Cracking the neural code: Neural data analysis on firing rates, neural encoding and decoding

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Abstract:

The neuronal analysis is the blend of theoretical neuroscience, data analysis, mathematical & computational modelling. Development of mathematical and computational models based on the theoretical neuroscience concepts helped to understand and analyse the mechanics of the central nervous system's functional unit, the neuron. The spike trains and firing rates were generated for the dataset employed. The computation models relied on 'Leaky integrate and fire model' to generate artificial spikes similar to the spikes generated by actual neurons in an experiment conducted on a rat with an application of a stimulus over multiple trials. The leaky integrated fire model does a decent job generating the spikes and calculating the firing rates at respective timed events. Despite the artificial spikes resembling the real spikes generated, the IF model cannot predict a real neuron's spike times. The passive IF model fails to adapt the neuron's electrical properties such as the refractory period and adaptive threshold unless initialised. The decoding process is very complex unless the data acquired is credible. The k fold loss helps to understand the SVM model's efficiency in predicting the stimulus. The accuracy of 72.12 is decent but not ideal to understand the stimulus thoroughly.

I. Introduction

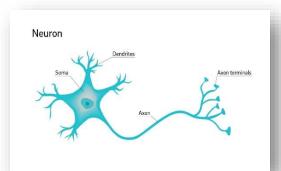


Figure 1 Source: www.medicalxpress.com (Why are neuron axons long and spindly? Study shows they're optimizing signaling efficiency, 2020)

response and reconstructs it (Dayan and Abbott 2001).

The composition of neurons includes three prominent parts, namely dendrites, soma and axon. Dendrites act as an input device as they receive signals from other neurons in the network. Soma acts as a processing unit. It processes the signal and passes onto the axon which acts as an output device transmitting the signal further to the next neuron through the synapses usually known as bridges between neurons. Usually, through synapses neurons communicate with each other in the network. Axons serve the purpose of transmission lines in the nervous system, and several axons together form

Neurons are the fundamental units of the nervous system, and they play a vital role in transmitting signals or fragments of information. They transmit the signals or information in the form of electric pulses popularly known as 'Action potential' or in other

words 'spikes'. These spikes help in the illustration of neural encoding and decoding. Neural encoding analysing the stimuli and building models to predict the response, whereas decoding, in contrast, analyses the



Figure 2 Source: https://qbi.uq.edu.au/brain/brainanatomy/central-nervous-system-brainand-spinal-cord (Central Nervous System: brain and spinal cord, 2020)

nerves which run all over the body receiving stimuli and transmitting the suitable response. Axons are 1mm to 1 meter in length. Axons of motor neurons extend from spinal cord till feet. The sensory organs are sensitive to stimuli. The sensory organ's sensory receptors detect the stimuli and transform them into action potentials with afferent neuron's intervention. The neurons transmit these action potentials to the brain where the stimuli's processing and classification take place. Figure (2) explains how the nerves run across the human body. In addition to these physical features, extracellular and intracellular solutions play an essential role in the action potential flow. The most important of them are sodium(Na+), Potassium (K+) and chloride(Cl-) ion channels. These ion channels enable the ions to flow in and out of the neuronal cells to conduct electric potential (Dayan and Abbott 2001).

II. Methodology

A. Organic action potential or spike generation:

The intracellular and extracellular solutions act as wires in the neurons. When dendrites of a neuron receive an incoming stimulation, they analyse if it is strong enough to transmit across the neuron. This transmission of an incoming signal is called an action potential, and the neuron fires. The transmission of the nerve impulse entirely depends on the flow of ions such as Na+ and K+. A neuron contains several ion channels across its length. These channels facilitate the flow of the ions in and out of the neuronal cell. A neuron is said to be in resting-state when there is no action potential flowing across it. At resting-state, the concentration of the Na+ ions is more outside the cell, and K+ concentration is more inside the cell. This results in more positively charged ions outside the cell and negatively charged ions inside the cell. The potential difference between inside and outside of

the cell is called the membrane potential. A neuron possesses a membrane potential of -70mV at resting-state which means the neuron has achieved electrochemical equilibrium (*Dayan and Abbott 2001*), (*Computation and OpenCourseWare 2021*).

