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Problem 1

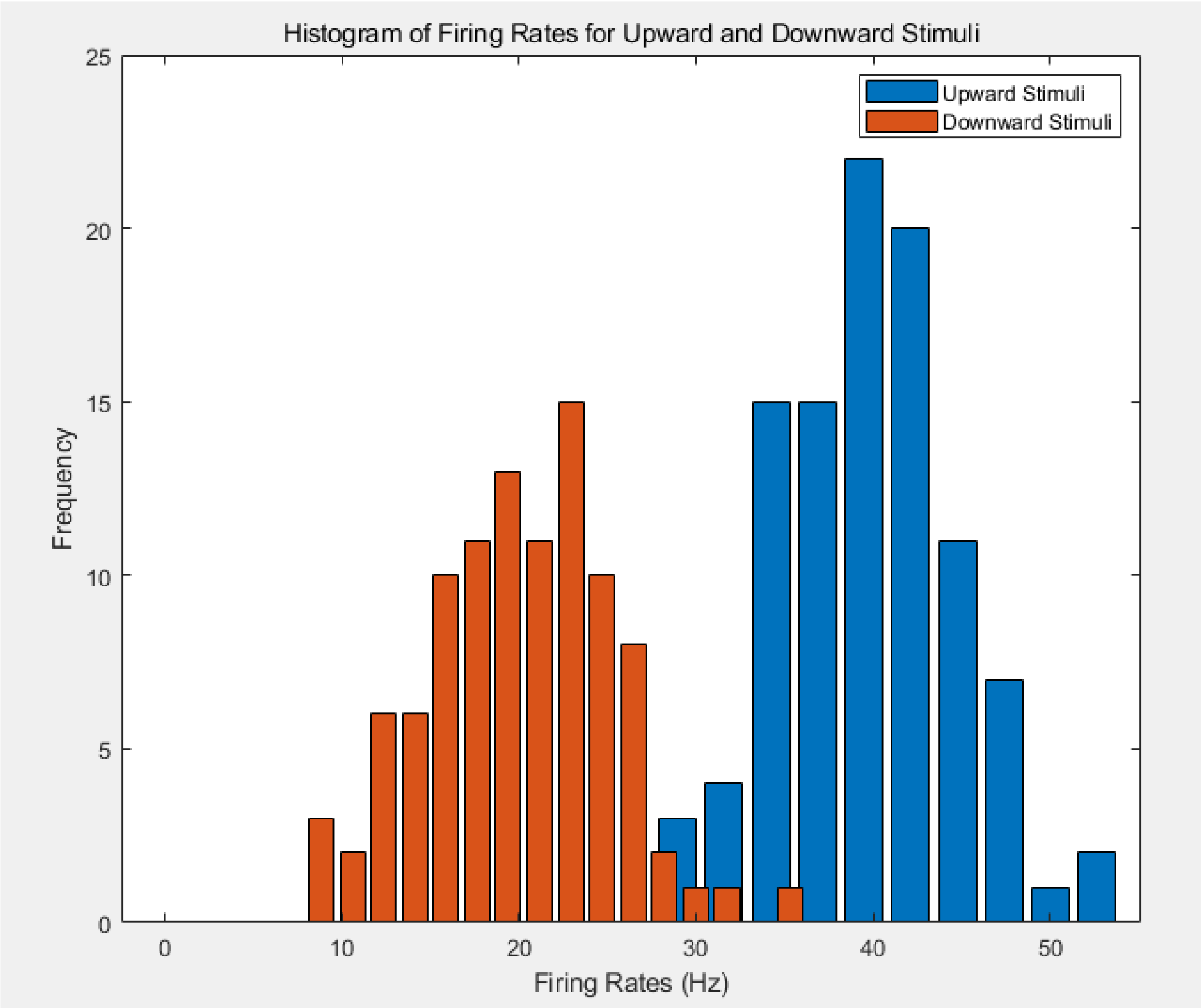
<u>Which physical connectomes contribute to generating memory?</u>

- Most important, in this case, refers to an unanswered question which has high relevance to understanding the dynamics underlying an important human function.
- Neuronal function is clearly generated by synapses between neurons, which indicates that the physical connectomes between neurons lead to different functions.
- While a great amount of effort is being put into determining physical connectomes in mammals, it is still unclear as to whether physical connectomes map to certain neural functions. It is not clear as to whether certain neural functions occur in localized brain areas.
- Memory is one of the core cognitive functions for which the underlying mechanism/dynamics are unknown. How physical connectomes map to memory, human memory in particular, appears to be salient for understanding not only memory but other cognitive functions.

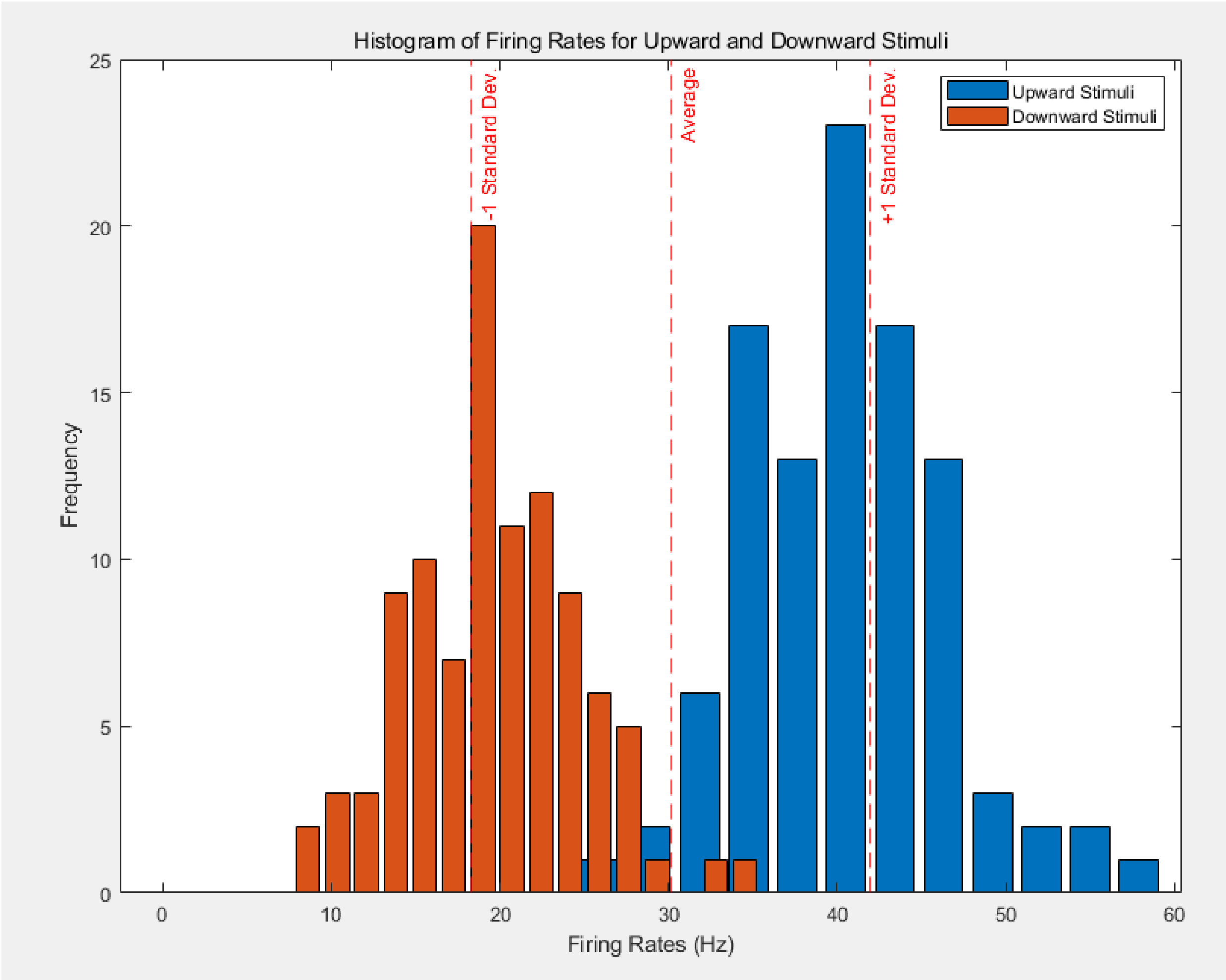
Problem 2

Activity of a neuron in MT is selective to the direction of stimulus motion, e.g. Up(+) or Down(-). The firing rate of each neuron is observed as a Gaussian with (μ_+, σ_+) and (μ_-, σ_-) Hz, where μ_x and σ_x are the mean and the s.d. of response firing rate to stimulus direction x.

a. For 15% correlated motion of stimulus (i.e. easy task), you observed (μ_+, σ_+) = (40, 5) and (μ_-, σ_-) = (20, 5). Generate the sample response of the neuron for 100 trials when the up- and down-ward stimuli appear by same chance. Plot the histogram of firing rates in all trials as in the figure.



b. Choose 3 arbitrary numbers as your threshold z of firing rate for decoding of the stimulus direction. Using the distribution in **a** and the value of each z, calculate the "hit rate" β and "false alarm rate" α, as in the lecture note. Show your estimated α, β and the probability of correct answer $p = (\beta+1- \alpha)/2$, for the z values above.



