RESEARCH ARTICLE

On modeling of a recurrent neural network from neural spiking data.

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HIGHLIGHTS

- *A fusion of statistical analysis, modeling, and biology*
- *Guides the computational neuroscientists in modeling of computational features of the neuron models from realistic neural spiking data.*
- *Assessment of the estimation accuracy under the existence of temporal only data (no amplitude)*

Keywords:

- Firing rate based neural networks
- Excitatory-inhibitory neurons
- Neural spiking,
- Kolmogorov-Smirnov tests
- İnterspike intervals

GRAPHICAL ABSTRACT

We present a theoretical and computational work aiming at the estimation of an excitatory and inhibitory recurrent neural network from realistic stimulus-response data. The neural network incorporates firing rates of the excitatory and inhibitory units as state variables. The stimulus and response recordings are taken from a previous study which performs a measurement on the H1 neurons of the order Diptera flies. The parameter estimation is performed by maximum likelihood method. As the stimulus-response data is a single recording of 20 minutes, it is segmented, and individual segments are superimposed on each other to increase the statistical content of information. The true values of the model parameters are unknown as we are not using synthetic data. Because of this fact, two sample Kolmogorov-Smirnov test is applied to compare the interspike intervals of the recorded and model responses. Estimation and analysis results are presented in tabular and graphical forms. In addition, a comparison with previous research employing a modified Fitzhugh-Nagumo model is made.

Figure A. The response of the H1 neurons of true flies of order Diptera to white noise visual stimulus

Aim of Article : *A theoretical study aiming at the modeling of an excitatory-inhibitory neural network from neural spiking data.*
Theory and Methodology: *The methodology is based on maximum likelihood method where the likelihood function is derived from the probability mass function of an Inhomogeneous Poisson Process. The optimization algorithm is of constrained type based on interior point methods. The measurement data sets are the neural spiking instants of the **H1 neurons of the order Diptera flies***.
Findings and Results: *As one does not know the true parameters of the model in consideration, the accuracy of the findings are assessed using two sample Kolmogorov-Smirnov tests.*
Conclusion : *The results suggests that the p-Value obtained from Kolmogorov-Smirnov tests has a dependence of the number of segments and the individual segment lengths. The estimated parameters appear to be closer to each other when the segment size is kept in the segment lengths stay in the range (10,25) seconds.*

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H I G H L I G H T S

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Keywords: *Firing rate based neural networks, Excitatory-inhibitory neurons, Neural spiking, Kolmogorov-Smirnov tests, interspike intervals*

I. INTRODUCTION

A. Literature survey

The science related to neuron modeling dates well back to 1950s. The related developments led to an emerging field called as "theoretical and computational neuroscience". The research community classified these models into three types namely the compartmental, cascade, and black box models. The compartmental models may involve single or multiple subsystems and thus are relatively complicated. They are used when one needs to simulate one or more biophysical features of realistic neurons. Compartmental neural modeling is appeared after the development of the well known Hodgkin-Huxley model [23] in 1952. This was a highly nonlinear fourth order differential equation aiming at the description of quantitative features such as membrane potentials and ion channel conductances Following that, simpler models such as Fitzhugh-Nagumo [18], Morris-Lecar [35] and Hindmarsh-Rose [22] models appeared. Also models with more emphasis on specific subsystems of a

neuron such as dendrites, soma or axon are also met (such as [3]).

The cascade models on the other hand are less complex and place lesser emphasis on the computational details. These models are chosen when biophysical characteristics are not important. They generally consist of a linear filter and a nonlinearity that include some dynamical features [13]. Examples of studies involving such models are [30,24,38,1]. These are specifically related to visual subsystem.

The third type of modeling that can be met in computational neuroscience is based on a black box approach. In this case, the models focus on the ability of the neurons to process signals and they have a reasonable set of statistical features. An example is the representing the neuron's response by a probability distribution when the neuron is triggered by stimulus. Associated examples are [4,2,17,20].

Efficiency and applicability of a suggested model depends explicitly on the researcher's aim and the related mechanism of data collection. In the case of in vivo experiments, it is difficult to measure membrane potentials directly by placing an electrode on the membrane of the neuron under examination. That may cause a damage of the neuron or change in its activities. Those will obviously lead to incorrect measurements [11]. Alternatively, it is possible to collect data from an examined cell without touching it by placing an electrode in an area surrounding the cell membrane. Although this approach does not give us the correct amplitudes of the membrane potential, it is likely to detect the bursts of successive action. In other words, that yields information as a time series of successive peaks rather than a value of potential levels. This set of data is called as a neural spike train (or trains) which is similar to bursts and idle times that would be formed based on the neuron's activity. Bursts could be defined as closely spaced spikes, whereas the idle periods can be represented by separate longer-term transactions. Although they may seem meaningless at a first look, they include valuable information about the activity of the investigated neuron. The work in [39] suggests that a sudden jump in data during an instant discovers what actually happened inside a neural cell. In addition, the random distribution of those spikes within a specific time interval largely obeys an Inhomogeneous Poisson Process (IPP). Therefore, it is possible to apply likelihood function derived from probability mass function of a Poisson distribution [36]. The studies by [5, 37] proposed a system identification approach that estimates internal parameters using maximum likelihood for integrating and firing neuron models. Firing probabilities are used to derive likelihood function based on a local Bernoulli approximation. Similarly, a study in [7] used maximum likelihood estimation to characterize functionality between neurons rather than study neurons individually. The study [40] presented a data analysis problem that deals with the stimulus-response experiments