A neuron fires when the incoming stimulation surpasses the threshold voltage of -55mV and any stimulation of a magnitude less than the threshold voltage is called graded potential. Here the neuron does not fire, instead resets to the equilibrium state. When the stimulation crosses -55mV, the neuron generates an action potential that travels down the axon's length triggering the Na+ channel to open, allowing the Na+ ions present outside the cell to flow inside. This inflow alters the membrane to become

(a) Resting potential.

(b) Presting potential, all vallage-gated Na* channels and most voltage-gated K* channels are closed. The Na*/K* transporter pumps K* one into the cell and Na* channels and most voltage-gated K* channels are closed. The Na*/K* transporter pumps K* one into the cell and Na* channels and most voltage-gated K* channels are closed. The Na*/K* transporter pumps K* one into the cell and Na* cross out.

(b) Depotentiation

In response to a depotentiation, some Na* channels open, allowing Na* (ms to order the cell. The membrane starts to depotentiate to the channels are considered in the transporter pumps K* channels in the start channels in the cell of the transporter pumps K* channels in the start channels open. (c) Hyperpolautization

(c) Hyperpolautization

(d) As 'K* transporter pumps K* transporter pumps K* channels in the start channels open. (d) the start

Figure 3 Source: https://courses.lumenlearning.com/boundless-biology/chapter/how-neurons-communicate/ (How Neurons Communicate | Boundless Biology, 2020)

more positive than negative crossing 0mV. This phase is called 'depolarisation'. Furtherly, the membrane potential crosses beyond 0mV mark

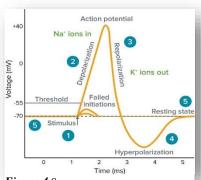


Figure 4 Source: https://www.moleculardevices.com/applications/patch-clamp-electrophysiology/whataction-potential#gref

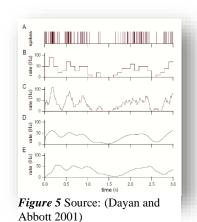
and overshoots up to +40mV (The amplitude of the membrane potential varies for different neurons). After achieving overshoot, the Na+ channel turns inactive thwarting any more Na+ ions to flow inside. Parallelly, the K+ channel opens up promoting the flow of K+ ions from inside of the cell to outside, thus altering it to be more negative and eventually falling below 0mV. This phase is called 'repolarisation'. The K+ channels are slow to close down entirely, so the membrane potential falls further than -70mV(resting-potential). This phase is called 'hyperpolarisation'. When activated by ATP(Adenosine Triphosphate) molecule, the sodium-potassium pump restores the membrane potential to -70mV by pumping out more Na+ ions than K+ ions let in (Feng 2004). After the hyperpolarisation, the Na+ channels are inactive, avoiding the triggering of another action potential and preventing action potential to flow backwards. This phase is known as 'absolute refractory period', and it lasts for approximately 10ms. For a particular neuron, the action potential's amplitude never changes concerning smaller or bigger stimuli. Instead, the only variation is the frequency of the spike occurrence. The spike rate may differ for different stimulus and

different trials. Figure 4 is a clear depiction of an action potential or spike

generation. (Dayan and Abbott 2001), (Computation and OpenCourseWare 2021), (Gerstner et al. 2014), (Feng 2004).

B. Spike firing rates:

The amplitude of action potential ranges between 30 mV to 100mV based on the type of neuron. The spike generated is the fundamental unit of signal transmission across the nerves, and the series of spikes generated by a neuron is called a spike train.