Threshold Value	β	α	Probability of Correct Answer
18.2960	1	0.6500	0.6750
30.1260	0.9800	0.0200	0.9800
41.9560	0.3800	0	0.6900

c. Find the optimal value of z for above condition and explain your method to determine it.

*Problem 2c has no corresponding script.

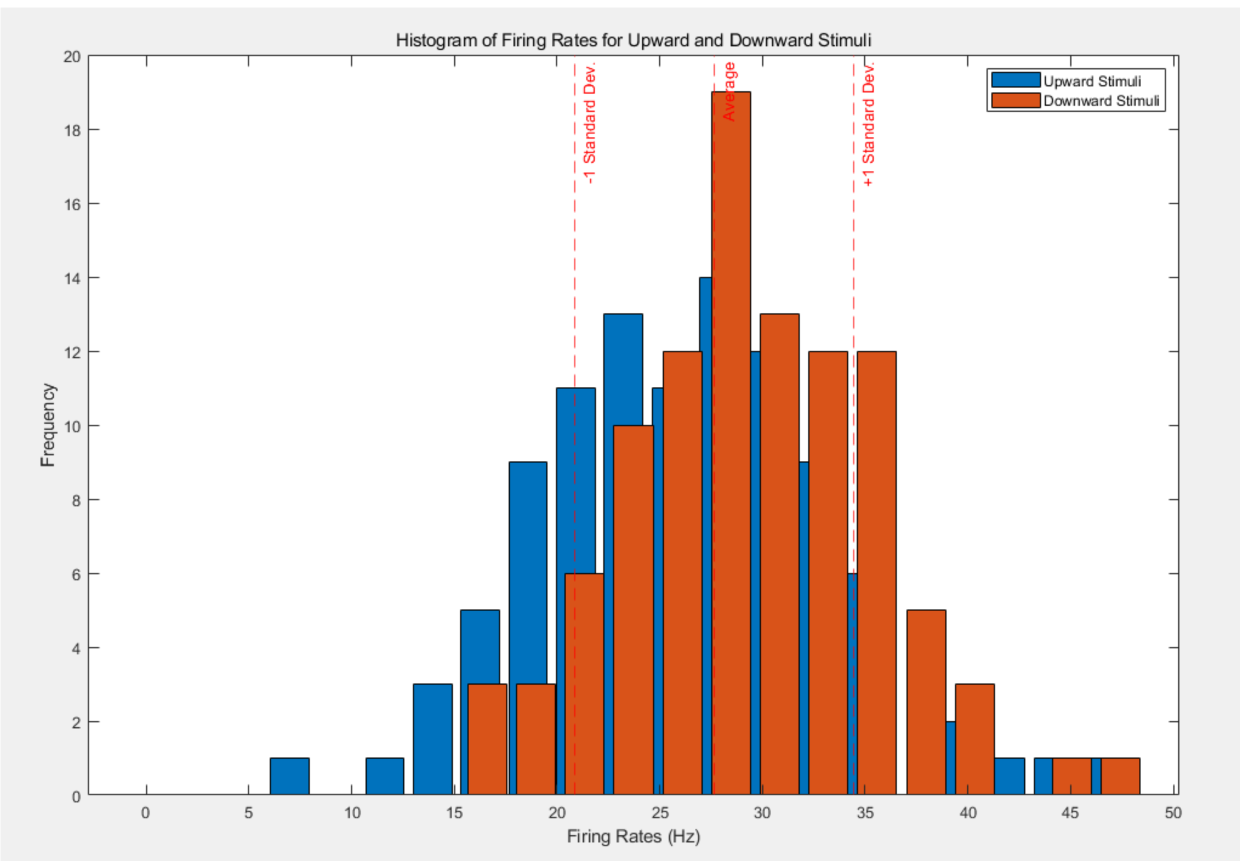
The optimal value for z was determined as the average between the means of the rate distributions for the two stimuli, 30 Hz.

The problem can be formulated such that an empirical distribution of firing rates is given and it is known that the prior distributions of the firing rates in response to the + and - stimuli are gaussian. As seen in b), the threshold value which led to the highest probability of correct answer was the average of the firing rates. This is because given the fact that the empirical distribution is the sum of two gaussian distributions whose means are separated - as such, the value of the threshold which best separates these two gaussian distributions is the midpoint between the two means: $z_{optimal} = \frac{\mu^+ + \mu^-}{2}$. In this case, the average of the two distributions is equal to the statistical average of the set of given firing rates.

Normalizing the histogram into a probability distribution, the net distribution can be thought of as the linear combination of two gaussian distributions weighted equally. $X_{net} = \frac{X_+ + X_-}{2}$, $X_+ \sim N(\mu_+, \sigma_+)$, $X_- \sim N(\mu_-, \sigma_-)$. Then $E[X_{net}] = \frac{E[X_-] + E[X_+]}{2}$.

d. Now, for 1% correlated motion of stimulus (i.e. hard task), you found (μ_+, σ_+) = (25, 6) and (μ_-, σ_-) = (30, 6). Repeat the process in from **a** to **c** for this condition.

*Note, problem 2d and 2e are answered together and all figures are



Threshold Value	β	α	Probability of Correct Answer
20.8713	0.7200	0.9300	0.3950
27.6512	0.3800	0.6600	0.3600
34.4311	0.0800	0.2200	0.4300

The task is difficult for two reasons. Firstly, the mean for the rate distribution of the upward stimulus is very similar to that of the rate distribution of the downward stimulus. As such, there is an inherent difficulty in using a single threshold to distinguish a given firing rate as belonging to either gaussian distribution. More importantly, the mean of the rates for the upward stimulus is lower than that of the mean for the downward stimulus. Hence, if downward stimuli are decoded as rates below the threshold, placing the threshold at the midpoint of the two means leads to a lower firing rate.

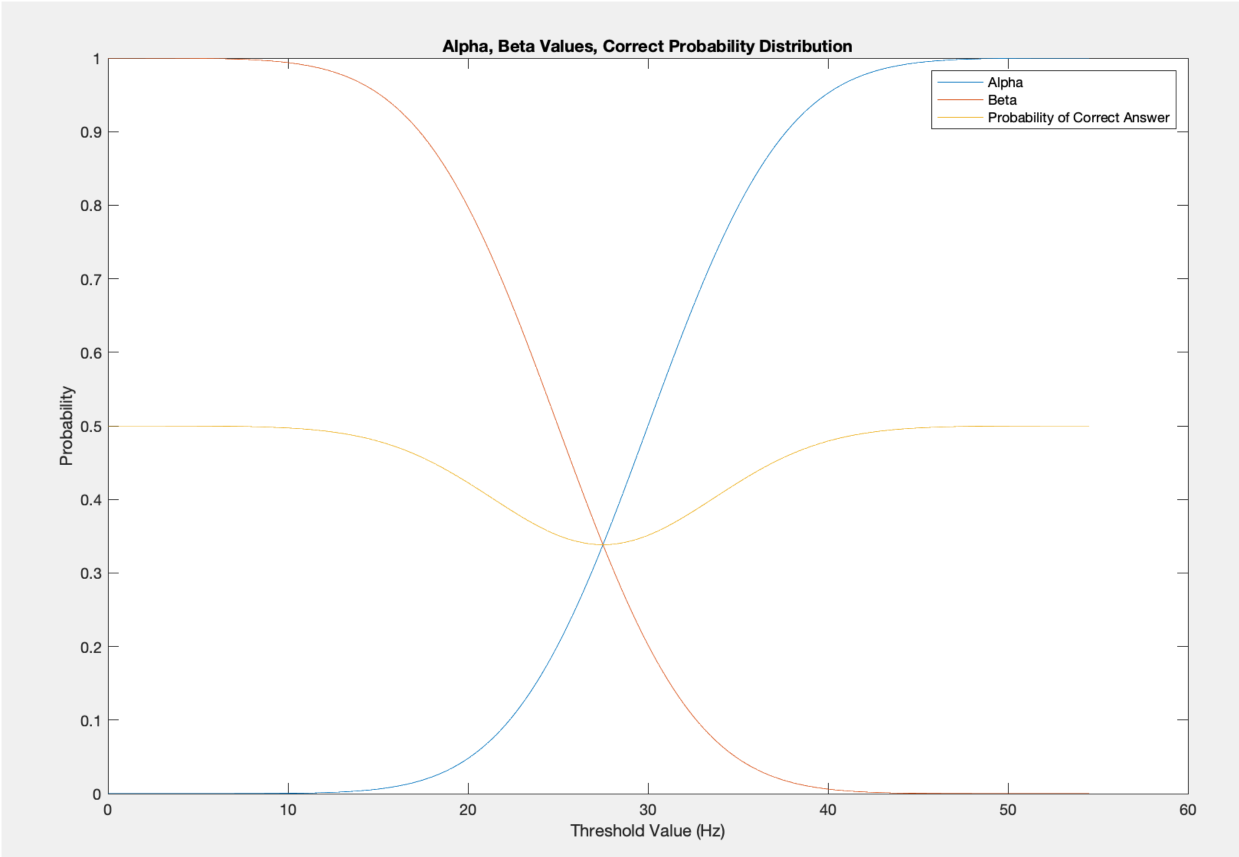
The theoretical correct probability found as $\frac{\beta + 1 - \alpha}{2}$ can be found analytically using the analytic expressions for Gaussian distributions. α given a threshold z is equal to the value of the cumulative probability distribution (cdf) of $X_- \sim N(\mu_-, \sigma_-)$ evaluated at z:

$$\alpha = \frac{1}{\sqrt(2\pi)\sigma_-} \int_{z_{threshold}}^{-\infty} e^{(\frac{x-\mu_-)^2}{\sigma_-^2}}$$