in neurophysiology. When the stimulus is known and the experiment is under the control, it is possible to record the spiking activities of the neurons. The study in concern proposed a state-space model to analyze response when the stimulus is implicit. Conditional intensity function is estimated based on general point processes that characterize spiking activities of neurons. This study also applied maximum likelihood algorithm to optimize parameters. The research in [21] claimed that the electrical signals in a biological neurons are random due to the chemical reactions in the ion channels and synaptic processes. The noise generated from the ion channels were described by mathematical models in some recent studies [33, 26, 41]. Other studies [28, 27, 42] stated that the movement of the ions in the channels produces electromagnetic fields that have influences on the membrane potential. However, the authors in [42] claimed that the operation of the heart can be determined through a magnetic fields produced by its electrical system.

Recently, the researchers have given more attention to the modeling of biological neurons by using artificial neural networks. For example, static feedforward neural networks are used by the researchers in some studies [10, 9, 8] to model auditory cortex. However, this type of neural networks does not sufficiently characterize the time dependent features of biological neurons such as action potentials and refractory periods. Therefore, dynamical neural networks seem to be better in the characterization of signal processing mechanisms of the biological neurons.

The literature regarding computational neuroscience has witnessed more attention to identify parameters of the neuron(s). Simple techniques such as minimum mean square estimation and spike synchronization could be utilized to calculate potential of membrane or firing rate when they are measurable. These methods become inapplicable when the collected data is discontinuous and there is no information about amplitude of amplitudes or rate of firing. Some studies such as [29] applied synchronization technique to spiking neurons. However, this technique requires a synchronization of two successive set of spikes that needs a reducing in inter-arrival time of spikes. The main problem in this method is the additional computational overhead introduced by the evaluation of the distance between two successive spikes. That will add extra complexity to the system.

B. *About this work*

As a difference from the studies performed by [15, 11, 13, 14] we will attempt to fit a firing rate based recurrent neural network model to a realistic stimulus-response data. One similar research is done by [12] where the response of H1 neurons of true flies of order Diptera [19] against a white noise visual stimulus is used. The data is available as a result of a research by [25]. In the aforementioned work ([12]), the model fitted to the H1 neuron stimulus-response pair is a modified Fitzhugh-Nagumo model [18] where the output

membrane potential is mapped to a firing rate variable by a specially formed sigmoid function. In this work, we will use an excitatory-inhibitory neural network model proposed by [34]. The model is formed by two differential equations representing the dynamics of the firing rates of excitatory and inhibitory units. The excitatory neuron's firing rate will be taken into consideration. The stimulus and neural spiking data will be the same as that of [12]. This will allow us to perform a comparison in the estimation performance of the two approaches. As we are not employing synthetically generated data from models with known parameters, no true parameter information will be available. After the estimation process is finalized, the model can be simulated with the estimated parameters, a firing rate profile and associated spike timings will be generated. The spike generation will make use of Inhomogeneous Point Process simulation with event rate being the firing rate of the excitatory neuron. The interspike intervals of the simulated spikes and the ones available from the data will be compared using Two Sample Kolmogorov-Smirnov statistical test [32, 31]. The p-values obtained from the tests will be presented in graphical forms. These results will be compared to the ones in [12].

II. MATERIALS AND METHODS

A. The neuron model

In this research, we will have a second order recurrent neural network model in the following form:

$$
\begin{aligned}
\dot{r}_e &= \beta_e \left[-r_e + \frac{F_e}{1+e^{-a_e(w_{ee}r_e - w_{ei}r_i + I)}} \right] \\
\dot{r}_i &= \beta_i \left[-r_i + \frac{F_i}{1+e^{-a_i(w_{ie}r_e - w_{ii}r_i + I)}} \right]
\end{aligned}
\tag{1}
$$

In the above the subscripts (e) and (i) represent the association of the related variables with the excitatory and inhibitory units respectively. The model have some differences from the one presented in [15]. Main difference appears in the choice of the state variables. [15] models the dynamics of the membrane potentials (v_e and v_i) whereas (1) presents the dynamics of the firing rates (r_e and r_i) directly. The discussion on both types of models can be found in the reference [34]. The definitions of the parameters in (1) is available in Table 1.

Table 1: The definitions and nominal values of the parameters of the neural network model in (1)

Parameter	Definition
β_e	The reciprocal time constant of the excitatory neuron
β_i	The reciprocal time constant of the inhibitory neuron
w_{ee}	Weight representing the strength of excitatory autaptic input
w_{ei}	Weight representing the strength of inhibitory synaptic input to excitatory unit
w_{ie}	Weight representing the strength of excitatory synaptic input to inhibitory unit
w_{ii}	Weight representing the strength of inhibitory autaptic input
F_e	Maximum firing rate of excitatory unit
F_i	Maximum firing rate of inhibitory unit
a_e	Excitatory slope
a_i	Inhibitory slope

B. Stimulus and response data

In this research, we will apply the same stimulus and response pair as in [12]. That is a white noise based visual stimulus and the associated response obtained from H1 neurons. This data set is a 20 minute recording of the experimental measurements on the H1 neurons of true flies [19, 25]. For convenience, a plot of the stimulus and associated response can be seen in **Figures 1** and **2** respectively.