These spike trains enable the nerves to transmit or receive signals from distant parts of the body. The number of spikes generated in a particular interval of time is vital in understanding the stimuli. Nonetheless, the spikes generated by a stimulus vary for each trial and for different time intervals, so the impulses are studied probabilistically. The probability of a spike to occur at a particular time instant is zero, so the calculation of the probability of a spike occurring within a time interval $(t + \Delta t)$ is trivial. The firing rate of a neuron r(t) is the probability density of the generation of spikes between t and Δt . The mathematical representation of spike train generated by

$$\rho(t) = \sum_{i=1}^{n} \delta(t - t_i)$$
 (Dayan and Abbott 2001)

The single spike probability density is the probability that a spike occurs between t and $t + \Delta t$. p[t] denotes single spike probability density equivalent to firing rate r(t). For a reasonable estimate of r(t) the same experiment is repeated for several trials.

The average of all the binned spikes over the number of trials is a trial-averaged neural function (Dayan and Abbott 2001).

a neuron:

$$r(t)\Delta t = \int_{t}^{t+\Delta t} d\tau \langle \rho(\tau) \rangle$$

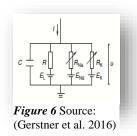
Another way of quantifying spike-count rate is by computing ratio the number of spikes generated during a trial and the trial duration. The calculation of spike-count rate (r) is

$$r = n / T$$

$$r = 1/T \int_0^T d\tau \, \rho(\tau)$$
Average firing rate $\langle r \rangle = \langle n \rangle / T$ (Dayan and Abbott 2001)
$$= 1/T \int_0^T dt \, r(t)$$

C. Spike generation and spike rates in computational models:

The spike generation is equivalent to the potential difference (membrane potential) between the intracellular and extracellular

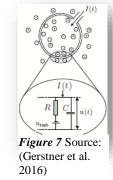


regions (difference in concentration gradient). The ion channels regulate the flow of selective ions in and out; they are sensitive to the voltage. The current injected into the neuron is responsible for the change in the voltage difference. Hodgkin and Huxley performed experiments on the axon of a giant squid and found three ionic currents: sodium current, potassium current, and leak current. They

proposed a neuron equivalent electrical model to explain its dynamics. They employed resistors which act as ion channels to regulate the flow of ions. Based on the varying Nernst potential for different ions, they included individual voltages for different channels. The equivalent electrical HH model in figure 6. The HH model is very complex, and a simplified model called 'Integrate and fire model' is used. A simple

spike generator replaces the sodium and potassium conductances in the HH model responsible for spike generation(Gerstner et al. 2014).

The circuit is a simple resistor and capacitor connected in parallel. The neuron continuously integrates its inputs and generates a spike when the voltage crosses the threshold voltage. To be more precise when the potential reaches the threshold, it fires a spike and resets to resting potential. When the neuron is injected with an input current I(t) the membrane potential sways away from the



resting the cell membrane. Hence, the cell membrane acts as a capacitor. The cell membrane is prone to leak charge over a while,

so the circuit is connected with a leak resistance to control the leak (figure 7). According to Kirchoff's law, the incoming current is equal to the outgoing potential (Gerstner et al. 2014), (Computation and OpenCourseWare 2021)

Therefore
$$I(t) = I_R + I_C$$

Considering Ohm's law, Current passing through the resistor $I_R = u_R / R$ and the potential across the resistor $u_R = u - u_{rest}$

Capacitance C = q/u and the current flowing through the capacitor is $I_c = dq/dt = C.du/dt$

$$\begin{split} &I(t) = (u(t) - u_{rest}) \, / \, R + C.du/dt \\ &\tau_m du/dt = u_{rest} - u(t) + R.I(t) \text{ where } \tau_m \text{ is time constant} \\ &\tau_m \, (u(t + \Delta t) - u(t)) / \, \Delta t \, = \, u_{rest} - u(t) + R.I(t) \quad \ \, (\textit{Gerstner et al. 2014}) \end{split}$$

The firing rate of a neuron generated by leaky integrate and fire model can be calculated by