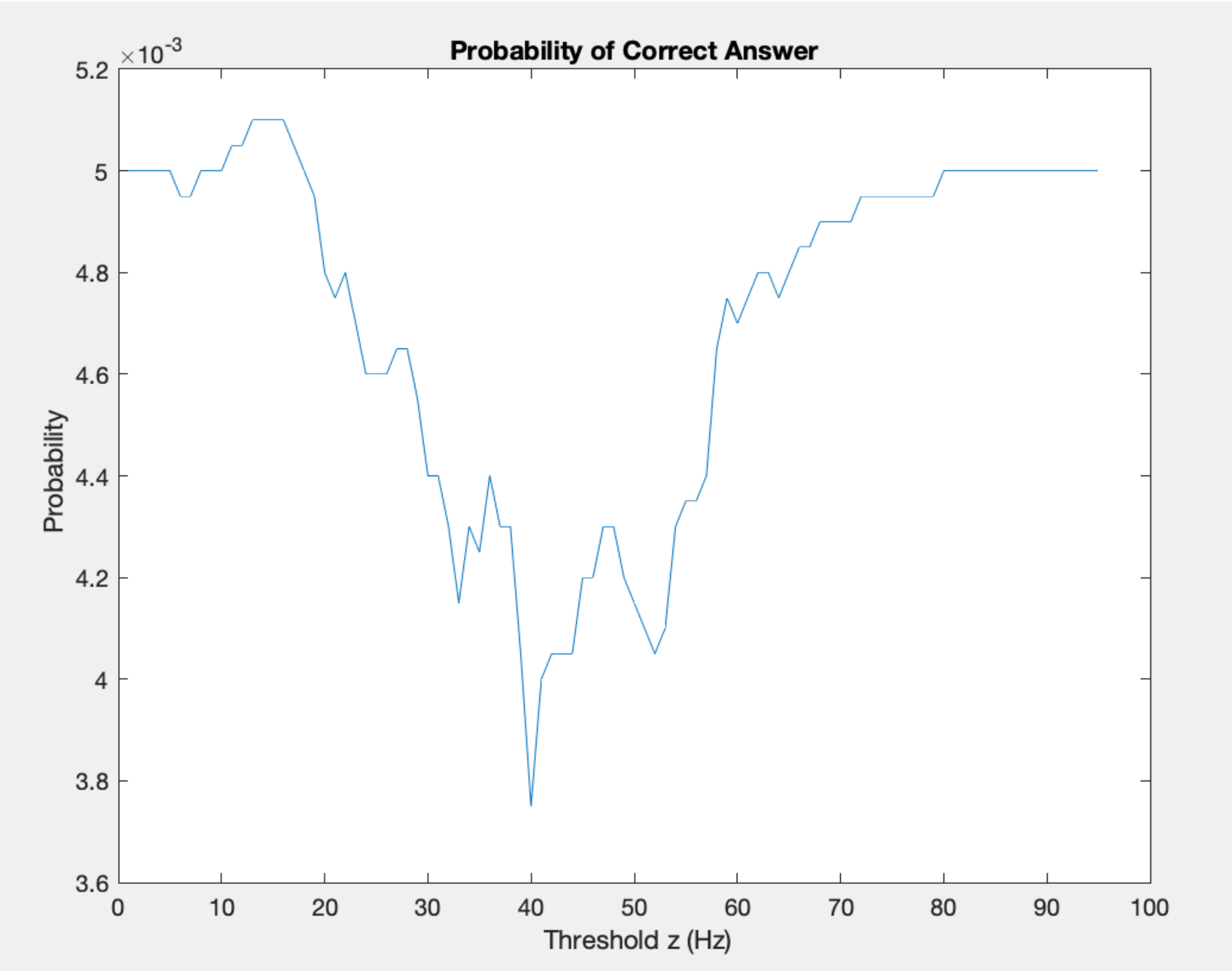
On the other hand, β given a threshold z is equal to the value of the cumulative probability distribution (cdf) of $X_+ \sim N(\mu_+, \sigma_+)$ evaluated at z subtracted from one:

$$\beta = 1 - \frac{1}{\sqrt(2\pi)\sigma_+} \int_{z_{threshold}}^{-\infty} e^{\frac{(x-\mu_+)^2}{\sigma_+^2}}$$

Varying the value of the threshold z and finding $\frac{\beta + 1 - \alpha}{2}$ using the above expressions leads to the analytic result below. It can be seen that the maximum correct probability occurs at either extreme values 0 and the maximum rate while the global minimum occurs at the midpoint between μ_+ and μ_-.



The fact that a global minimum occurs can also be seen empirically. The threshold value was varied from 0 to the maximum firing rate and the probability of correct answer was calculated as $\frac{\beta + 1 - \alpha}{2}$. The result below corroborates the analytic result: the global minimum in correct probability occurs at the mean of the rates.

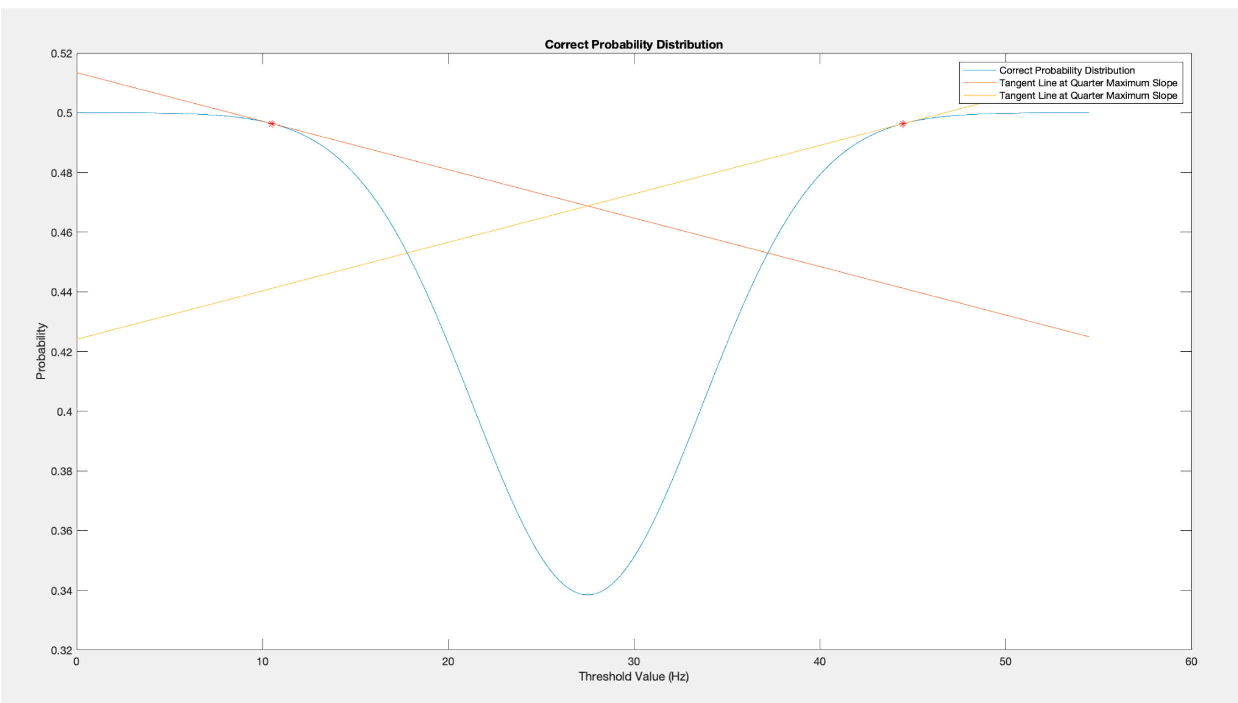


Using a single threshold z, the maximal correct probability of 0.5 occurs at 0 or the maximum observed firing rate. However, using 0 or the maximum observed firing rate as the threshold value drives either β or $1-\alpha$ to zero, which is equivalent to assuming that all rates correspond to one type of stimulus. As such, it is more desirable to select a threshold value which allows for both types of stimuli while attaining a theoretical maximal correct probability value of 0.5.

e. Compare the process of finding the optimal value of **z** in **c** and **d**, and discuss your strategy to find the optimal threshold value under the "hard task" condition.

In d), the mean of the distribution for the upward stimulus is lower and closer in absolute value to the mean of the distribution for the downward stimulus. As such, the distributions of the two stimuli are not well-separated by a single threshold. Under the conditions in d), the theoretical maximal correct probability is 0.5. One way of determining the threshold value is to find the point at which the probability of correct answer begins to decrease from or increase to the maximum theoretical correct probability, which occurs at the lowest and highest rate values.

