Tutorial 1: The Leaky Integrate-and-Fire (LIF) Neuron Model

Contents

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Week 2, Day 3: Biological Neuron Models

By Neuromatch Academy

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Estimated timing of tutorial: 1 hour, 10 min

This is Tutorial 1 of a series on implementing realistic neuron models. In this tutorial, we will build up a leaky integrate-and-fire (LIF) neuron model and study its dynamics in response to various types of inputs. In particular, we are going to write a few lines of code to:

- simulate the LIF neuron model
- drive the LIF neuron with external inputs, such as direct currents, Gaussian white noise, and Poisson spike trains, etc.
- study how different inputs affect the LIF neuron's output (firing rate and spike time irregularity)

Here, we will especially emphasize identifying conditions (input statistics) under which a neuron can spike at low firing rates and in an irregular manner. The reason for focusing on this is that in most cases, neocortical neurons spike in an irregular manner.

Tutorial slides

These are the slides for the videos in all tutorials today

```
# Imports

import numpy as np
import matplotlib.pyplot as plt
```

Figure Settings

Plotting Functions

Video 1: Reduced Neuron Models

Youtube | Bilibili

```
Video available at https://youtube.com/watch?v=rSExvwCVRYg
```

This video introduces the reduction of a biological neuron to a simple leaky-integrate-fire (LIF) neuron model.

▶ Click here for text recap of video

Note that you have seen the LIF model before if you looked at the pre-reqs Python or Calculus days!

The LIF model captures the facts that a neuron:

- performs spatial and temporal integration of synaptic inputs
- generates a spike when the voltage reaches a certain threshold
- goes refractory during the action potential
- has a leaky membrane

The LIF model assumes that the spatial and temporal integration of inputs is linear. Also, membrane potential dynamics close to the spike threshold are much slower in LIF neurons than in real neurons.

Coding Exercise 1: Python code to simulate the LIF neuron

We now write Python code to calculate our equation for the LIF neuron and simulate the LIF neuron dynamics. We will use the Euler method, which you saw in the linear systems case yesterday to numerically integrate this equation:

$$\tau_m \frac{dV}{dt} = -(V - E_L) + \frac{I}{g_L}$$

where V is the membrane potential, g_L is the leak conductance, E_L is the resting potential, I is the external input current, and τ_m is membrane time constant.

The cell below initializes a dictionary that stores parameters of the LIF neuron model and the simulation scheme. You can use `pars=default_pars(T=simulation_time, dt=time_step)` to get the parameters. Note that, `simulation_time` and `time_step` have the unit `ms`. In addition, you can add the value to a new parameter by `pars['New_param'] = value`.

