MULTITAPER ANALYSIS OF EVOLUTIONARY SPECTRAL DENSITY MATRIX FROM MULTIVARIATE SPIKING OBSERVATIONS

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ABSTRACT

Extracting the spectral representations of the neural processes that underlie spiking activity is key to understanding how the brain rhythms mediate cognitive functions. While spectral estimation of continuous time-series is well studied, inferring the spectral representation of latent processes from spiking observations is a challenging problem. In this paper, we address this issue by proposing a spectral estimation methodology that can be directly applied to multivariate spiking observations in order to extract the evolutionary spectral representation of the latent non-stationary processes. We compare the performance of our proposed technique with several existing methods using simulated data, which reveals significant gains in terms of the bias-variance trade-off.

***Index Terms*—** Evolutionary spectral density matrix, point process model, multivariate non stationary latent process, multitaper analysis, binary spiking observations

1. INTRODUCTION

Neural oscillations are known to play a significant role in mediating the cognitive and motor functions of the brain [1, 2, 3]. The advent of high-density electrophysiology recordings [4, 5, 6] from multiple locations in the brain has opened a unique window of opportunity to probe these oscillations at the neuronal scale. In order to exploit such experimental data for inferring the mechanisms of brain function, spectral analysis techniques tailored for such neuronal spiking data are required [7].

Existing techniques for spectral analysis of neuronal data use point process theory [8, 9, 10] to capture the spiking statistics. Due to the time-domain smoothing procedures used by existing techniques [11, 12, 13] for recovering the latent processes that drive spiking activity, the power spectral density (PSD) estimates obtained by these methods results in distortion in the spectral domain. An alternative approach for directly estimating the PSD from spiking data has recently been proposed in [14].

These existing methods consider univariate spiking observations and assume the latent process to be second-order stationary during the observation period. However, it is known that the brain oscillations that drive neuronal spiking are non-stationary and may exhibit rapid changes corresponding to the brain state or behavioral dynamics [12, 15]. Non-stationary time series analysis has been well studied for multivariate continuous signals and various methods have been proposed to quantify the energy-frequency-time distributions [16, 17, 18, 19]. One notable example is the evolutionary power spectral characterization [17], which defines a non-stationary spectral density matrix in order to quantify the local spectral energy distributions of a multivariate process. A unified approach that considers multivariate spiking observations driven by non-stationary latent processes is lacking, but highly desired due to the emerging demands of modern neuronal data acquisition.

In this paper, we close this gap by developing a framework to estimate the evolutionary spectral density matrix of a multivariate non-stationary latent process, given spiking observations. We model the spiking observations as multiple realizations of point processes with logistic links to the latent continuous processes. We then pose the problem of spectral estimation within a multitapering framework. Multitapering is a widely-used PSD estimation technique with desirable bias-variance trade-off performance [20, 21, 22]. Therefore, the goal is to estimate the multivariate eigen-spectra of the latent processes corresponding to a set of discrete prolate spheroidal sequences [23] used as tapers.

We next employ a state-space model to characterize the dynamics of the evolutionary spectra, with the underlying states pertaining to the eigen-spectra of the multivariate latent processes. We derive an Expectation-Maximization (EM) algorithm for efficiently computing the maximum a posteriori (MAP) estimate of the latent variables and states given the spiking observations, which we then use to construct the evolutionary spectral density matrix. We provide theoretical bounds on the bias-variance performance of our proposed method. Finally, we present simulation results that reveal the superior spectral estimation performance of our proposed methodology, as compared with several existing techniques.

2. PROBLEM FORMULATION

Let $N(t)$ and $H(t)$ denote the point process representing the number of spikes and spiking history of a neuron in $[0, t)$, respectively, where $t \in [0, T]$ and T denotes the observation duration. The Conditional Intensity Function (CIF) [8] of a point process $N(t)$ is defined as:

$$\lambda(t|H_t) := \lim_{\Delta \to 0} \frac{P[N(t+\Delta) - N(t) = 1 | H_t]}{\Delta}. \tag{1}$$

To discretize the continuous process, we consider time bins of length Δ, small enough that the probability of having two or more spikes in an interval of length Δ is negligible. Thus, the discretized point process can be modeled by a Bernoulli process with success probability $\lambda_k := \lambda(k\Delta|H_k)\Delta$, for $1 \le k \le K$, where $K := T/\Delta$ is an integer (with no loss of generality). We refer to λ_k as CIF hereafter for brevity.

In a similar fashion, we consider spiking observations from an ensemble of J neurons, with CIFs $\{\lambda_{k,j}\}_{k=1}^{K}$, for $j = 1, 2, \cdots, J$. Suppose that for each neuron, L independent realizations of the spiking activity is observed. The collection of the binary spiking observations are represented as $\{n_{k,j}^{(l)}\}_{l=1,k=1,j=1}^{L,K,J}$. We model the j^{th} CIF by a logistic link to a latent random process, $\mathbf{X}_j =$

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$[X_{1,j}, X_{2,j}, \cdots, X_{K,j}]^\top$, which needs not be stationary in general. Accordingly, for $1 \le j \le J$, $1 \le k \le K$ and $1 \le l \le L$, we have $n_{k,j}^{(l)} \sim \mathrm{Bern}(\lambda_{k,j})$, where $\lambda_{k,j} = 1/(1+\exp(-X_{k,j}))$. Further, we assume the non-stationary processes to be quasi-stationary [19].