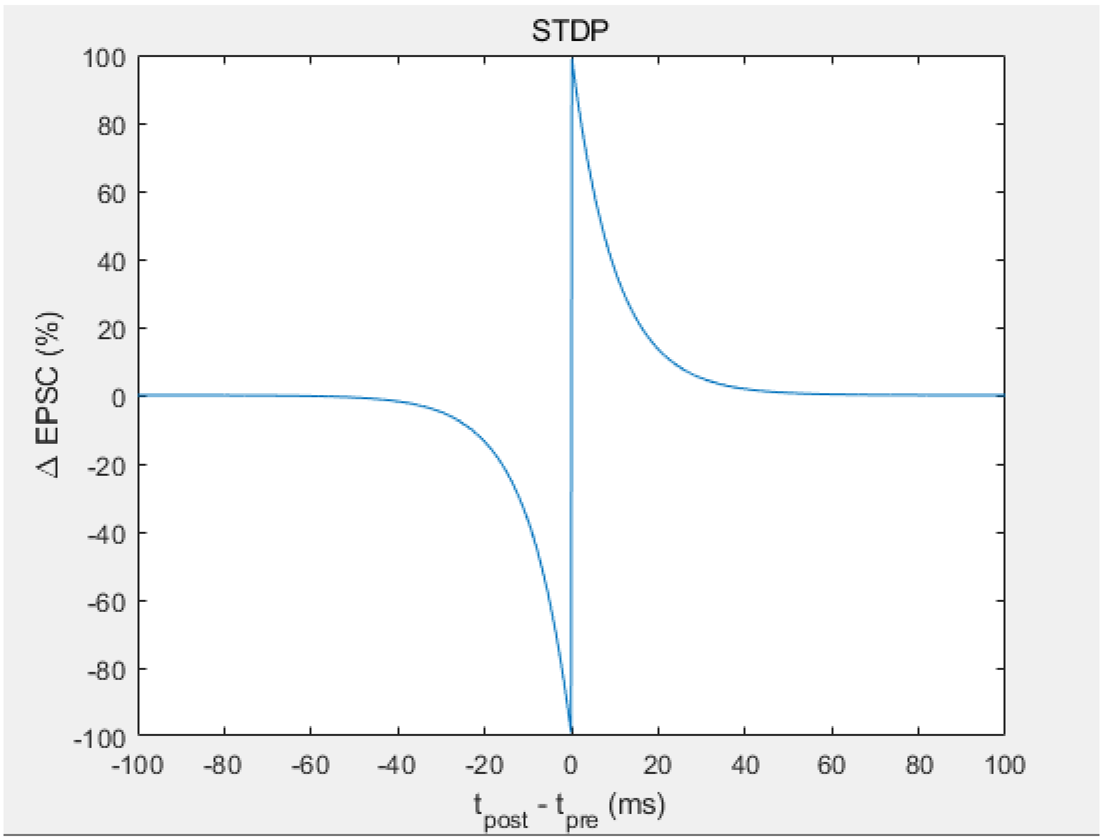
This approach assumes that the values of $\mu_+, \sigma_+, \mu_-, \sigma_-$ are known and uses the analytic form of correct probability found as $\frac{\beta + 1 - \alpha}{2}$ using the expressions $\alpha = \frac{1}{\sqrt{(2\pi)}\sigma_-} \int_{z_{threshold}}^{-\infty} e^{(\frac{x-\mu_-)^2}{\sigma_-^2}}$ and $\beta = 1 - \frac{1}{\sqrt{(2\pi)}\sigma_+} \int_{z_{threshold}}^{-\infty} e^{\frac{(x-\mu_+)^2}{\sigma_+^2}}$. As discussed previously, the minimum correct probability occurs at the mean of all observed rates. As such, the points at which the rates begin to decrease to or increase from the minimum sink are determined: the points at which the slope is a tenth of the slope of the maximal slope value of $\frac{\beta + 1 - \alpha}{2}$ are found. If the threshold is set to either of these values, a correct probability close to 0.5 can be achieved.



Problem 3

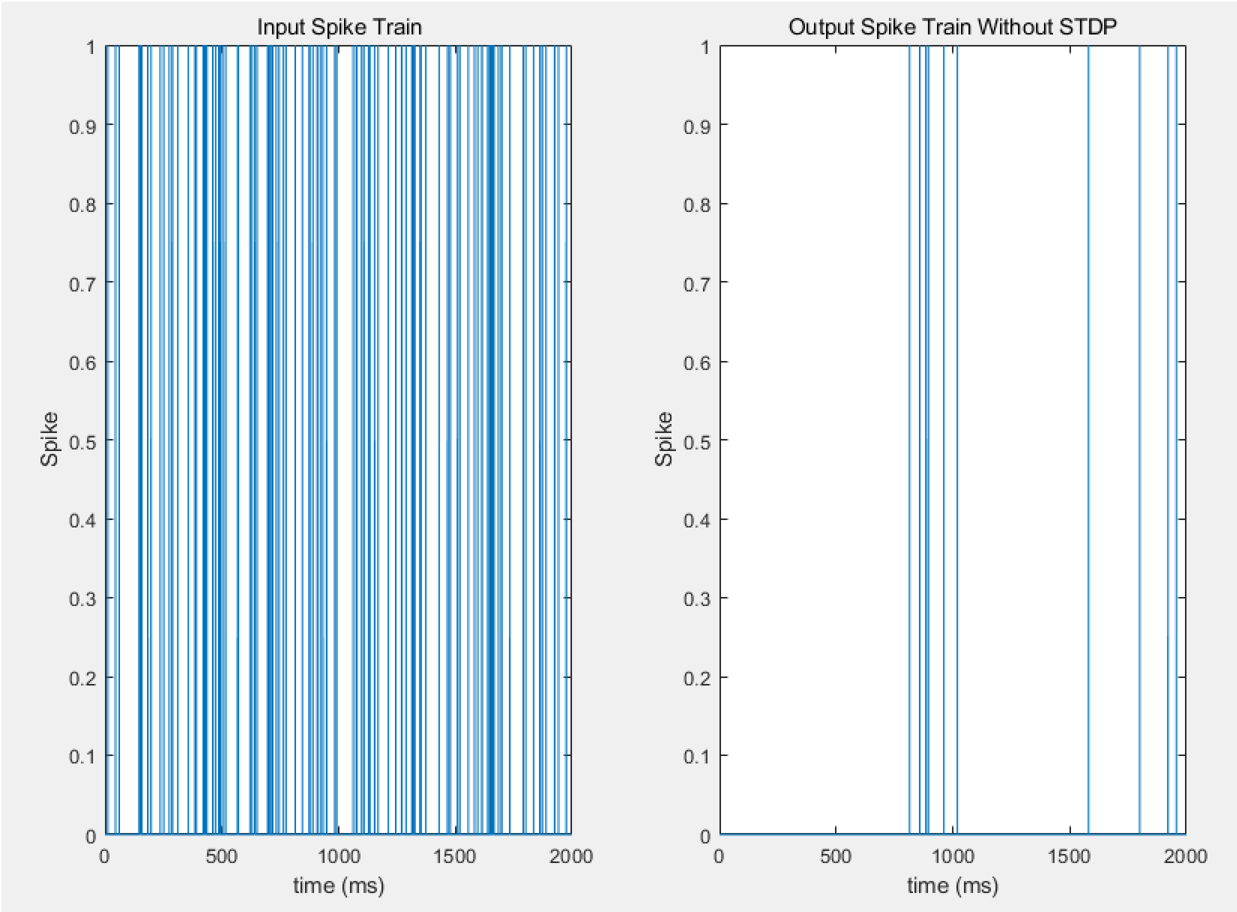
a. Design your equation and choose parameters, to implement the STDP as shown. Plot your result for Δt = [-100, 100] ms.

The exponential STDP is modeled as follows: $STDP(t^{post} - t^{pre}) = e^{\mp\frac{t^{post} - t^{pre}}{\tau^{\pm}}}\theta(\pm[t^{post} - t^{pre}])$, where $\theta(\pm[t^{post} - t^{pre}])$ is the step function. $\theta(\pm[t^{post} - t^{pre}]) = 1$ when $t^{post} - t^{pre} > 0$ and $\theta(\pm[t^{post} - t^{pre}]) = -1$ when $t^{post} - t^{pre} < 0$. The value of τ was set to 10 such that the STDP would be $1/e * \Delta EPSC(\Delta t = 0ms)$ at Δt = 10ms.



b. Suppose your pre-synaptic input is a random Poisson spike train of firing rate r^{pre}=50Hz, and your post-synaptic output is a random Poisson spike train of firing rate $r^{post}(\tau)$ = (mean input firing rate between τ-100ms and τ) * (EPSC amplitude, initially 0.1). When there is no synaptic plasticity (no change in EPSC), simulate your model spike trains and plot the pre- and post- spike trains for T=2sec.