Execute this code to initialize the default parameters

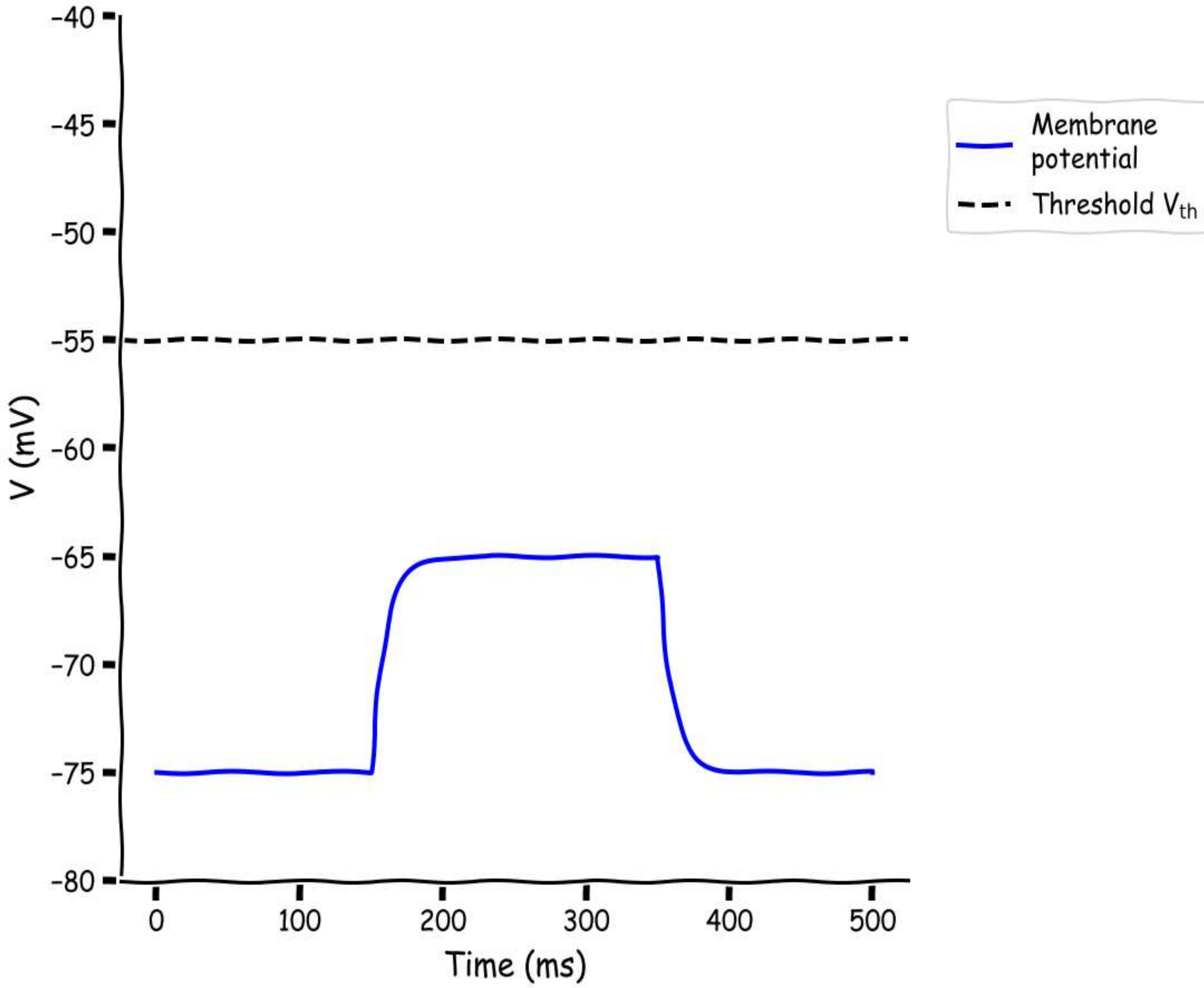
```
{'V_th': -55.0, 'V_reset': -75.0, 'tau_m': 10.0, 'g_L': 10.0, 'V_init': -75.0, 'E_L':
-75.0, 'tref': 2.0, 'T': 400.0, 'dt': 0.1, 'range_t': array([0.000e+00, 1.000e-01, 2.000e-
01, ..., 3.997e+02, 3.998e+02,
       3.999e+02])}
```

Complete the function below to simulate the LIF neuron when receiving external current inputs. You can use `v, sp = run_LIF(pars, Iinj)` to get the membrane potential (`v`) and spike train (`sp`) given the dictionary `pars` and input current `Iinj`.

```python
def run_LIF(pars, Iinj, stop=False):
  """
  Simulate the LIF dynamics with external input current

  Args:
    pars       : parameter dictionary
    Iinj       : input current [pA]. The injected current here can be a value
                 or an array
    stop       : boolean. If True, use a current pulse

  Returns:
    rec_v      : membrane potential
    rec_sp     : spike times
  """

  # Set parameters
  V_th, V_reset = pars['V_th'], pars['V_reset']
  tau_m, g_L = pars['tau_m'], pars['g_L']
  V_init, E_L = pars['V_init'], pars['E_L']
  dt, range_t = pars['dt'], pars['range_t']
  Lt = range_t.size
  tref = pars['tref']

  # Initialize voltage
  v = np.zeros(Lt)
  v[0] = V_init

  # Set current time course
  Iinj = Iinj * np.ones(Lt)

  # If current pulse, set beginning and end to 0
  if stop:
    Iinj[:int(len(Iinj) / 2) - 1000] = 0
    Iinj[int(len(Iinj) / 2) + 1000:] = 0

  # Loop over time
  rec_spikes = []  # record spike times
  tr = 0.  # the count for refractory duration

  for it in range(Lt - 1):

    if tr > 0:  # check if in refractory period
      v[it] = V_reset  # set voltage to reset
      tr = tr - 1 # reduce running counter of refractory period

    elif v[it] >= V_th:  # if voltage over threshold
      rec_spikes.append(it)  # record spike event
      v[it] = V_reset  # reset voltage
      tr = tref / dt  # set refractory time

    ########################################################################
    ## TODO for students: compute the membrane potential v, spike train sp #
    # Fill out function and remove
    raise NotImplementedError('Student Exercise: calculate the dv/dt and the update
step!')
    ########################################################################

    # Calculate the increment of the membrane potential
    dv = ...

    # Update the membrane potential
    v[it + 1] = ...

  # Get spike times in ms
  rec_spikes = np.array(rec_spikes) * dt

  return v, rec_spikes


# Get parameters
pars = default_pars(T=500)

# Simulate LIF model
v, sp = run_LIF(pars, Iinj=100, stop=True)

# Visualize
plot_volt_trace(pars, v, sp)
```