Our goal is to estimate the time-varying power spectral density matrix of the J CIFs directly from the spiking observations. Following the formation of Priestley's evolutionary spectra [17], each random process $X_{k,j}$, with mean $\mu_{k,j}$, will have a representation of the form,

$$X_{k,j} - \mu_{k,j} = \int_{-\pi}^{\pi} e^{ik\omega} A_{k,j}(\omega)\, dZ_{k,j}(\omega), \tag{2}$$

where $A_{k,j}(\omega)$ is the time-varying amplitude function and $dZ_{k,j}(\omega)$ is an orthogonal increment process. To define a discrete-parameter harmonic process, we approximate $Z_{k,j}(\omega)$ by a jump process over N frequency bins [14], and thereby replace it with $\frac{\pi}{N}(a_{j,n} + ib_{j,n})$, at $\omega_n = n\pi/N, 1 \le n \le N-1$, where $a_{j,n}$ and $b_{j,n}$ are random variables. Given that the random processes are real-valued, we use the symmetry $Z_{k,j}(\omega) = Z_{k,j}(-\omega)$, and express the discretized version of Eq. (2) as

$$X_{k,j} = \mu_{k,j} + \frac{2\pi}{N} \sum_{n=1}^{N-1} A_{k,j}(\omega_n)\,(a_{j,n}\cos(\omega_n k) - b_{j,n}\sin(\omega_n k)).$$

To explicitly model the quasi-stationarity, we further assume the J-variate random process $\{X_{k,j}\}_{k=1}^{K}$ to be jointly stationary in windows of small enough length W, and divide the data duration K into M non-overlapping segments of length W, with $K = MW$. The vector process $[X_{k,1}, X_{k,2}, \cdots, X_{k,J}]$ is assumed to be jointly stationary for $(m-1)W + 1 \le k \le mW, 1 \le m \le M$. Under this quasi-stationarity assumption, we get

$$X_{k,j} = \mu_{m,j} + \frac{2\pi}{N} \sum_{n=1}^{N-1} (p_{m,j,n}\cos(\omega_n k) - q_{m,j,n}\sin(\omega_n k)),$$

for $(m-1)W + 1 \le k \le mW$, $1 \le m \le M$ and $1 \le j \le J$ where $p_{m,j,n}$ and $q_{m,j,n}$ are random variables.

The evolutionary spectrum of $X_{k,j}$ at frequency ω_n is defined as $f_{k,j}(\omega_n)\, d\omega_n = |A_{k,j}(\omega_n)|^2 \mathbb{E}|dZ_{k,j}(\omega_n)|^2$ [17]. Moreover, for a J-variate vector-valued orthogonal increment process $\mathbf{Z}(\omega_n) := [Z_1(\omega_n), \cdots, Z_J(\omega_n)]^\top$, the spectral density matrix can be formulated as $\boldsymbol{f}(\omega_n) d\omega_n := \mathbb{E}[d\mathbf{Z}(\omega_n) d\mathbf{Z}(\omega_n)^H]$ [24]. Extending this to the evolutionary spectra, the evolutionary spectral density matrix according to our model can be formulated as

$$\boldsymbol{f}_m(\omega_n) = \frac{\pi}{N}\, \mathbb{E}[(\mathbf{p}_{m,n} + i\mathbf{q}_{m,n})(\mathbf{p}_{m,n} + i\mathbf{q}_{m,n})^H], \tag{3}$$

where $\mathbf{p}_{m,n} := [p_{m,1,n}, \cdots, p_{m,J,n}]^\top$ and $\mathbf{q}_{m,n} := [q_{m,1,n}, \cdots, q_{m,J,n}]^\top$, for $1 \le m \le M$ and $1 \le n \le N-1$. Defining $\mathbf{X}_{m,j} := [X_{(m-1)W+1,j}, \cdots, X_{mW,j}]^\top$, $\mathbf{v}_{m,j} := [\frac{N}{2\pi}\mu_{m,j}, p_{m,j,1}, q_{m,j,1}, \cdots, p_{m,j,N-1}, q_{m,j,N-1}]^\top$, $\widetilde{\mathbf{X}}_m := [\mathbf{X}_{m,1}, \cdots, \mathbf{X}_{m,J}]$, $\mathbf{V}_m := [\mathbf{v}_{m,1}, \cdots, \mathbf{v}_{m,J}]$, we can write $\widetilde{\mathbf{X}}_m = \mathbf{A}_m \mathbf{V}_m$, for $1 \le m \le M$, in which $\mathbf{A}_m$ is a $W \times 2N-1$ matrix with the first column filled with all ones, and the $(w, 2u)^{\text{th}}$ and $(w, 2u+1)^{\text{th}}$ elements given by $\cos(\frac{\pi u((m-1)W+w)}{N})$ and $-\sin(\frac{\pi u((m-1)W+w)}{N})$, respectively, for $w = 1, 2, \cdots, W$ and $u = 1, 2, \cdots, N-1$.