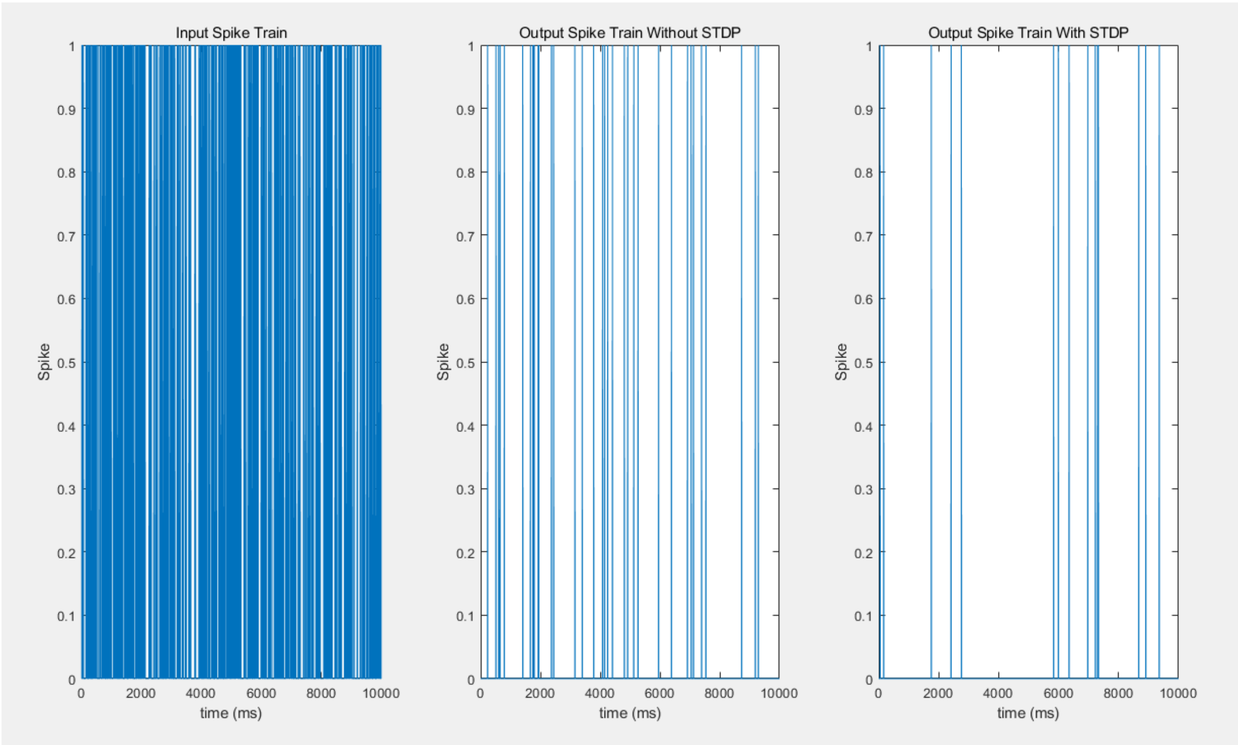
The output spike train was generated by iterating through the input spike train in 100 ms intervals. In each 100 ms interval, the average input firing was measured by finding the number of spikes and dividing the number by 0.1 s (100 ms). The corresponding 100 ms of the output spike train was generated as a 100 ms Poisson spike train with rate $r^{post}(\tau) =$ (mean input firing rate between τ - 100 ms and τ) * (0.1) without any STDP component.



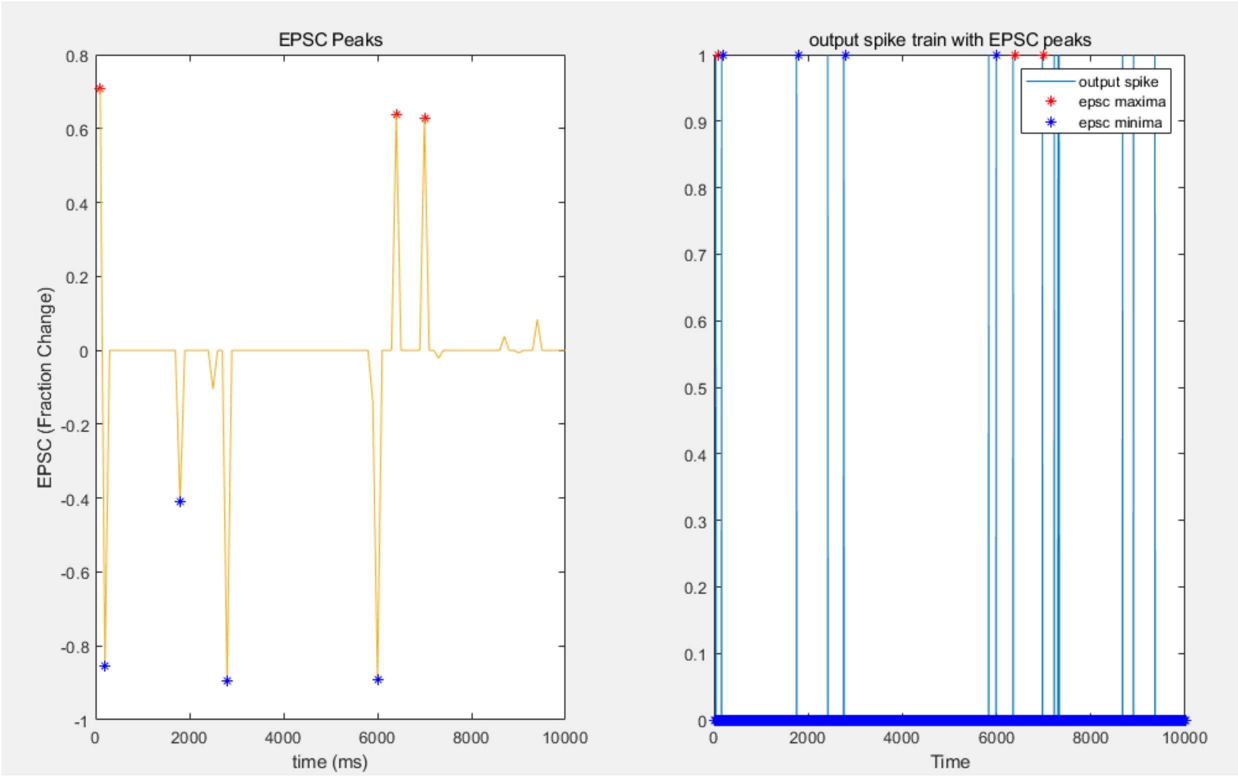
c. Now turn on the STDP in **a**. Simulate your model spike trains and plot the pre- and post- spike trains with the (instantaneously changing) value of EPSC. Choose proper values of simulation length and timescale to demonstrate your result effectively.

The STDP was turned on by comparing the average input spike timing to the average output spike timing in 100 ms intervals. To begin with, a 2 second input spike train was generated and the first 100 ms of the output spike was generated using the rate 0.1*(mean rate of first 100 ms of the input spike train). The next 100 ms of the output spike train was then generated using $r^{post}(\tau) =$ (mean input firing rate between τ - 100 ms and τ) * (0.1)*(1 + $STDP(t^{post} - t^{pre})$). The rest of the output spike was generated by iterating through 100ms of the input and generating 100ms intervals of the output using the average spike time differences between the input and output within each 100ms interval.

In order to observe the effect of turning on STDP, the output spike with and without STDP were compared. The same input spike train was used to generate an output spike train with and without STDP over a 10 s time interval.