[Click for solution](#)

Example output:



Estimated timing to here from start of tutorial: 20 min

In the following section, we will learn how to inject direct current and white noise to study the response of an LIF neuron.

Video 2: Response of the LIF neuron to different inputs

Youtube | Bilibili

```
Video available at https://youtube.com/watch?v=preNGdab7Kk
```

Section 2.1: Direct current (DC)

Estimated timing to here from start of tutorial: 30 min

Interactive Demo 2.1: Parameter exploration of DC input amplitude

Here's an interactive demo that shows how the LIF neuron behavior changes for DC input (constant current) with different amplitudes. We plot the membrane potential of an LIF neuron. You may notice that the neuron generates a spike. But this is just a cosmetic spike only for illustration purposes. In an LIF neuron, we only need to keep track of times when the neuron hit the threshold so the postsynaptic neurons can be informed of the spike.

How much DC is needed to reach the threshold (rheobase current)? How does the membrane time constant affect the frequency of the neuron?

Make sure you execute this cell to enable the widget!

I_dc 50.00

tau_m 10.00

```
---------------------------------------------------------------------------
NotImplementedError                       Traceback (most recent call last)
/opt/hostedtoolcache/Python/3.7.12/x64/lib/python3.7/site-
packages/ipywidgets/widgets/interaction.py in update(self, *args)
    255                     value = widget.get_interact_value()
    256                     self.kwargs[widget._kwarg] = value
--> 257                 self.result = self.f(**self.kwargs)
    258                 show_inline_matplotlib_plots()
    259                 if self.auto_display and self.result is not None:

/tmp/ipykernel_3995/2402907096.py in diff_DC(I_dc, tau_m)
     12   pars = default_pars(T=100.)
     13   pars['tau_m'] = tau_m
---> 14   v, sp = run_LIF(pars, Iinj=I_dc)
     15   plot_volt_trace(pars, v, sp)
     16   plt.show()

/tmp/ipykernel_3995/3866942583.py in run_LIF(pars, Iinj, stop)
     52     ## TODO for students: compute the membrane potential v, spike train sp #
     53     # Fill out function and remove
---> 54     raise NotImplementedError('Student Exercise: calculate the dv/dt and the
update step!')
     55     ########################################################################
```

```
     56

NotImplementedError: Student Exercise: calculate the dv/dt and the update step!
```

[*Click for solution*]()

Section 2.2: Gaussian white noise (GWN) current

Estimated timing to here from start of tutorial: 38 min

Given the noisy nature of neuronal activity *in vivo*, neurons usually receive complex, time-varying inputs.

To mimic this, we will now investigate the neuronal response when the LIF neuron receives Gaussian white noise $\xi(t)$ with mean 0 ($\mu = 0$) and some standard deviation σ.

Note that the GWN has zero mean, that is, it describes only the fluctuations of the input received by a neuron. We can thus modify our definition of GWN to have a nonzero mean value μ that equals the DC input, since this is the average input into the cell. The cell below defines the modified gaussian white noise currents with nonzero mean μ.