If the voltage of the neuron is greater than V_{th} (threshold voltage) the amount of current needed to trigger a spike is $I_{th} = G_1(V_{th} - E_i)$ (threshold current)

So, the firing rate in a Leaky integrate neuron model $f = \frac{1}{c \Delta v} [I_e - I_{th}]$ (Computation and OpenCourseWare 2021)

As the cell membrane acts as a good insulator, little current enters the neuron and remaining charge charges. Where $I_{th} = G_l(V_{th}-E_l)$ and G_l is leak conductance; E_l is the voltage of the leak fragment; I_e is the injected current.

III. Data

Washington University prepared the dataset, and it holds the recordings of different behaviours of a rat while performing a decision-making experiment. The behaviours' classification was based on whether the rat approaches the reward correctly or not upon hearing the stimulus. Value 1 denotes the correctness of the response and 2,3,4 denote incorrectness of the response.

Figure 8 demonstrates the classification of each behaviour. The current dataset has over 1000 correct responses (value 1) and more than 2600(values 2,3,4) incorrect responses

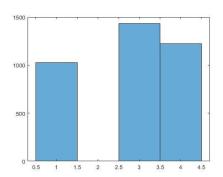


Figure 8

IV. Results

MATLAB was extensively used to analyse the dataset for understanding spike generation and spike rates in both real and artificial neurons. As the neural encoding is the mapping from stimulus to response, analysis is implicitly based on the rat's different behaviours. Figure 9(a) shows the spike generation and six real neurons' spike rates during the experiment. Each neuron has a different spike train generation and spike rates. Here the spike rates are calculated using a time window and averaging it over the period by sliding it for 1ms until the last instance. The spike trains' variation in each neuron for different trials proves that every neuron has a different stimulus behaviour. The spikings differ for different trials, even if the neuron remains the same(Balaguer-Ballester 2017). The gaps between each spike train denote either a refractory period or stimulation interval. It is a complicated task to predict precisely whether the gap refers to a refractory period of stimulation interval.

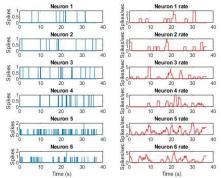
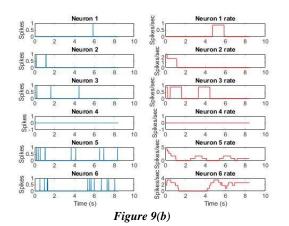


Figure 9(a)

A. Evaluation of similarity between spikes generated by real neuron and computational neuron

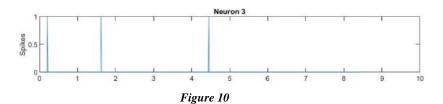


For the analysis, the combination of Trial 1 and Trial 2 recordings in neuron three and neuron five are considered. Figure 10 demonstrates each of six neurons' spikes and their spike rates for Trial 1 and 2, respectively. Neuron 1 and Neuron 2 were barely firing over the trials, so they were excluded from the analysis. The correlation occurred at the window size of 1.15secs and utilised to calculate the spike rates. The p-test values were significantly below 0.05 (Figure 23). Figures 11 and 12 are plots for individual neurons 3 and 5 for trial 1 and 2. The artificial neurons are generated using Leaky integrate and fire model. The parameters used for the implementation are: τ (membrane time constant) = 0.02; resistance R = 3e7 ohms; Resting potential E = -0.07V; threshold of depolarization (theta) = -0.030V; value of spike in volts = 0.1; time step dt = 0.0001; absolute refractory period = 0.008; noise input current = 3e-9; adaptive threshold = 0.15. The mathematical equation used for this computational model is:

$$\tau_{m} \frac{u(t+\Delta t)-u(t)}{\Delta t} = u_{rest} - u(t) + R(\alpha I(t) + I_{noise}(t))$$