Figure 1: The white noise visual stimulus applied to the H1 neurons of true flies of order Diptera by [25]. Only the first two seconds are shown here to for the sake of proper displaying of its variation. Here the bin size is $\delta t = 2$ ms.

the number of spikes in the interval $[t, t + \Delta t)$. That is statistically related to the firing rate $r(t)$ and λ will represent the mean spike count corresponding to the time dependent firing rate $r(t)$. In (2), $N(\tau)$ stands for the cumulative total number of spikes up to time τ, thus making $N(t + \Delta t) - N(t)$ equal to the number of spikes for the time interval $[t, t + \Delta t)$.

Now, suppose that one has a spike train $(t_1, t_2, \ldots, t_K)$ in the time interval $(0, T)$. Here, $0 \leq t_1 \leq t_2 \leq \cdots \leq t_K \leq T$, and so t and Δt become 0 and T. The spike train can be considered as a time series (including the time stamps for K spikes). So a likelihood function associated with any spike train $(t_1, t_2, \ldots, t_K)$ can be derived from an Inhomogeneous Poisson Process [16, 6] in the following way:

$$p(t_1, t_2, \ldots, t_K) =$$
$$\exp\left(-\int_0^T r(t, x, \theta) dt\right) \prod_{k=1}^K r(t_k, x, \theta) \qquad (4)$$

The function yields the likelihood of a given spike train $(t_1, t_2, \ldots, t_K)$ that occurs with the rate function $r(t, x, \theta)$ which obviously is relying mainly upon model parameters and the stimulus.

An important point that is to be discussed here is the generation of test spikes for the statistical analysis. As we don't have any firing rates available from experimental measurements we will need to apply a statistical analysis on the spike timings. The estimated model's firing rate output should be converted to spike timings. In order to obtain those, one needs to perform an Inhomogeneous Poisson Process simulation using the firing rate output(s) of the model in (1) with the estimated parameters. The stimulus should be the same as the one used in the generation of the experimental data (provided by [25]). The simulation can be performed using the following scheme [16]:

(1). Given the firing rate of a neuron as $r(t)$,

(2). Find the probability of firing at time t_i by evaluating $p_i = r(t_i) \delta t$ where δt is the integration interval. It should be a small real number such as one milliseconds,

(3). Draw a random number $x_{rand} = U[0,1]$ which is uniformly distributed in the interval $[0,1]$. Here, U stands for a uniform distribution,

(4). If $p_i > x_{rand}$ fire a spike at $t = t_i$, else do nothing,

(5). Collect spikes as $S = [t_1, \ldots, t_{N_s}]$ where N_s will be the total number of spikes collected from one simulation.

Note that the above scheme requires sufficiently small bin sizes like 1 or 2 milliseconds.

Figure 2: The response of the H1 neurons of true flies of order Diptera to white noise visual stimulus. The data is provided by [25]. Only the first two seconds are shown here to for the sake of proper displaying of its variation. Here the response is shown as spikes and each occurence of a spike is shown in a binary fashion. i.e. A **1** for an existing spike and a **0** for no spike.

C. Inhomogeneous Poisson Processes

While introducing this study, it is stated that the neural spiking process largely obeys the Inhomogeneous Poisson Processes. In its simplest sense, it is a discrete random process characterized by an event rate λ and has a probability mass function defined by:

$$Prob\left[N(t + \Delta t) - N(t) = k\right] = \frac{e^{-\lambda} \lambda^k}{k!} \qquad (2)$$

where k is the number of events that occur in the interval $[t, t + \Delta t)$. In homogeneous versions of the Poisson processes the λ is constant in that interval. In neural operation on the other hand, the process is much more complex and assuming a constant event rate will mostly be not sufficient and thus a time varying rate is needed. That actually is equivalent to the firing rate $r(t)$ of the neuron under examination. One can refer to r_e or r_i in (1). This will be an Inhomogeneous Poisson Point Process with the event rate λ replaced by a mean firing rate defined by:

$$\lambda = \int_t^{t+\Delta t} r(\tau) d\tau \qquad (3)$$

where $r(t)$ will be $r_e(t)$ if the neural spiking of the excitatory neuron is considered. For the inhibitory neuron $r(t)$ should be replaced by $r_i(t)$. Now the term k represents

D. Maximum Likelihood Approaches

The parameters in consideration is vectorized as follows:

$$\theta = [\beta_e, \beta_i, w_{ee}, w_{ei}, w_{ie}, w_{ii}, a_e, a_i, F_e, F_i] \qquad (5)$$