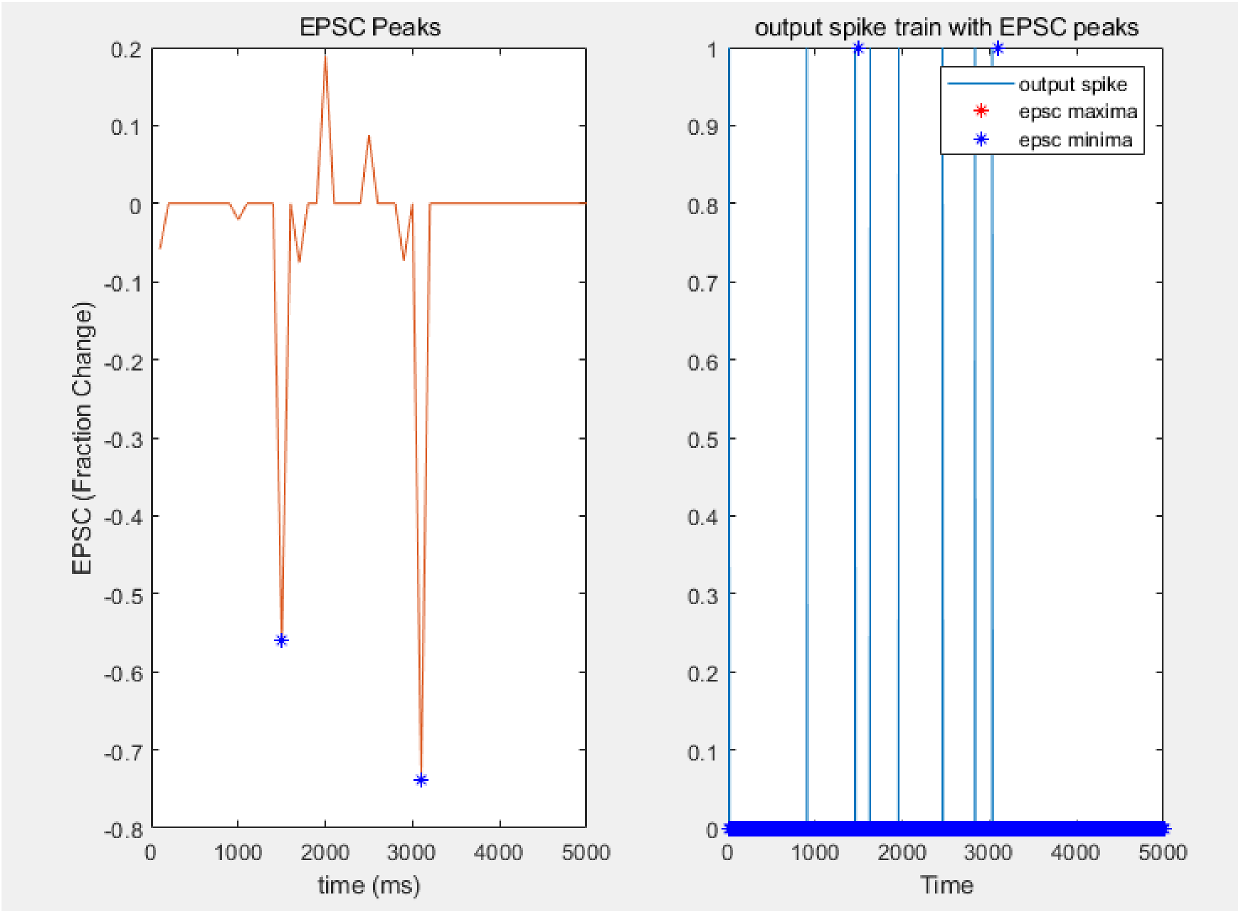


It can be seen that the spike train with STDP has a region with near zero spike rate. This is likely due to long term depression caused by the spikes in the output spike train occurring on average before spikes in the input. This can be verified by recording the EPSC across time. Below, it can be seen that there are negative minima in the change in EPSC prior to the section where no spikes occur in the spike train without STDP. As such, it can be seen that STDP weakens the connection between the input and output neurons.



(Figure generated in Prob3c_1.m)

It can be seen that there is no sustained long-term change occurs as both long term potentiation and long term depression may occur. Above, after the EPSC change is negative, there are 100 ms intervals where the EPSC change has positive local maxima, leading to an increase in output firing rate. As the average spike timing difference $t^{post} - t^{pre}$ in the 100 ms interval constantly changes as new 100 ms intervals of the postsynaptic spike train are generated stochastically. The instantaneous strengthening and weakening of the input-output connection is dependent on the stochastic spike timing. In order for a long-lasting change to occur between the input and the output, multiple peaks in EPSC change must occur in the same direction. An example of such a case can be seen below for a lower time interval of 5 s: after two negative minima in EPSC change occur in succession, no output spikes occur.

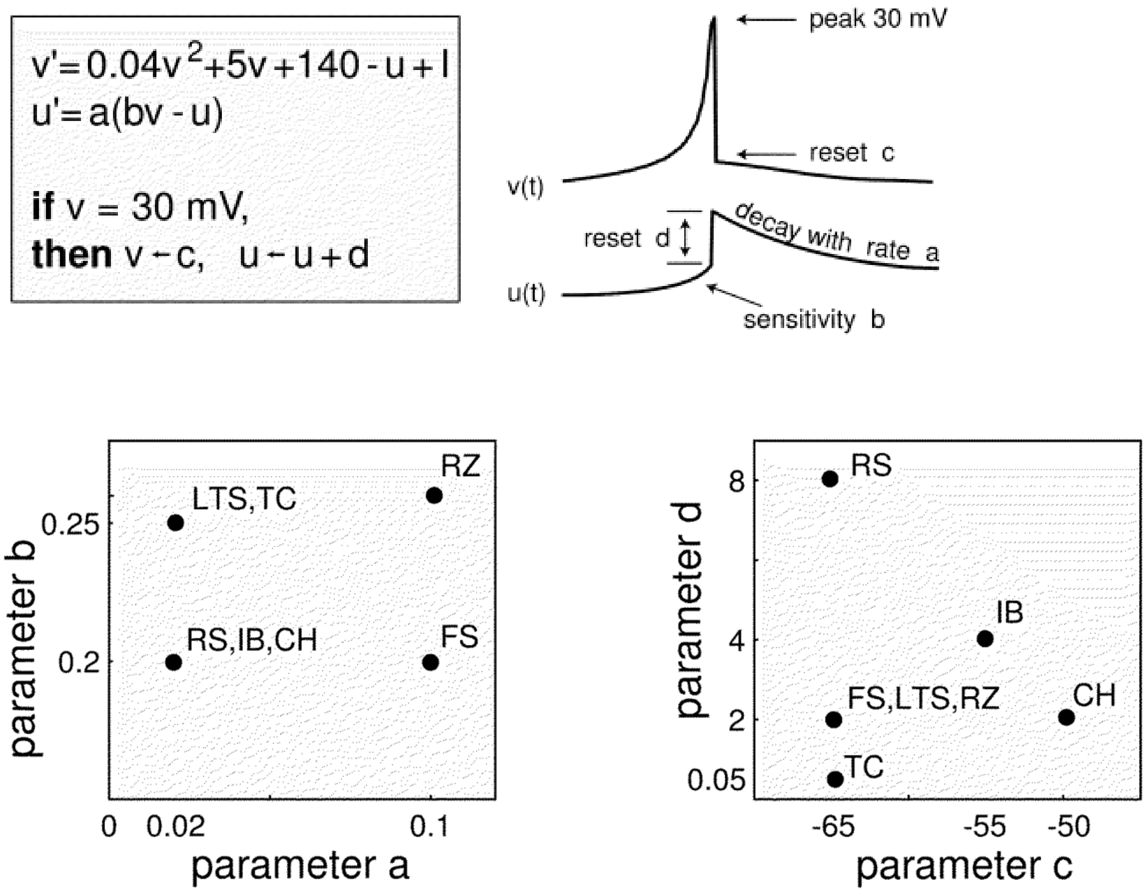


(Figure generated in Prob3c_2.m)

Problem 4

a. For $I(t)$= 10mA, find a set of parameters (a,b,c,d) such that the neuron fires at f~50Hz in "fast spiking" mode as shown. Plot V(t) and ISI (inter-spike-interval) histogram for 500ms.

The default parameters for regular spiking in the original paper for the Izhikevich neuron (https://www.izhikevich.org/publications/spikes.pdf)) were adjusted to achieve fast, regular spiking. In the paper, the values for regular spiking are a = 0.02, b=0.2, c = -65mV, d = 8. Fast spiking is achieved by increasing the value of a. Since a "describes the time scale of the recovery variable u", increasing a has the effect of increasing the frequency of spike occurrence since u decays more quickly; since the update for v includes -u, a faster decay in u corresponds to faster increases in v.