Further, we define $\mathbf{w}_{m,n} := [\mathbf{p}_{m,n}^\top, \mathbf{q}_{m,n}^\top]^\top$ for $1 \le n \le N-1$, $\mathbf{w}_{m,0} := [\mu_{m,1}\ \mu_{m,2}\ \ldots\ \mu_{m,N}]^\top$ and $\mathbf{w}_m := [\mathbf{w}_{m,0}^\top, \mathbf{w}_{m,1}^\top, \cdots, \mathbf{w}_{m,N-1}^\top]^\top$. Note that $\mathbf{w}_m$ is the vectorization of the matrix $\mathbf{V}_m$ and both are equivalent representations, for the discrete parameter harmonic process driving the spiking observations in the time window m. The evolutionary spectral density matrix as in Eq. (3) is determined by computing $\mathbb{E}[\mathbf{w}_{m,n}\mathbf{w}_{m,n}^T]$ for $1 \le n \le N-1$. Thus, the task of determining the evolutionary power spectra of the J-variate random process can be reduced to computing $\mathbb{E}[\mathbf{w}_m \mathbf{w}_m^T]$, for $m = 1, 2, \cdots, M$, given the spiking data $\{n_{k,j}^{(l)}\}_{l=1,k=1,j=1}^{L,K,J}$.

3. PROPOSED MULTITAPER ESTIMATE OF THE SPECTRAL DENSITY MATRIX

It is known that direct estimates of the spectral density suffer from high bias and variance [22]. The bias can be significantly reduced by using tapered estimates, and the variability can be mitigated by using multitaper estimates [21]. The multitaper spectral estimate of a time series $x_1, x_2, \cdots, x_K$ is defined as

$$S^{mt}(\omega) = \frac{1}{P} \sum_{p=1}^{P} \left| \sum_{k=1}^{K} \nu_k^{(p)} x_k\, e^{-i\omega k} \right|^2, \tag{4}$$

where $\{\nu_k^{(p)}\}_{k=1}^{K}$ is the p^{th} discrete prolate spheroidal sequence (dpss) [23], for $1 \le p \le P$. Multitapering can be extended to multivariate time series as in a natural fashion [25], for cross spectral estimation.

First, we note that due to the independence of the L realizations of each point process, the ensemble mean, $\{\overline{n}_{k,j}\}_{k,j=1}^{K,J}$ is a sufficient statistics. Thus, if the effect on the ensemble mean when tapering the latent time series can be determined, we can assess the impact of tapering on our spectral estimation framework. Given that $n_{k,j}^{(l)} \sim \mathrm{Bern}(\lambda_{k,j})$, it is evident that the ensemble average $\overline{n}_{k,j} = \frac{1}{L}\sum_{l=1}^{L} n_{k,j}^{(l)}$, almost surely converges to the expected value $\lambda_{k,j}$, by the strong law of large numbers. Further, considering that $\lambda_{k,j} = \mathrm{logistic}(X_{k,j})$, we get $X_{k,j} = \mathrm{logit}(\lambda_{k,j}) = \log(\lambda_{k,j}/(1-\lambda_{k,j}))$. Thus, for L sufficiently large, it is reasonable to consider $\mathrm{logit}(\overline{n}_{k,j})$ as an approximation to $X_{k,j}$. Hence, if we define $\overline{n}_{k,j}^{(p)}$ to be the ensemble mean that would have been generated if the random process $X_{k,j}$ were tapered by the p^{th} dpss, we have:

$$\overline{n}_{k,j}^{(p)} \quad \approx \quad \mathrm{logistic}\,(\,\mathrm{logit}(\overline{n}_{k,j})\ \nu_k^{(p)}\,). \tag{5}$$

However, note that $\mathrm{logit}(\overline{n}_{k,j})$ is not finite when $\overline{n}_{k,j} = 0$ or $\overline{n}_{k,i} = 1$. Hence, for $1 \le p \le P$, we estimate $\overline{n}_{k,j}^{(p)}$ as in Eq. (5) if $\overline{n}_{k,i} \neq 0$ and $\overline{n}_{k,i} \neq 1$. We thus need to compute the evolutionary spectra corresponding to each of the P tapers, and finally derive the multitaper estimate by averaging the P spectra. In the next subsection, we consider estimating the power spectral density matrix of the untapered process first, and then extend it to the P tapers by replacing the ensemble average of spiking data $\{\overline{n}_{k,j}\}$ with the tapered ensemble mean $\{\overline{n}_{k,j}^{(p)}\}$, for $p = 1, 2, \cdots, P$.

3.1. Proposed Estimator

In order to efficiently compute $\mathbb{E}[\mathbf{w}_m \mathbf{w}_m^T]$, we need to model the evolution of the spectra. We impose a stochastic continuity constraint on the random variables $\mathbf{w}_m$ in the form of a discrete state-space model $\mathbf{w}_m = \boldsymbol{\Phi}\mathbf{w}_{m-1} + \boldsymbol{\eta}_m$, where the state transition matrix $\boldsymbol{\Phi}$ is a constant matrix and $\boldsymbol{\eta}_m \sim \mathcal{N}(\mathbf{0}, \mathbf{Q}_m)$. We consider a special case where $\boldsymbol{\Phi} = \alpha\mathbf{I}$ is fixed, and therefore need to estimate $\mathbf{Q}_m$. We perform this task via the Expectation-Maximization (EM) algorithm.