The maximum probability here relies on the function proposed in (4) and includes each spike timing as well. Estimation theory asserts that determining maximum likelihood is asymptotically effective and goes as far as the Cramér-Rao bound when the data size increases. Thus, in order to expand the likelihood function in (4) to further cover settings with numerous spike trains initiated by numerous stimuli, a series of M stimuli should be assumed. Take the m-th stimulus $(m = 1, ..., M)$ to initiate a spike train containing K_m spikes in the time window $[0, T]$, and the spike timings are given by $S_m = \left(t_1^{(m)}, t_2^{(m)}, ..., t_{K_m}^{(m)}\right)$. By (4). According to (4), the probability function for the spike train S_m can be determined as:

$$p(S_m|\theta) = \exp\left(-\int_0^T r^{(m)}(t)dt\right)\prod_{k=1}^{K_m} r^{(m)}\left(t_k^{(m)}\right) \qquad (6)$$

in which $r^{(m)}$ represents the firing rate against the m-th stimulus. Here it should be noted that the rate function $r^{(m)}$ entirely relies on the parameters related to neuron parameters θ and the applied stimulus. Supposing the stimulus and its elicited responses in each mth trial are independent one can derive a joint likelihood function as:

$$L(S_1, S_2, ..., S_M|\theta) = \prod_{m=1}^M p(S_m|\theta) \qquad (7)$$

To improve its convexity, we can make use of natural logarithm and derive a log likelihood function as shown below:

$$\begin{aligned} l(S_1, S_2, ..., S_M|\theta) \quad &= -\sum_{m=1}^M \int_0^T r^{(m)}(t)dt \\ &+ \sum_{m=1}^M \sum_{k=1}^{K_m} \ln r^{(m)}\left(t_k^{(m)}\right) \end{aligned} \qquad (8)$$

Finally, the maximum likelihood estimates of the parameter vector θ is obtained by:

$$\hat{\theta}_{ML} = \underset{\theta}{\arg\max}[l(S_1, S_2, ..., S_M|\theta)] \qquad (9)$$

E. Analysis approaches

As the true values of the parameters in Table 1 are not available to us, the only viable approach seems to perform a statistical analysis on the measured and simulated spike trains. One such approach is the Kolmogorov-Smirnov test [32, 31] which assesses whether two samples are drawn from the same distribution or not. MATLAB's [h,p,ks2stat] = kstest2(x1,x2) routine can perform this test for two arrays x_1 and x_2 respectively. The routine tests the null hypothesis that the data in vectors x_1 and x_2 are from the same continuous distribution using the two-sample Kolmogorov-Smirnov test. The alternative hypothesis is that x_1 and x_2 are from

different distributions. MATLAB routine can return both the h value and p value at 5% significance level. Here h value appears to be **1** when the test rejects the null hypothesis. The p value behaves reversely as it is the probability of observing a test statistic as extreme as, or more extreme than, the observed value under the null hypothesis. As a result it will be closer to **1** when the null hypothesis is not rejected.

In this research, the test is performed on the interspike intervals (ISI) of the measured and simulated neural spike trains.

(1). After the parameter identification by maximum likelihood method completed, the model in (1) is simulated with the estimated parameters against the stimuli used in the estimation process (i.e. the one in **Figure 1**).

(2). The firing rate is recorded and an Inhomogeneous Poisson Process simulation is performed using the method introduced in **Section 2.C**.

(3). The interspike intervals (ISI) of both simulated spikes obtained in **Step 2** and the measured ones available from the data provided by [25] are evaluated.

(4). The interspike intervals are provided to two sample Kolmogorov-Smirnov test and the p-values are recorded.

(5). During the tests, the stimulus-response pair is segmented and the measured and simulated responses are superimposed. Different number of segments are examined. This is performed as a single train of spikes may not be statistically sufficient to reflect the statistical content of the response.

(6). In [h,p,ks2stat] = kstest2(x1,x2), x_1 corresponds to ISI of measured spikes and x_2 corresponds to the ISI of the simulated spikes obtained in **Step 2**. The p values are taken into consideration in this research.

III. RESULTS

In this study, we attempt to estimate the parameters of an firing rate based neural network model representing excitatory and inhibitory behaviors. The mathematical model of this network is presented in (1) and the parameters to be estimated are available in Table 1. The stimulus-response pair is a realistic data obtained as a result of an experiment performed by [25]. Here the stimulus is a visual input of white noise type recorded for 20 minutes (First two seconds is available in **Figure 1**). The response is the firing instants received from the H1 neurons of the true flies of order Diptera (First two seconds is available in **Figure 2**). As we are not using synthetically generated data, we have no information on true parameters. The performance of the estimation is assessed using two sample Kolmogorov-Smirnov test on the interspike intervals of the recorded spiking data and responses of the model with estimated parameters.

The parameters are estimated by maximizing the joint likelihood function in (8). Optimization will be performed by MATLAB's fmincon routine. This allows the user to define constraints and we apply a lower bound of zero to ensure all the parameters remain in positive region. This will both ensure the stability of the algorithm and also the excitatory-inhibitory nature of the model in (1) is not disturbed. We only have a single recording of a relatively longer duration. Thus, one will need to partition the stimulus and response into segments of predetermined length. The segmentation will be beneficial as responses falling into individual segments can be superimposed to increase statistical content of information. One can observe in **Table 2** the results obtained from maximum likelihood estimation of parameters.