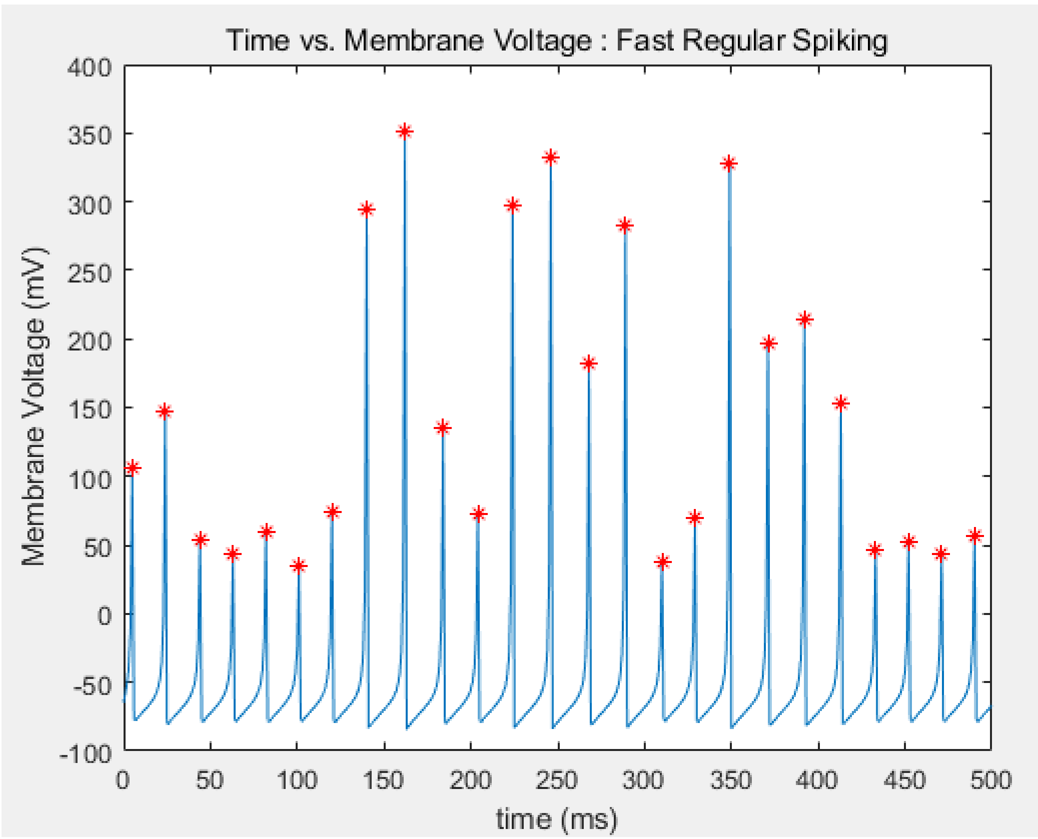


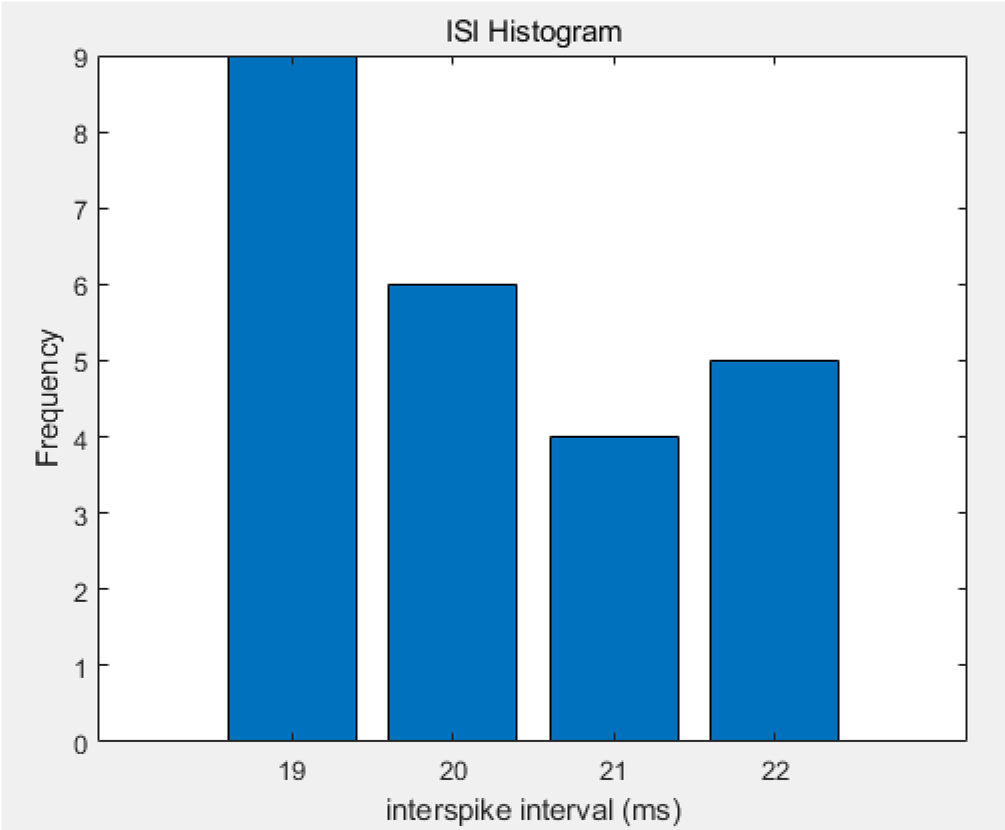
(figure taken from https://www.izhikevich.org/publications/spikes.pdf)

Fast, Regular Spiking:			
a	**b**	**c**	**d**
0.1	0.2	-65	13
Bursting Spiking:			
a	**b**	**c**	**d**
0.02	0.2	-50	3

The only parameter which was tuned further after setting the parameters to the default values a = 0.1, b=0.2, c = -65mV, d = 8 was d. It was observed that using the default parameter values, the number of spikes in the 500 ms interval, counted as local maxima in the voltage, was 33. This corresponds to a rate of 66 Hz. The value of d was increased to decrease the rate down to the desired 50 Hz, which has 25 spikes in the 500 ms interval. Increasing d has the effect of decreasing rate because resetting u to a higher value increases the time required for u to decay sufficiently to cause a large spike in v. Grid search starting from the default value d=8 was used to determine the value of d=13 which leads to 25 spikes in the 500 ms interval.

It can be seen that the ISI histogram reflects the regularity of the spike timing. It can be seen that the ISI is consistently around 20, which corresponds to a 50 Hz firing rate.

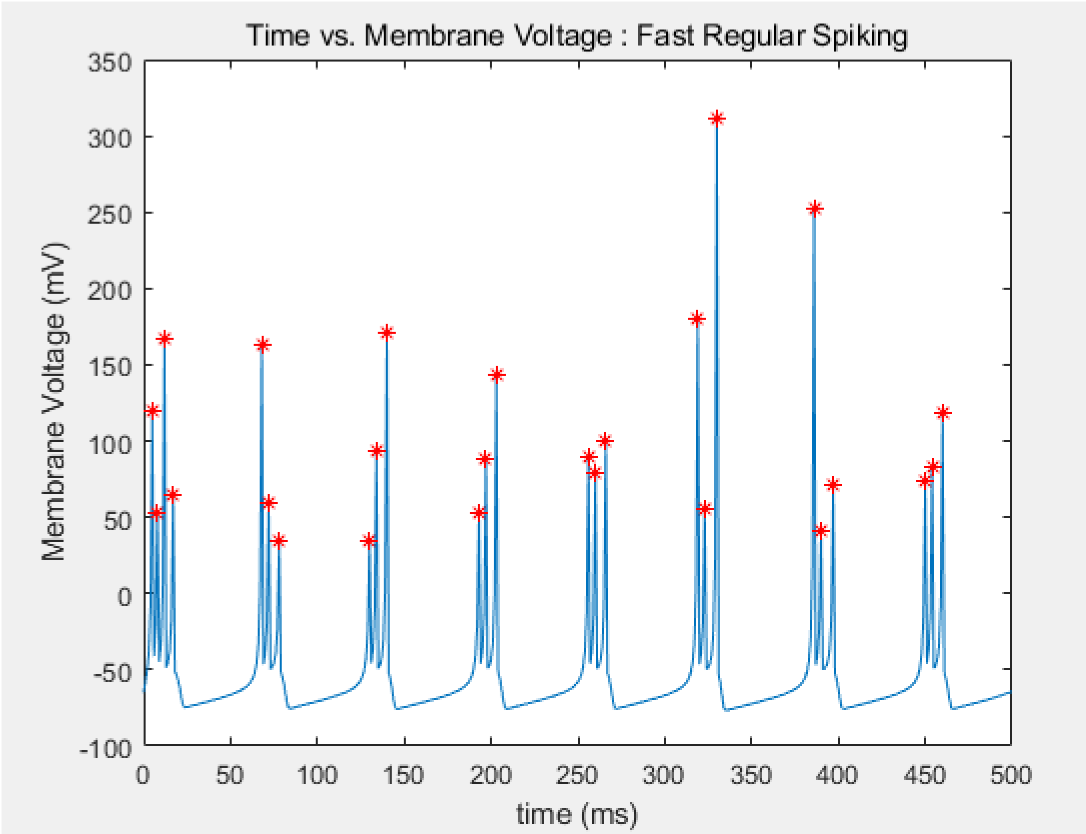




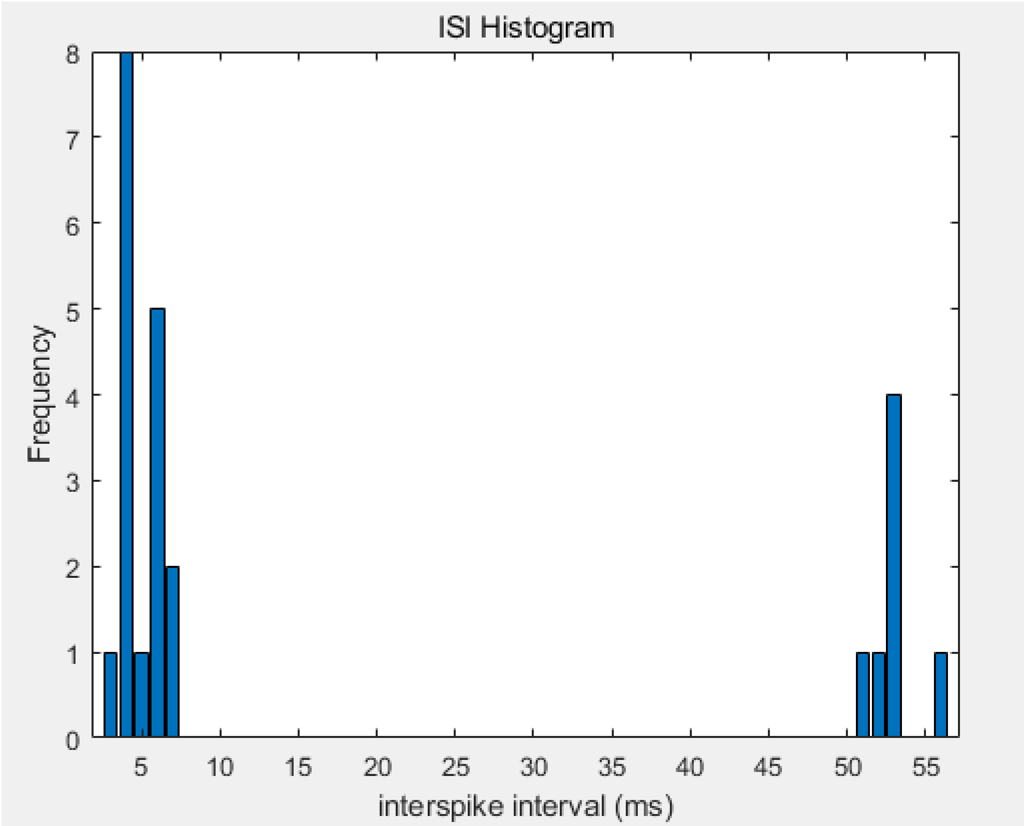
b. For $I(t)$= 10mA, find a set of parameters (a,b,c,d) such that the neuron fires at f~50Hz in "bursting" mode as shown. Plot V(t) and ISI histogram for 500ms.