The parameters to be estimated are $\boldsymbol{\theta} = \{\mathbf{Q}_m,\ 1 \le m \le M\}$ and the observations are binary spiking data $\mathcal{D} = \{n_{k,j}^{(l)}\}_{k,j,l=1}^{K,J,L}$. Suppose that the current estimate of $\boldsymbol{\theta}$ at the r^{th} iteration is $\hat{\boldsymbol{\theta}}^{(r)}$. In order to ensure convergence and to eliminate undesired coupling we enforce $\mathbf{Q}_m$ to be diagonal, with the n^{th} diagonal entry being $Q_{m,n}$. Further, we assume $\mathbf{Q}_m$ to be independent and identically distributed for $1 \le m \le M$, with a distribution of the form,

$$f(\mathbf{Q}_m) \propto \exp\left(-\gamma \sum_{j=1}^{2J}\sum_{n=1}^{N-2} \left(\log(Q_{m,J(2n-1)+j}) - \log(Q_{m,J(2n+1)+j})\right)^2\right).$$

This prior distribution encourages continuity of the spectral estimates of the adjacent frequency bins corresponding to each latent process in log scale, and can be controlled by appropriately selecting the parameter γ.

Accordingly, considering $(\mathcal{D}, \mathbf{V})$ to be the set of complete data, the complete data likelihood is given by,

$$\log f(\mathcal{D}, \mathbf{V}, \boldsymbol{\theta}) = -\frac{1}{2}\sum_{m=1}^{M}\Big\{(\mathbf{w}_m - \boldsymbol{\Phi}\mathbf{w}_{m-1})^T \mathbf{Q}_m^{-1}(\mathbf{w}_m - \boldsymbol{\Phi}\mathbf{w}_{m-1}) + \log|\mathbf{Q}_m| - \gamma \log f(\mathbf{Q}_m)\Big\} + C, \tag{6}$$

where $\mathbf{w}_0 = \mathbf{0}$ and C represents terms that are not a function of $\boldsymbol{\theta}$.

The E-step of the r^{th} EM iteration requires the Q-function $\mathcal{Q}^{(r)} := \mathbb{E}[\log\ f(\mathcal{D}, \mathbf{V}, \boldsymbol{\theta})|\mathcal{D}, \hat{\boldsymbol{\theta}}^{(r)}]$ to be evaluated. To this end, we assess the conditional expectations $\mathbf{w}_{m|M} := \mathbb{E}[\mathbf{w}_m|\mathcal{D}, \hat{\boldsymbol{\theta}}^{(r)}]$, $\boldsymbol{\Sigma}_{m|M} := \mathbb{E}[(\mathbf{w}_m - \mathbf{w}_{m|M})(\mathbf{w}_m - \mathbf{w}_{m|M})^H|\mathcal{D}, \hat{\boldsymbol{\theta}}^{(r)}]$ and $\boldsymbol{\Sigma}_{m,m-1|M} := \mathbb{E}[(\mathbf{w}_m - \mathbf{w}_{m|M})(\mathbf{w}_{m-1} - \mathbf{w}_{m-1|M})^H|\mathcal{D}, \hat{\boldsymbol{\theta}}^{(r)}]$ utilizing the Fixed Interval and Covariance Smoothing algorithms [26, 27]. However, considering that the forward model is not Gaussian, we cannot directly use Kalman filtering to estimate $\mathbf{w}_{m|m}$ and $\boldsymbol{\Sigma}_{m|m}$ as in [26].

Hence, we employ an alternative method to estimate these conditional moments, utilizing the distribution $f(\{\mathbf{V}\}_1^m|\mathcal{D}_1^m, \hat{\boldsymbol{\theta}}^{(r)})$, where $\{\mathbf{V}\}_1^m = [\mathbf{V}_1, \mathbf{V}_2, \ldots, \mathbf{V}_m]$ and $\mathcal{D}_1^m = \{n_{k,j}^{(l)}\}_{k,j,l=1}^{mW,J,L}$. Note that this is proportional to the product of the two distributions, $f(\mathcal{D}_1^m|\{\mathbf{V}\}_1^m, \hat{\boldsymbol{\theta}}^{(r)})$ and $f(\{\mathbf{V}\}_1^m|\hat{\boldsymbol{\theta}}^{(r)})$, which are Binomial and Gaussian distributed, respectively. Observing the distribution $\{\mathbf{V}\}_1^m|\mathcal{D}_1^m, \hat{\boldsymbol{\theta}}^{(r)}$ to be unimodal, we approximate it by a multivariate Gaussian, and derive the mean of the distribution, $\mathbf{w}_{m|m}^{(r)}$ by the mode of $\log\ f(\{\mathbf{V}\}_1^m|\mathcal{D}_1^m, \hat{\boldsymbol{\theta}}^{(r)})$:

$$\underset{\mathbf{w}_m}{\operatorname{argmax}}\left(\sum_{j,s,w=1}^{J,m,W} L\Big\{\overline{n}_{(s-1)W+w,j}(\mathbf{A}_s\mathbf{V}_s)_{w,j} - \log\left(1+\exp(\mathbf{A}_s\mathbf{V}_s)_{w,j})\right)\Big\} - \frac{1}{2}\sum_{s=1}^{m}\Big\{\log|\mathbf{Q}_s^{(r)}| + (\mathbf{w}_s - \boldsymbol{\Phi}\mathbf{w}_{s-1})^T(\mathbf{Q}_s^{(r)})^{-1}(\mathbf{w}_s - \boldsymbol{\Phi}\mathbf{w}_{s-1})\Big\}\right),$$