Table 2: The estimated parameters θ_{ML} and their dependence to the length of the segments (T_{seg}). The number of segments are indicated by N_{seg}.

T_{seg}	N_{seg}	$\widehat{\beta}_e$	$\widehat{\beta}_i$	w_{ee}	w_{ei}	w_{ie}	w_{ii}	a_e	a_i	F_e	F_i
600.0	2	188.50	279.52	315.24	64.68	271.54	236.12	153.84	60.42	44.67	289.09
400.0	3	23.54	260.10	178.55	16.63	457.98	90.23	243.11	294.44	44.67	103.13
300.0	4	181.63	352.44	415.08	19.04	121.46	75.13	411.93	186.02	44.67	294.13
200.0	6	15.11	154.32	226.83	13.54	210.41	56.20	86.12	197.90	44.68	136.20
150.0	8	111.80	117.90	243.51	350.43	474.50	170.36	446.64	160.09	44.67	19.42
120.0	10	16.70	498.80	79.12	431.33	90.73	123.66	120.03	129.57	89.40	265.75
100.0	12	164.52	117.64	243.50	350.60	486.09	170.23	447.39	159.94	44.67	16.24
80.0	15	93.89	298.27	418.81	19.21	274.78	233.81	128.49	29.33	44.67	300.95
60.0	20	132.89	345.36	433.38	52.32	409.45	338.66	464.99	421.40	44.68	378.80
50.0	24	105.35	243.59	183.07	13.42	379.81	265.20	353.56	29.84	44.68	169.42
40.0	30	68.27	116.33	422.60	41.86	403.69	469.93	76.69	284.45	44.68	258.11
30.0	40	102.12	293.87	322.42	24.72	274.87	233.75	125.00	24.04	44.68	301.16
25.0	48	111.04	17.59	405.97	482.82	150.12	352.77	340.92	312.97	44.68	52.77
20.0	60	95.52	21.35	480.33	188.89	476.42	415.38	410.33	231.41	44.69	466.87
15.0	80	83.48	19.78	485.35	188.49	483.46	415.68	410.61	231.39	44.69	467.84
12.0	100	117.87	21.53	480.75	188.56	476.67	415.39	410.34	231.41	44.69	466.91
10.0	120	104.81	25.79	486.65	186.30	485.18	415.65	410.59	231.39	44.71	467.76
8.0	150	94.14	116.14	461.20	77.55	226.71	467.42	158.95	119.61	44.72	212.01
6.0	200	135.70	29.57	336.38	169.75	125.37	223.65	256.82	16.09	44.71	331.76
5.0	240	90.23	70.67	450.14	62.48	269.97	192.39	360.96	277.86	44.75	37.13
4.0	300	126.92	244.80	122.57	13.70	380.86	265.27	354.33	17.67	44.75	197.02
3.0	400	122.45	357.09	418.17	3.05	411.64	339.47	475.62	424.06	44.77	380.12
2.0	600	124.77	164.32	150.83	17.40	353.63	263.02	40.09	81.77	44.84	168.31
1.0	1200	110.37	7.46	340.41	165.29	349.10	388.43	499.99	155.79	45.04	278.53
0.5	2400	121.30	343.46	484.86	68.36	18.48	13.92	228.91	318.02	45.52	239.72

For the Kolmogorov-Smirnov analysis one can refer to the **Figures 3 - 17**. The figure explanations comment on the variation of p value with the super imposed number of samples (or samples N_{seg}). The test results show that regardless of the length of the segments (T_{seg}), the p value exceeds $p = 0.95$ level when number of samples are at least equal to $N_{seg} = 40$. When the length of the segments are restricted to a minimum of $T_{seg} = 5$ seconds, most of the cases yield $p > 0.95$ when we have a sample size of $N_{seg} = 30$ or more.

IV. CONCLUSION

A. Summary

In this work, we presented a framework for estimation of the parameters of a firing rate based excitatory-inhibitory dynamical neural network from a realistic set of stimulus-response data. The model is of second order type and has a total of 10 parameters that are to be estimated (1). The stimulus is a 20 minute recording of white noise visual excitation. The response is a binary array of neural spikes
that are received from H1 neurons of true flies of order Diptera [19, 25]. As a result, only the temporal locations of the spikes are available to us. Thanks to the evidence that the neural spiking phenomenon largely obeys the Poisson processes, we can employ a point process likelihood function such as (7) to perform an estimation of our model parameters. Contrary to the studies like [15, 13, 11, 14] we do not know the true value of our parameters (as we do not employ synthetic data here) and thus needed to apply two sample Kolmogorov-Smirnov statistical test to compare the interspike intervals of the recorded response and the one obtained after the simulation of the model in (1) with the estimated parameters.

B. Discussion of the results

In the analysis by Kolmogorov-Smirnov method, the resultant p value which shows the probability that the interspike interval distribution comes from two similar distributions. In the case that 5% significance level is sufficient, $p = 0.95$ level should be achieved to conclude that our spiking procedures are coming from two point

processes with the same event (thus firing) rate. If the significance level is pushed to 10%, then $p = 0.90$ should be reached. However, higher percentages for the significance level should be avoided.