Apart from these for neuron 3 spike generation (post synaptic current) psc = [0.21:dt:0.22, 1.62:dt:1.63, 4.46:dt:4.47] as the three spikes were generated at the instances 0.21, 1.62 and 4.47 secs in the time duration of 10 seconds. For neuron 5 spike generation psc = [0.18:dt:0.19, 0.33:dt:0.34, 0.54:dt:0.55, 1.02:dt:1.025, 3.65:dt:3.66, 4.12:dt:4.13, 6.52:dt:6.53, 6.94:dt:6.95, 8.32:dt:8.33] as the 9 spikes were fired by real neurons at the respective instances. (Figure 11)

The Leaky integrate and fire model was decent enough to generate spike artificially. The spikes look similar to the ones generated by real neurons and fired at the same instances. Though the results are convincingly satisfactory, yet the fact remains that the spikes were hardcoded to achieve the similarity. The model may not be useful in predicting the spike trains based on the specific stimulus. It is a passive model which means the membrane potential is made constant and does not change over time.



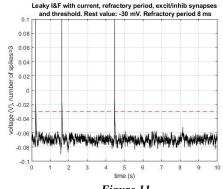


Figure 11

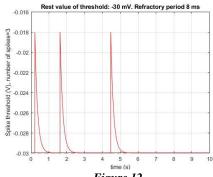
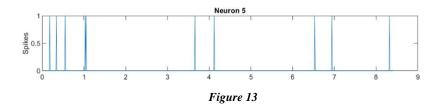
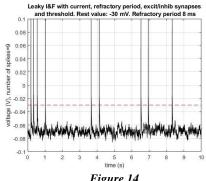


Figure 12





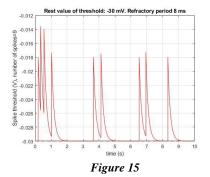
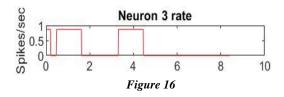
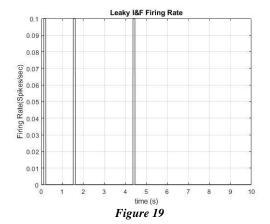
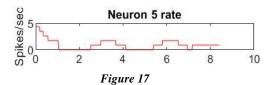


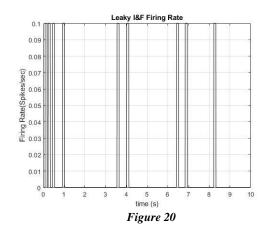
Figure 14

Comparison of firing rates in real and artificial neurons









The firing rates of real neurons (3 & 5) and artificial neurons seem similar, but IF model fails to predict the spike times and their rates for a real neuron. One observation is that the firing rate grows linearly with increase in input current, which means more spikes are generated for the same neuron and the same trials (Knight 1972). This computational model differs from the passive model as the refractory period is initialised to forbid the neuron to fire continuously. Spike rate adaption is achieved by including other incoming currents and noisy inputs(Gerstner et al. 2014), (Heeger 1997).

C. Decoding the types of behaviours based on real firing rates

Decoding is the mapping from response to the stimulus. It is useful in the case of understanding and classifying the stimulus based on the response generated. In reality, the electric potential is recorded in the neuron's vicinity but not inside the neuron. So the aggregation of spike rates generated over time is more viable to decode the stimulus because the spike's origin is very vague. Using local field potentials to record ensemble firing rates of a collective set of neurons unless the information on which neuron generated the spike is known. This analysis employs firing rates to perform neural decoding.