and the covariance by the negative of the inverse of its Hessian. Note that the collection of ensemble average of the binary realizations, $\overline{n}_{k,j} = \frac{1}{L}\sum_{l=1}^{L} n_{k,j}^{(l)}$, for $1 \le k \le K, 1 \le j \le J$ is a sufficient statistic. Observing that the objective function is a combination of convex functions and is differentiable, we perform the above optimization using the Newton-Raphson method. Further, we concurrently estimate $\boldsymbol{\Sigma}_{m|m}^{(r)}$, using the Hessian matrix.

Next, we evaluate the updates $\hat{\boldsymbol{\theta}}^{(r+1)}$ in the M-step of the r^{th} EM iteration, by maximizing the Q-function. The function $\mathcal{Q}^{(r)}$ is separable in $\mathbf{Q}_m$'s, which allows independent updates for $\mathbf{Q}_m$ for $1 \le m \le M$. Taking the convexity of the problem into consideration, we employ the multivariate Newton-Raphson method to perform the maximization and derive an update for $\mathbf{Q}_m, 1 \le m \le M$.

Following convergence, we use the final estimates of $\mathbf{w}_{m|M}$ and $\boldsymbol{\Sigma}_{m|M}$ derived through the above EM iterations, to estimate the evolutionary spectral density matrix as in Eq. (3). The same EM procedure can be carried out for $\{\overline{n}_{k,j}^{(p)}\}$, for $p = 1, 2, \cdots, P$, and finally the multitaper spectral estimates can be evaluated by averaging the tapered estimates as outlined in Algorithm 1.

Algorithm 1 Estimation of Multitaper Evolutionary Spectra

Inputs: Collection of ensemble averages of the spiking observations $\{\overline{n}_{k,j}\}_{k,j=1}^{K,J}$, the set of P dpss tapers of length W $\{\nu_w^{(p)}\}_{w,p=1}^{W,P}$, parameters γ and α

Outputs: The multitaper estimates of the evolutionary spectral density matrices $\hat{\boldsymbol{f}}_m^{mt}(\omega_n)$ for $1 \le m \le M, 1 \le n \le N-1$

for $p = 1, 2, \ldots, P$ **do**
  for $1 \le w \le W,\ 1 \le m \le M,\ 1 \le j \le J$ **do**
    $k = ((m-1)W + w)$
    if $\overline{n}_{k,j} \neq 0$ and $\overline{n}_{k,j} \neq 1$ **then**
      $(\overline{n}_{k,j})^{(p)} \quad = \quad \text{logistic}\left(\text{logit}(\overline{n}_{k,j})\,\nu_w^{(p)}\right)$
    else
      $(\overline{n}_{k,j})^{(p)} \quad = \quad \overline{n}_{k,j}$
    end if
  end for
  Compute the p^{th} tapered spectral density matrix estimate, $\hat{\boldsymbol{f}}_m^{(p)}(\omega_n)$ for $1 \le m \le M, 1 \le n \le N-1$, employing the proposed EM procedure on the tapered ensemble mean, $\{\overline{n}_{k,j}^{(p)}\}_{k,j=1}^{K,J}$
end for
for $1 \le m \le M,\ 1 \le n \le N-1$ **do**
  $\hat{\boldsymbol{f}}_m^{mt}(\omega_n) = \frac{1}{P}\sum_{p=1}^{P}\hat{\boldsymbol{f}}_m^{(p)}(\omega_n)$
end for
return $\hat{\boldsymbol{f}}_m^{mt}(\omega_n)$ for $1 \le m \le M, 1 \le n \le N-1$;

3.2. Performance Bounds

Here, we present performance bounds of the PSD estimates in the stationary case. Consider a stationary uni-variate bounded random process $x_1, x_2, \ldots, x_K$, with spiking observations $\{n_k^{(l)}\}_{k,l=1}^{K,L}$, where $n_k^{(l)} \sim \text{Bern}(\lambda_k)$ and $\lambda_k = \text{logistic}\,(x_k)$. Let $\hat{S}^{mt}(\omega)$ be the multitaper PSD estimated by using the ensemble mean, $\overline{n}_k$ as an approximation for λ_k:

$$\hat{S}^{mt}(\omega) \quad = \quad \frac{1}{P}\sum_{p=1}^{P}\left|\sum_{k=1}^{K}\nu_k^{(p)}\ \text{logit}(\overline{n}_k)\,e^{-i\omega k}\right|^2.$$

It can be shown that for sufficiently large L and under a saddle-point approximation to the log-likelihoods, the bias and variance of $\hat{S}^{mt}(\omega)$ can be bounded with respect to those of the direct multitaper estimate $S^{mt}(\omega)$ given in Eq. (4) as follows:

$$|\text{bias}(\hat{S}^{mt}(\omega))| \le |\text{bias}(S^{mt}(\omega))| + \mathcal{O}\left(K\frac{\log L}{\sqrt{L}}\right),$$

$$\text{Var}(\hat{S}^{mt}(\omega)) \le \left\{\sqrt{\text{Var}(S^{mt}(\omega))} + \mathcal{O}\left(K\frac{\log L}{\sqrt{L}}\right)\right\}^2.$$

The proof as well as extension to the non-stationary and multivariate case are omitted for brevity.