Based on the results in **Figures 3-17**, one can note that the p value obtained from the two sample Kolmogorov-Smirnov analysis stays in ranges higher than $p = 0.95$ if the sample size (number of segments) remains at least $N_{seg} = 40$ for all cases. When the segment size is larger than $T_{seg} = 5$ seconds, the required number of samples is even smaller i.e. $N_{seg} = 30$. In **Table 2**, parameters appear to be closer to each other when the segment size is kept in the range $10 \leq T_{seg} \leq 25$ seconds. Interesting coincidence is that, the minimum required sample size is also lower than $N_{seg} = 40$.

When the results of [12] is examined, it appears that the required sample size to have p values higher than $p = 0.95$ requires larger number of samples. In **Table 3**, one is able to see some results from [12] which bears the segment sizes T_{seg} in seconds and required number of samples N_{seg} to have p values higher than $p = 0.95$. It is pretty obvious that, the model in [12] requires more samples to yield p values higher than $p = 0.95$. The minimum required sample size is $N_{seg} = 50$ and obtained when the segment size is $T_{seg} = 0.5$ seconds. For larger segment sizes, the required number of samples is even larger. So one can say that, the model in (1) has a better modeling capacity for H1 neurons of Diptera flies.

Table 3: The required sample size N_{seg} v.s. the segment size T_{seg} which yields p values higher than $p = 0.95$ for the model in [12].

T_{seg} (s)	N_{seg}
0.5	50
1	170
2	130
3	140
4	130
6	150

CONFLICTS OF INTEREST

They reported that there was no conflict of interest between the authors and their respective institutions.

RESEARCH AND PUBLICATION ETHICS

In the studies carried out within the scope of this article, the rules of research and publication ethics were followed.

FIGURES
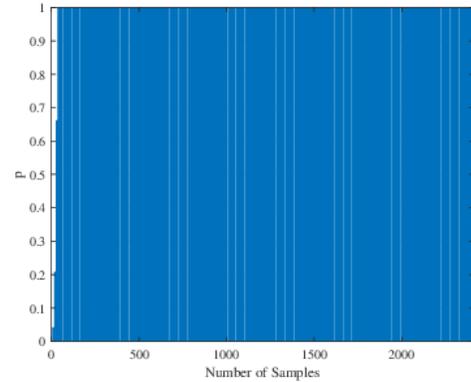
Figure 3: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 0.5$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger.
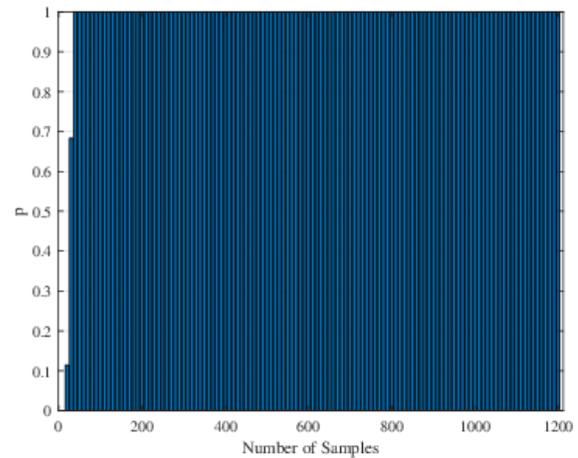
Figure 4: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 1$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger.
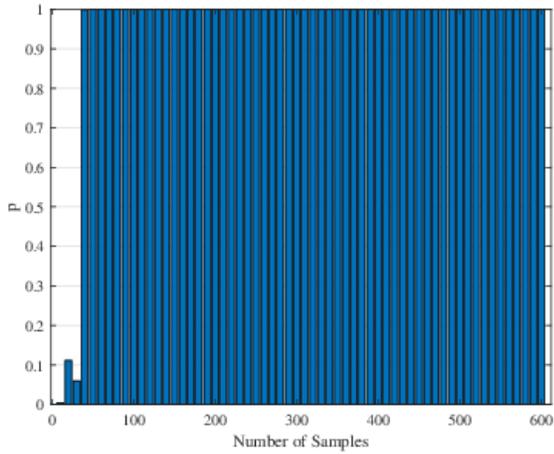
Figure 5: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 2$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger.
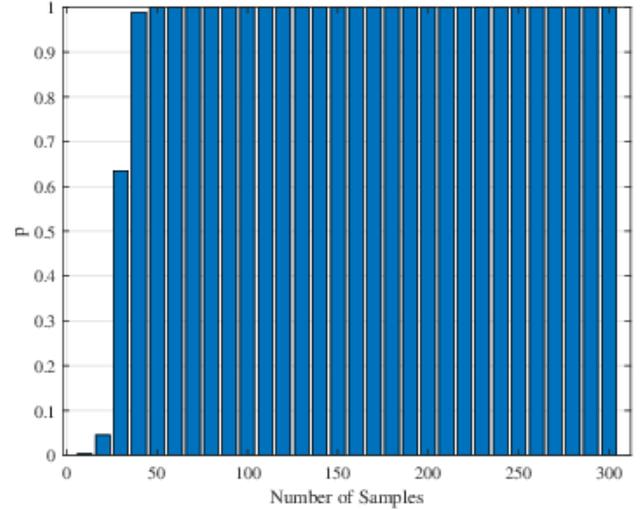
Figure 7: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 4$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger.
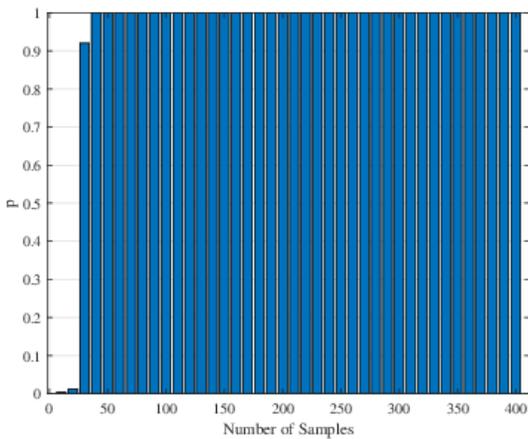
Figure 6: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 3$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger. Considering 10% significance p value reaches $p = 0.90$ when number of segments reach $N_{seg} = 30$.
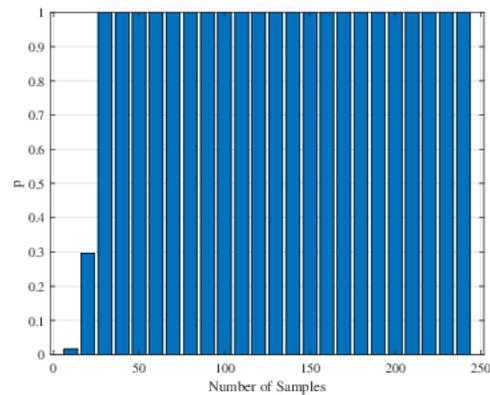
Figure 8: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 5$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.