Value	Count	Percent
1	1027	27.91%
3	1432	38.91%
4	1221	33.18%

Figure 21

```
Fit template for classification SVM.
                            Alpha: [0×1 double]
                 BoxConstraint:
                       CacheSize:
                 CachingMethod
                     ClipAlphas:
     DeltaGradientTolerance:
                  Epsilon:
GapTolerance:
                   KKTTolerance:
               IterationLimit:
KernelFunction:
KernelScale:
                  KernelOffset:
      KernelPolynomialOrder:
NumPrint:
              OutlierFraction:
              RemoveDuplicates:
ShrinkagePeriod:
Solver:
StandardizeData:
          SaveSupportVectors:
VerbosityLevel:
                         Version:
                          Method: 'SVM'
                             Type: 'classification'
classioss = 0.5981
     0.5981
```

Figure 22

The dataset is quite imbalanced as per figure 8, which shows the histogram of each behaviour's count. The frequency table also asserts that the correct behaviour occurred only 27.91% in the overall experiment, which is significantly low compared to incorrect behaviour. This process involved support vector machines algorithm which searches for a hyperplane which distinguishes the data points.

The k-fold loss delineates the difference between the readings in the folds and the predictions. The k-fold loss achieved during this analysis was 0.5981, which means the accuracy is around 40.19%. The loss is very high, so it is quite difficult to decode the stimulus or predict the spike trains.

Transforming the analysis to Value Count Percent 1027 27.91% 1 classification will rectify the loss. Value = 4 replaced 4 2653 72.09% the value = 4, as behaviour values 3 and 4 denote incorrectness. The loss has decreased to 0.2788, with a classLoss = 0.2788prediction accuracy of 72.12. Balancing the imbalanced dataset 0.2788 might further enhance accuracy.

Figure 18

V. CONCLUSION

The thorough analysis of the rat's behaviour based on the several neuron's spiking delineates that analysing neural responses is not only complicated but quite erratic. The reproducibility of the results for the same experiment for several trials is dissimilar. The actual neuron firing is not solely about the potential difference fluctuation. However, many other chemical and electrical reactions such as ion flow through the ion channels, ion concentration gradients, synaptic transmission, threshold voltage, refractory period, noise, and potential passed on from presynaptic neurons to postsynaptic neurons. The neuron model employed in the analysis 'Leaky integrate and fire model' is accurate in generating the spikes for a particular timed event but works poorly to predict the spikes generated by a real neuron. It fails to explain the biophysics of neuroscience concerning the electrical properties of a neuron. This neuron model might be a good option in understanding the spikes generated in the soma but not at the dendritic level due to the complexity involved. The decoding process is viable only with the firing rates, and additionally, it is quite a significant task to achieve high accuracy in prediction levels. Nonetheless, the analysis provides an accurate analysis of neural responses concerning the rat's responses to a stimulus.

Acknowledgement

This neuronal analysis would not have been possible without Dr Emili Balaguer-Ballester's support and the proprietary MATLAB code(along with mathematical equations) he has provided. His enthusiasm for computational neuroscience and clear explanation of the concepts enabled me to gain expertise in this field. His generosity to clarify the doubts and attention to detail has made it easier to carry on the research.

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APPENDIX A - Methodology

The action potential is transmitted from neuron to the adjacent along the path to respond or receive a stimulus. This transmission between one neuron and the other happens at a junction called a synapse, and the transmission is called synaptic transmission (Bear. 2015). The neuron passing on the neural signal is called a presynaptic neuron, and the neuron receiving it is called a postsynaptic neuron. Along with the ion-channels mentioned earlier, the third type of ion channel called transmitter-activated ion channel is responsible for synaptic transmission. The presynaptic neuron on the activation releases the neurotransmitters into the postsynaptic neuron at the synaptic cleft. The neurons are classified into inhibitory and excitatory. GABA_A and GABA_B are the vital inhibitory synapses, and GABA_B channels are responsible for opening K⁺ channels. The excitatory synapses employ glutamate as the neurotransmitter and open Na⁺, K⁺ and sometimes Cl⁻ ion channels. The synaptic currents are responsible for fluctuating the membrane potential, resulting in diffusion of ions to generate an action potential (Gerstner et al. 2014).