4. SIMULATION RESULTS

We simulated data consisting of spiking observations from a bivariate random process ($J = 2$). The processes $\mathbf{X}_1$ and $\mathbf{X}_2$ are formed by different linear combinations of a set of AR(6) processes, $\{\mathbf{y}^{(i)} = \{y_k^{(i)}\}_{k=1}^{K}, 1 \le i \le 5\}$, where $\mathbf{y}^{(i)}$ has been tuned around the frequency f_i, with $f_1 = 1.15$ Hz, $f_2 = 0.95$ Hz, $f_3 = 1.5$ Hz, $f_4 = 0.65$ Hz and $f_5 = 1.85$ Hz. Further, one component of $\mathbf{X}_1$ has been amplitude modulated by a low frequency cosine signal at $f_0 = 0.0008$ Hz. All signals have been sampled at 32 Hz ($f_s = 32$

Hz) and a duration of 2000 seconds ($K = 64000$) is considered for the analysis. The following combinations are used to induce non-stationarity and spectral coupling:

$$X_{k,1} = y_k^{(1)} \cos(2\pi f_0 k/f_s) + 1.2 y_k^{(3)} + 1.2 y_k^{(4)} u_{k-0.4K} + \nu_{1,k}$$
$$X_{k,2} = 0.83 y_k^{(2)} + 0.83 y_{k-6}^{(3)} + 0.83\, y_k^{(4)} + 0.83\, y_k^{(5)} + \nu_{2,k},$$

where u_k is the unit step function, and $\nu_{j,k}$ for $j = 1, 2$ are non-zero mean white Gaussian noise components. The noise power is chosen to maintain an SNR of 20 dB for each signal. We generated spike trains for $L = 20$ realizations per CIF, following the logistic link model. The noise means have been set to -5.5 so that the average spiking rate of the ensemble corresponding to each signal is around 0.28 spikes per second. A 30 second sample window of the signal $X_{k,1}$ and the raster plot generated using it is shown in Fig. 1.

We assume the signals to be stationary within windows of duration 100 seconds ($W = 3200$), resulting the total number of windows M, to be 20. The parameter α has been fixed at 0.4 to have optimal dependency across time windows and the prior γ has been set to 0.2. Further we set $N = 800$, the time-bandwidth product of the dpss tapers to 2, and use the first three tapers when computing the estimates.

We compare the results of the proposed PSD estimate with four others, namely, the theoretical PSD, oracle PSD estimate, SS-PSD estimate and PSTH-PSD estimate. The theoretical spectra has been derived using the closed form expression for the PSD of an AR process, and the oracle PSD estimates correspond to the non-overlapping sliding window multitaper estimates of the actual processes $X_{k,j}$. Assuming joint stationarity within windows of length W, the oracle PSD estimates are obtained by evaluating the multitaper PSD estimates of $\mathbf{X}_{m,j}$, for $1 \leq m \leq M$ and $1 \leq j \leq J$.

The other two estimates are derived based on spiking observations, where SS-PSD estimate is based on the approach in [11]. The MAP estimate of each latent process $\mathbf{X}_{m,j}$ is obtained using an EM algorithm based on spiking observations as proposed in [11], followed by computing the the sliding window multitaper estimate of the inferred processes. The PSTH-PSD estimate is derived by directly considering the ensemble mean of the spiking observations $\overline{n}_{k,j}$, often referred to as the peristimulus time histogram (PSTH), to be an estimate of the random signals $X_{k,j}$, followed by sliding window multitapering.

Fig. 2 shows the different spectral estimates from the simulated data. It is evident that the proposed spectral estimator (third column) closely follows the theoretical and oracle estimates (first and second column). The power of SS-PSD estimate decays with frequency, as a result of its time-domain smoothing (Fig. 2-B), and as a result the high frequency components are not accurately identified. The PSTH-PSD estimates have a significant bias and are not able to capture the dynamics of the evolutionary spectra (Fig. 2-B). It is notable that the proposed estimator results in much less background noise compared to all the others, while the dynamic evolution of the spectra are precisely captured and all frequency components are properly discriminated. The relative Mean Squared Errors (MSE) of the estimates with respect to the true theoretical PSD are reported in Table 1. Accordingly, we ascertain that the proposed PSD estimate has the closest MSE to that of the oracle PSD, compared to the other spectral estimates obtained from spiking data.

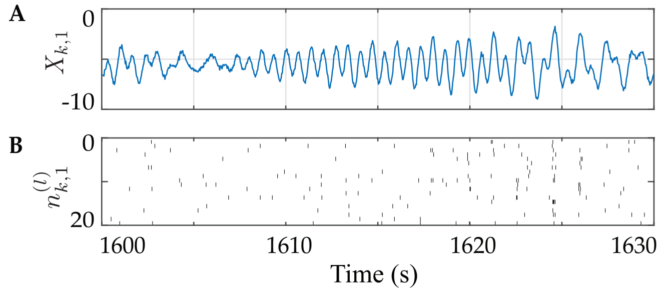

Fig. 1. (A) Samples of the signal $X_{k,1}$ from $t = 1600s$ to $t = 1630s$, (B) The corresponding spiking raster plot.