value reaches $p = 0.90$ when number of segments reach $N_{seg} = 30$.
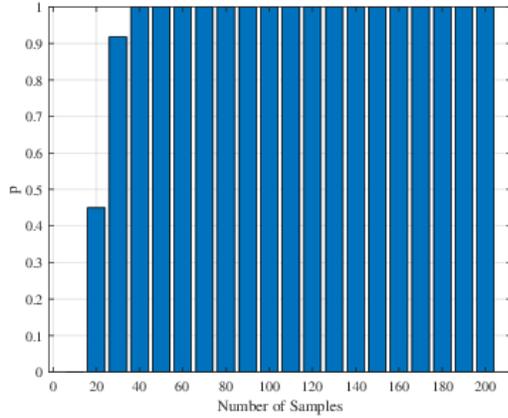
Figure 9: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 6$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.
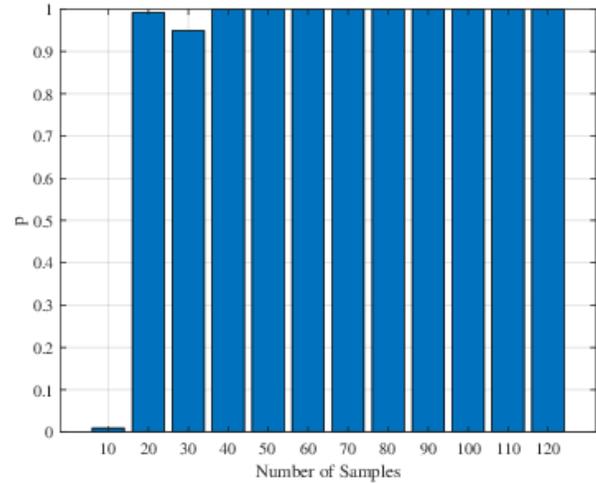
Figure 11: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 10$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 20$ or larger.
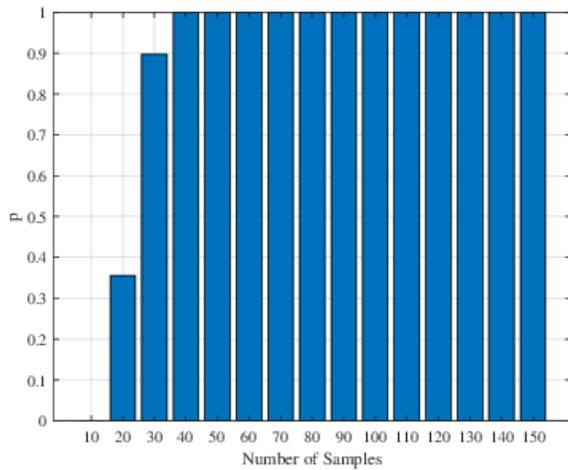
Figure 10: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 8$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 40$ or larger. Considering 10% significance p
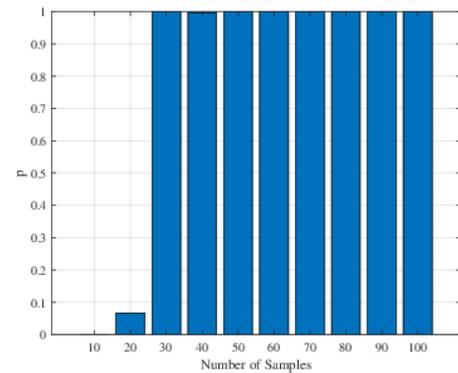
Figure 12: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 12$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.
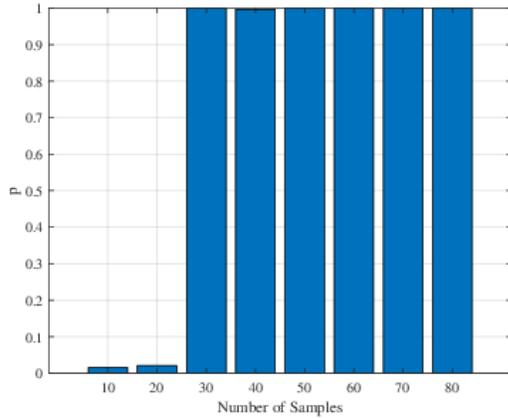
Figure 13: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 15$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.
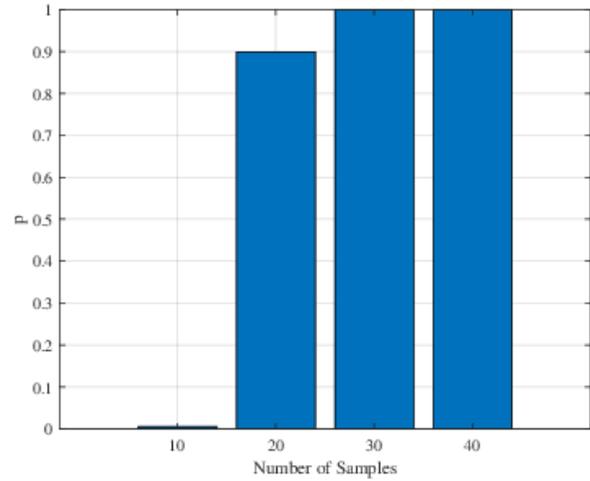