The default parameters for chattering were adjusted to create “bursting” mode. In a bursting neuron, the value of a is lower than that for fast, regular spiking. The default value is set to 0.02. The value of c is also higher (set to -50), which indicates that the membrane voltage is reset to a higher value. Overall, the bursting neuron has a higher rate of decay of the reset parameter u while resetting the membrane voltage to a higher value.

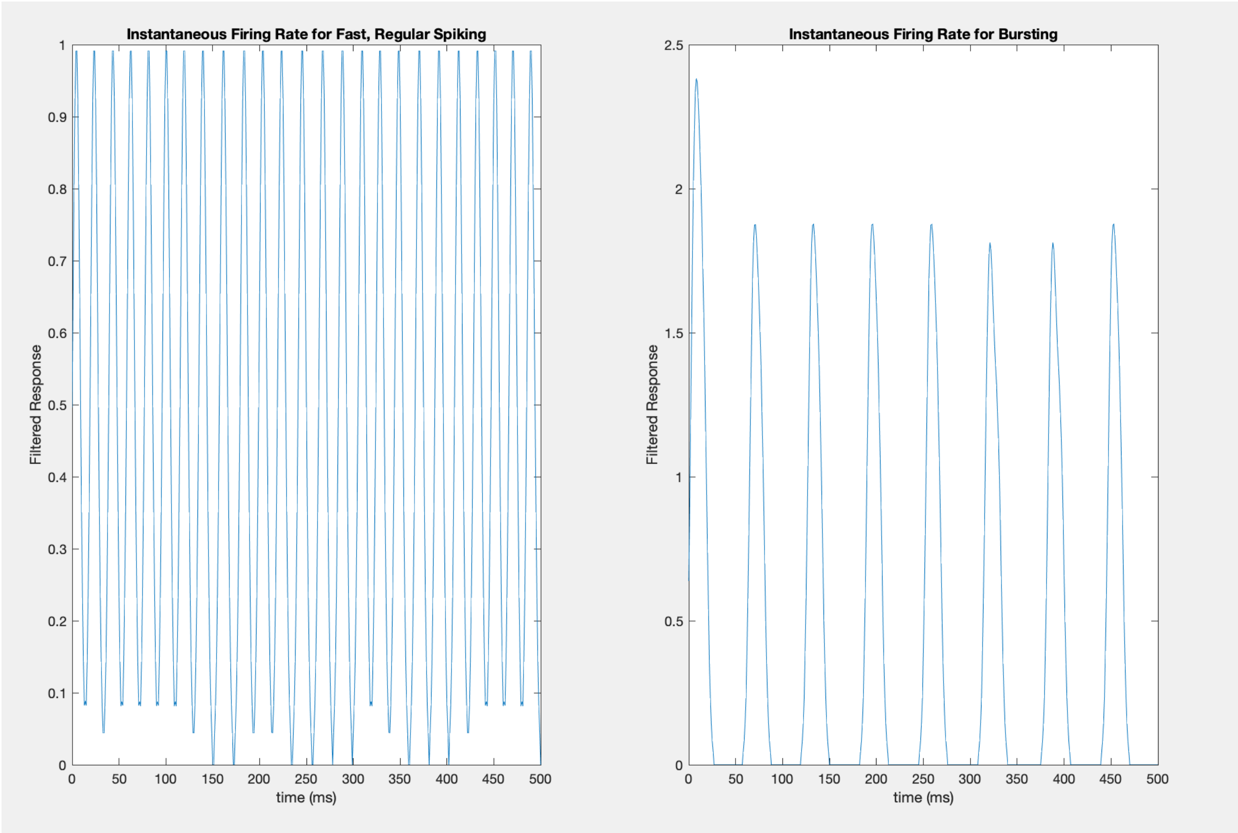
The only parameter which was tuned was d, which was increased from the default value of 2 in order to decrease the average firing rate to 50 Hz.



It can be seen that the ISI histogram has two distinct clusters. The first cluster consists of spikes in the bursting sections of the spike train, where spikes occur rapidly in succession in short bursts. The second cluster of larger ISIs corresponds to the relatively longer intervals between the series of bursts.



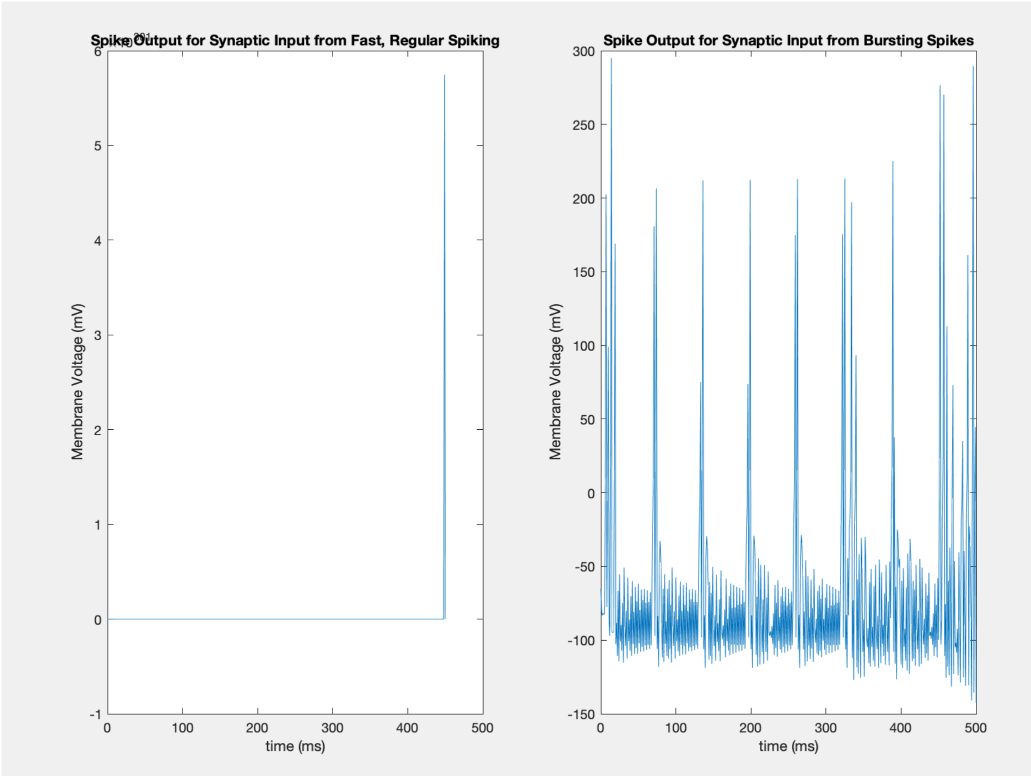
c. Estimate the instantaneous firing rate of two conditions by applying a proper size of Gaussian filter to spike raster. Discuss whether you can describe each condition using the average firing rate.



In order to apply a gaussian filter, the spike train was convolved with a gaussian function with a standard deviation set to 20 ms, which is the interspike interval when completely regular spiking occurs at 50 Hz. For fast, regular spiking, applying the gaussian filter leads to 25 clearly separated gaussian functions appearing as the filtered result. On the other hand, for the bursting spike train, the result shows 8 gaussian functions centered at the time points when the membrane voltage bursts occurred. The peak values of these gaussians for the bursting spike trains, which indicates the maximum firing rate within the width of the gaussian window, is roughly twice that of the peak firing rate for the fast, regular spiking neuron.

Overall, different spike train modes can be distinguished by the width of the gaussian curves as well as the peak instantaneous firing rate. For a bursting spike train, the instantaneous firing rate is higher and the width of each gaussian is larger due to the closely spaced spikes during bursts.

d. Now suppose this neuron provides presynaptic input to another (target) model neuron. Find a condition that this target neuron fires with the input in **b**, but not fire with the input in **a**. Implement your simulation to realize this, and plot the response of the target neuron for the two input conditions.



a	b	c	d
0.01	0.01	-55	9

In order for the target neuron to not respond to the fast, regular spiking profile, the rate of decay of u must be low such that u does not decrease sufficiently to cause a spike. Without any input current, the target neuron only receives current input from the synaptic current generated from the input neuron. From $\frac{dv}{dt} = -u + I_{syn}$, it can be seen that membrane voltage v increases sufficiently to cause a spike when the reset variable u is continuously negative and the synaptic current occurs. To achieve the same effect, the value of the parameter b was also decreased in order to decouple voltage v from the reset parameter u; in this way, an increase in voltage would not lead to any decrease in u. At the same time, the reset value d of the variable u should be high for the same reason that u should not decrease sufficiently to cause large increases in v. Increasing the value of d also has the effect of suppressing increases in v, since the -u term in the update for $v = v + \Delta t \frac{dv}{dt}$ becomes a highly negative value at reset. Overall, a, b, and d were adjusted to reduce the effect of u on increasing v for fast, regular spike inputs.

With low values of a and b and a high value of d, the target neuron only responds to bursting spike inputs. This is because when spikes occur rapidly in succession, the voltage can increase sufficiently even without any additional assistance from u.