APPENDIX A - Figures

```
Trial 1 Neuron 3 correlation = 0.15228 (9.4423e-07)
Trial 2 Neuron 3 correlation = NaN (NaN)
Trial 3 Neuron 3 correlation = 0.074359 (0.0048727)
Trial 4 Neuron 3 correlation = 0.10067 (0.00042673)
All trials Neuron 3 correlation = 0.099986 (1.2123e-09)
Trial 1 Neuron 4 correlation = 0.23925 (7.793e-15)
Trial 2 Neuron 4 correlation = NaN (NaN)
Trial 3 Neuron 4 correlation = 0.07052 (0.007594)
Trial 4 Neuron 4 correlation = 0.089026 (0.0018469)
All trials Neuron 4 correlation = 0.091212 (2.9756e-08)
Trial 1 Neuron 5 correlation = 0.12792 (3.9322e-05)
Trial 2 Neuron 5 correlation = NaN (NaN)
Trial 3 Neuron 5 correlation = 0.091275 (0.00054375)
Trial 4 Neuron 5 correlation = 0.0563 (0.049202)
All trials Neuron 5 correlation = 0.094562 (9.0666e-09)
Trial 1 Neuron 6 correlation = 0.090727 (0.0036146)
Trial 2 Neuron 6 correlation = NaN (NaN)
Trial 3 Neuron 6 correlation = 0.10993 (3.058e-05)
Trial 4 Neuron 6 correlation = 0.11216 (8.5808e-05)
All trials Neuron 6 correlation = 0.10335 (3.2923e-10)
                   Figure 23
APPENDIX B – Live script snippets
   I.
          Spikes and spike rates for trials [1,2] for real neurons:
                    Spikes = load("DataSetCoursework_KAM.txt");
                    dat5 = Spikes(1:841, 1:end-2); % Only for trial 1 + trial 2
                    window_size = 1.15; %0.22
                    %max resolution = 0.01;
                    Rate1 = Rates_0(dat5, window_size);
  II.
          Spikes and spike rates for all trials for all real neurons:
                    Spikes = load("DataSetCoursework_KAM.txt");
                    dat1 = Spikes(1:841, 1:end); % Only for trial 1 + trial 2
                    window_size = 1.15; %0.22
                    %max resolution = 0.01;
                    Rate1 = Rates_0(dat1, window_size);
 III.
          Behavior classes and their distribution:
                    Spikes = load("DataSetCoursework KAM.txt");
                    dat3 = Spikes(: , 7);
                    h = histogram(dat3);
 IV. Leaky IF model for neuron 3:
                    % Neuron 3 (Trial 1 + Trial 2)
                    dt = 0.0001
                    psc = [0.21:dt:0.22, 1.62:dt:1.63, 4.46:dt:4.47]
                    input_currents.V_0 = 0.3;
                    input_currents.ipsc = 0;
```

input_currents.psc = psc;

LeakyIF_3_act(input_currents, 10);

V. Leaky IF model for neuron 5:

```
% Neuron 5 (Trial 1 + Trial 2)

dt = 0.0001

psc = [0.18:dt:0.19, 0.33:dt:0.34, 0.54:dt:0.55, 1.02:dt:1.025,
3.65:dt:3.66, 4.12:dt:4.13, 6.52:dt:6.53, 6.94:dt:6.95, 8.32:dt:8.33]

input_currents.V_0 = 0.3;
input_currents.ipsc = 0;
input_currents.psc = psc;

LeakyIF_3_act(input_currents, 10);
```

VI. Decoding classes:

```
Spikes = load("DataSetCoursework_KAM.txt");
Rate=Rates_0(Spikes);

X= Rate(:, 1:end-2);
Y= Rate(:, end);

t = templateSVM('Standardize',true)
Decoder= fitcecoc(X,Y,'Learners',t,'ClassNames',{'1','2','3','4'});

CV_model= crossval(Decoder);
classLoss= kfoldLoss(CV_model)

disp(classLoss)
```

VII. Class frequency table

```
labels = unique(Y)
nlabel = numel(labels)
tabulate(categorical(Y))
```