Figure 15: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 25$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger. Considering 10% significance p value reaches $p = 0.90$ when number of segments reach $N_{seg} = 20$.
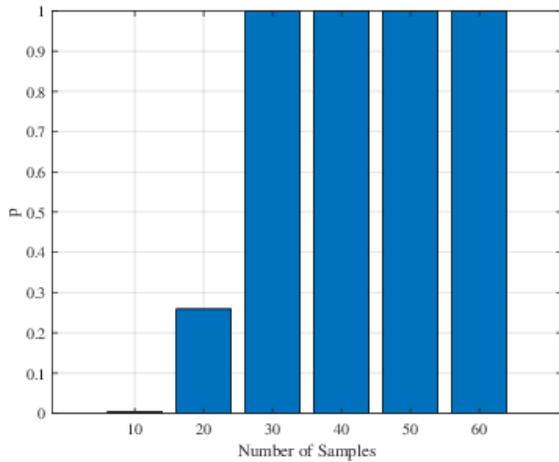
Figure 14: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 20$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.
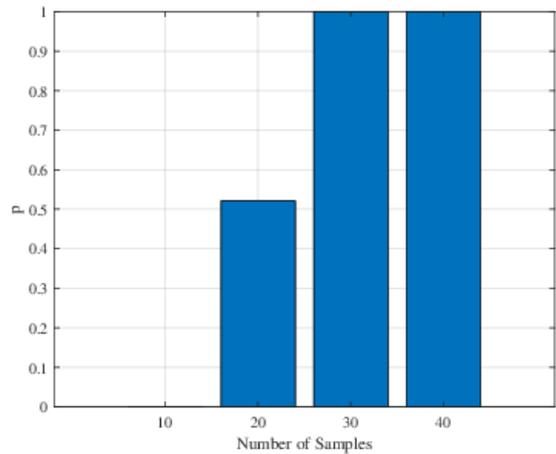
Figure 16: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 30$ seconds. The p value exceeds $p = 0.95$ level (5%

significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.
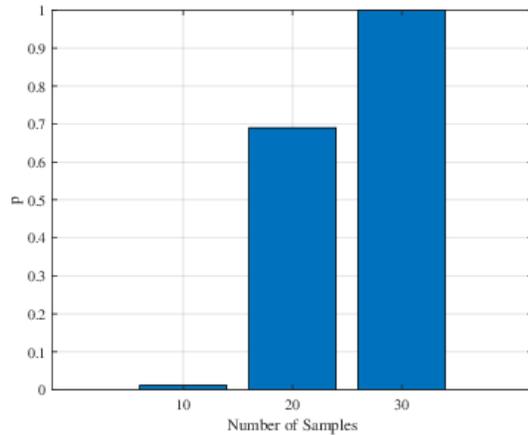
Figure 17: The variation of the p value for two sample Kolmogorov-Smirnov test when the segment size is $T_{seg} = 40$ seconds. The p value exceeds $p = 0.95$ level (5% significance level) when number of samples or segments reach $N_{seg} = 30$ or larger.

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