Table 1. Relative MSE of different spectral estimates

Estimation method	Relative MSE
Oracle PSD Estimate	0.0507
Proposed PSD Estimate	0.1464
SS-PSD Estimate	0.3957
PSTH-PSD Estimate	1.4597

5. CONCLUSION

In this paper, we proposed a spectral estimation technique that is capable of extracting the evolutionary spectral density matrix of a latent multivariate non-stationary process from spiking observations. To this end, we integrated techniques from state-space modeling, multitaper analysis, and point processes. We provided theoretical guarantees on the bias-variance of the proposed method, benchmarked by the classical multitapering framework. We also evaluated the performance of the proposed methodology through a simulation study, which revealed significant gains in terms of the bias-variance trade-off in comparison to several existing techniques.

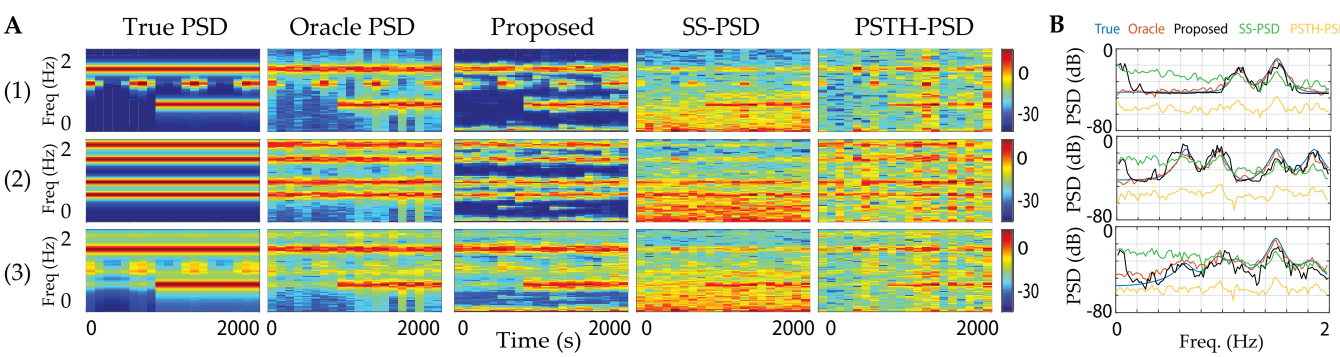

Fig. 2. Estimation of the evolutionary spectra from the simulated data. (A) Columns from left to right correspond to the true theoretical PSD, oracle PSD estimate, the proposed method, SS-PSD, and PSTH-PSD estimates. Rows from top to bottom show $(\boldsymbol{f}_m)_{1,1}(\omega)$, $(\boldsymbol{f}_m)_{2,2}(\omega)$, $(\boldsymbol{f}_m)_{1,2}(\omega)$ (cross-spectral PSD). Color scales are in decibels. (B) snapshots of the evolutionary spectral estimates at a given time (time window $m = 8$, corresponding to $t = 700s - 800s$).

6. REFERENCES

[1] A. Schnitzler and J. Gross, "Normal and pathological oscillatory communication in the brain," *Nature Reviews Neuroscience*, vol. 6, pp. 285–296, 2005.

[2] P. J. Uhlhaas and W. Singer, "Neural synchrony in brain disorders: Relevance for cognitive dysfunctions and pathophysiology," *Neuron*, vol. 52, no. 1, pp. 155 – 168, 2006. [Online]. Available: http://www.sciencedirect.com/science/article/pii/S0896627306007276

[3] L. M. Ward, "Synchronous neural oscillations and cognitive processes," *Trends in Cognitive Sciences*, vol. 7, no. 12, pp. 553 – 559, 2003. [Online]. Available: http://www.sciencedirect.com/science/article/pii/S1364661303002894

[4] R. P. Vertes and R. W. Stackman, *Electrophysiological Recording Techniques*. Humana Press, 2011, vol. 54.

[5] J. J. Jun, N. Steinmetz, J. H. Siegle, D. J. Denman, M. Bauza, B. Barbarits, A. K. Lee, C. Anastassiou, A. Andrei, C. Aydin, M. Barbic, T. Blanche, V. Bonin, J. Couto, B. Dutta, S. Gratiy, D. Gutnisky, M. Husser, B. Karsh, and T. D. Harris, "Fully integrated silicon probes for high-density recording of neural activity," *Nature*, vol. 551, pp. 232–236, 11 2017.

[6] J. Du, T. J. Blanche, R. R. Harrison, H. A. Lester, and S. C. Masmanidis, "Multiplexed, high density electrophysiology with nanofabricated neural probes," *PLOS ONE*, vol. 6, no. 10, pp. 1–11, 10 2011. [Online]. Available: https://doi.org/10.1371/journal.pone.0026204

[7] E. N Brown, R. Kass, and P. P Mitra, "Multiple neural spike train data analysis: state-of-the-art and future challenges," *Nature neuroscience*, vol. 7, pp. 456–61, 06 2004.

