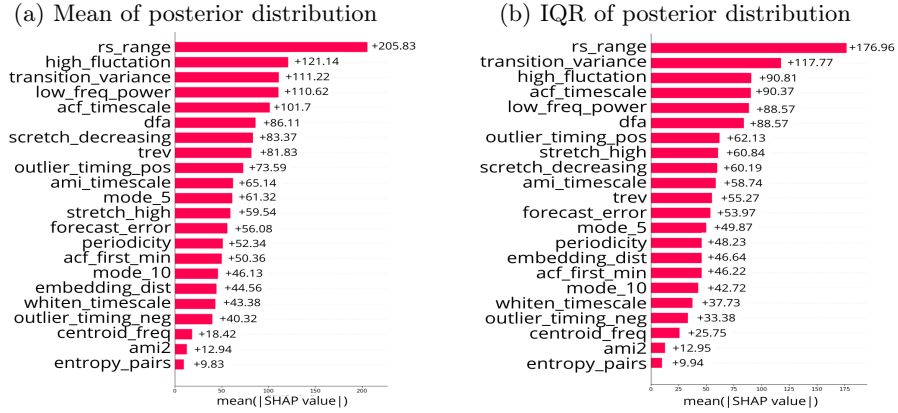


Fig. 4: Mean SHAP values for τ_{synI} .

4 Discussion

This study aimed to assess feature importance in SBI-based predictions using SHAP values to interpret and explain model outcomes. We evaluated the effectiveness of this approach for predicting parameters of a spiking cortical circuit model using simulated LFP data. Our results highlight the efficacy of this method in identifying crucial features from electrophysiological data, such as

Fig. 5: Mean SHAP values for J_{ext} .

dfa, *rs_range*, *low_freq_power* or *transition_variance*, which are essential for accurately predicting key parameters of cortical circuit activity.

To further refine our analysis, it will be important to compare the SHAP results with those obtained using a technique specifically developed for evaluating feature importance in SBI models, e.g., the FSLM technique combined with a greedy feature selection algorithm [3]. This comparison will help determine whether the feature importance metrics derived from the FSLM algorithm, which quantify how a feature impacts posterior uncertainty, differ from those obtained using SHAP values. Testing these methods on real datasets involving controlled changes in neural activity, such as optogenetic manipulation of cortical activity, will allow us to evaluate which approach reveals important features more effectively for inferring cortical circuit parameters. Additionally, incorporating additional sets of features, such as those from the hctsa library [11] or other relevant features that have been shown to be robustly linked to properties of cortical circuit activity, such as the 1/f slope or microstates [1], will enhance our ability to fully capture and characterize the range of features relevant to describing circuit parameters.

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