[8] E. N. Brown, "Course 14 theory of point processes for neural systems," *Les Houches*, vol. 80, 12 2005.

[9] W. Truccolo, U. T. Eden, M. R. Fellows, J. P. Donoghue, and E. N. Brown, "A point process framework for relating neural spiking activity to spiking history, neural ensemble, and extrinsic covariate effects," *Journal of Neurophysiology*, vol. 93, no. 2, pp. 1074–1089, 2005, pMID: 15356183. [Online]. Available: https://doi.org/10.1152/jn.00697.2004

[10] L. Paninski, "Maximum likelihood estimation of cascade point-process neural encoding models," *Network: Computation in Neural Systems*, vol. 15, no. 4, pp. 243–262, 2004, pMID: 15600233. [Online]. Available: https://doi.org/10.1088/0954-898X_15_4_002

[11] A. C. Smith and E. N. Brown, "Estimating a state-space model from point process observations," *Neural Computation*, vol. 15, no. 5, pp. 965–991, 2003. [Online]. Available: https://doi.org/10.1162/089976603765202622

[12] L. D. Lewis, V. S. Weiner, E. A. Mukamel, J. A. Donoghue, E. N. Eskandar, J. R. Madsen, W. S. Anderson, L. R. Hochberg, S. S. Cash, E. N. Brown, and P. L. Purdon, "Rapid fragmentation of neuronal networks at the onset of propofol-induced unconsciousness," *Proceedings of the National Academy of Sciences*, vol. 109, no. 49, pp. 19 891–19 892, 2012. [Online]. Available: https://www.pnas.org/content/109/49/E3377/1

[13] D. M. Halliday and J. R. Rosenberg, *Time and Frequency Domain Analysis of Spike Train and Time Series Data*. Berlin, Heidelberg: Springer Berlin Heidelberg, 1999, pp. 503–543. [Online]. Available: https://doi.org/10.1007/978-3-642-58552-4_18

[14] S. Miran, P. L. Purdon, E. N. Brown, and B. Babadi, "Robust estimation of sparse narrowband spectra from neuronal spiking data," *IEEE Transactions on Biomedical Engineering*, vol. 64, no. 10, pp. 2462–2474, Oct 2017.

[15] S. Grn, M. Diesmann, and A. Aertsen, "Unitary events in multiple single-neuron spiking activity: Ii. nonstationary data," *Neural Computation*, vol. 14, no. 1, pp. 81–119, 2002. [Online]. Available: https://doi.org/10.1162/089976602753284464

[16] N. E. Huang, Z. Shen, S. R. Long, M. C. Wu, H. H. Shih, Q. Zheng, N.-C. Yen, C. C. Tung, and H. H. Liu, "The empirical mode decomposition and the hilbert spectrum for nonlinear and non-stationary time series analysis," *Proceedings of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences*, vol. 454, 1998.

[17] M. B. Priestley, "Evolutionary spectra and non-stationary processes," *Journal of the Royal Statistical Society. Series B (Methodological)*, vol. 27, no. 2, pp. 204–237, 1965. [Online]. Available: http://www.jstor.org/stable/2984191

[18] W. Martin and P. Flandrin, "Wigner-Ville spectral analysis of nonstationary processes," *IEEE Transactions on Acoustics, Speech, and Signal Processing*, vol. 33, no. 6, pp. 1461–1470, December 1985.

[19] P. Das and B. Babadi, "Dynamic Bayesian multitaper spectral analysis," *IEEE Transactions on Signal Processing*, vol. 66, no. 6, pp. 1394–1409, March 2018.

[20] D. J. Thomson, "Spectrum estimation and harmonic analysis," *Proceedings of the IEEE*, vol. 70, no. 9, pp. 1055–1096, Sept 1982.

[21] D. B. Percival and A. T. Walden, *Spectral Analysis for Physical Applications*. Cambridge University Press, 1993.

[22] B. Babadi and E. N. Brown, "A review of multitaper spectral analysis," *IEEE Transactions on Biomedical Engineering*, vol. 61, pp. 1555–1564, 2014.

[23] D. Slepian, "Prolate spheroidal wave functions, Fourier analysis, and uncertainty v: the discrete case," *The Bell System Technical Journal*, vol. 57, no. 5, pp. 1371–1430, May 1978.

[24] P. J. Brockwell and R. A. Davis, *Time Series: Theory and Methods*. Berlin, Heidelberg: Springer-Verlag, 1986.

[25] A. T. Walden, "A unified view of multitaper multivariate spectral estimation," *Biometrika*, vol. 87, no. 4, pp. 767–788, 2000. [Online]. Available: http://www.jstor.org/stable/2673609

[26] H. E. Rauch, C. T. Striebel, and F. Tung, "Maximum likelihood estimates of linear dynamic systems," *AIAA Journal*, vol. 3, no. 8, pp. 1445–1450, aug 1965. [Online]. Available: https://doi.org/10.2514

[27] P. D. Jong and M. J. Mackinnon, "Covariances for smoothed estimates in state space models," *Biometrika*, vol. 75, no. 3, pp. 601–602, 1988. [Online]. Available: http://dx.doi.org/10.1093/biomet/75.3.601