Interactive Demo 2.2: LIF neuron Explorer for noisy input

The mean of the Gaussian white noise (GWN) is the amplitude of DC. Indeed, when $\sigma = 0$, GWN is just a DC.

So the question arises how does σ of the GWN affect the spiking behavior of the neuron. For instance we may want to know

1. how does the minimum input (i.e. μ) needed to make a neuron spike change with increase in σ
2. how does the spike regularity change with increase in σ

To get an intuition about these questions you can use the following interactive demo that shows how the LIF neuron behavior changes for noisy input with different amplitudes (the mean μ) and fluctuation sizes (σ). We use a helper function to generate this noisy input current: `my_GWN(pars, mu, sig, myseed=False)`. Note that fixing the value of the random seed (e.g., `myseed=2020`) will allow you to obtain the same result every time you run this. We then use our `run_LIF` function to simulate the LIF model.

Execute to enable helper function `my_GWN`

```
Help on function my_GWN in module __main__:

my_GWN(pars, mu, sig, myseed=False)
    Function that generates Gaussian white noise input

    Args:
      pars       : parameter dictionary
      mu         : noise baseline (mean)
      sig        : noise amplitute (standard deviation)
      myseed     : random seed. int or boolean
                   the same seed will give the same
                   random number sequence

    Returns:
      I          : Gaussian white noise input
```

Make sure you execute this cell to enable the widget!

mu_gwn 200.00

sig_gwn 2.50

```
---------------------------------------------------------------------------
NotImplementedError                       Traceback (most recent call last)
/opt/hostedtoolcache/Python/3.7.12/x64/lib/python3.7/site-
packages/ipywidgets/widgets/interaction.py in update(self, *args)
    255                     value = widget.get_interact_value()
    256                     self.kwargs[widget._kwarg] = value
--> 257                 self.result = self.f(**self.kwargs)
    258                 show_inline_matplotlib_plots()
    259                 if self.auto_display and self.result is not None:

/tmp/ipykernel_3995/2904493659.py in diff_GWN_to_LIF(mu_gwn, sig_gwn)
     15   pars = default_pars(T=100.)
     16   I_GWN = my_GWN(pars, mu=mu_gwn, sig=sig_gwn)
---> 17   v, sp = run_LIF(pars, Iinj=I_GWN)
     18   plt.figure(figsize=(12, 4))
     19   plt.subplot(121)

/tmp/ipykernel_3995/3866942583.py in run_LIF(pars, Iinj, stop)
     52     ## TODO for students: compute the membrane potential v, spike train sp #
     53     # Fill out function and remove
---> 54     raise NotImplementedError('Student Exercise: calculate the dv/dt and the
update step!')
     55     ########################################################################
     56

NotImplementedError: Student Exercise: calculate the dv/dt and the update step!
```

Click for solution

Think! 2.2: Analyzing GWN Effects on Spiking

- As we increase the input average (μ) or the input fluctuation (σ), the spike count changes. How much can we increase the spike count, and what might be the relationship between GWN mean/std or DC value and spike count?
- We have seen above that when we inject DC, the neuron spikes in a regular manner (clock like), and this regularity is reduced when GWN is injected. The question is, how irregular can we make the neurons spiking by changing the parameters of the GWN?

We will see the answers to these questions in the next section but discuss first!

Estimated timing to here from start of tutorial: 48 min

When we plot the output firing rate as a function of GWN mean or DC value, it is called the input-output transfer function of the neuron (so simply F-I curve).

Spike regularity can be quantified as the **coefficient of variation (CV) of the inter-spike-interval (ISI)**:

$$\text{CV}_{\text{ISI}} = \frac{std(\text{ISI})}{mean(\text{ISI})} \tag{256}$$

A Poisson train is an example of high irregularity, in which $\mathbf{CV_{ISI}= 1}$. And for a clocklike (regular) process we have $\mathbf{CV_{ISI}= 0}$ because of **std(ISI)=0**.

Interactive Demo 3A: F-I Explorer for different `sig_gwn`

How does the F-I curve of the LIF neuron change as we increase the σ of the GWN? We can already expect that the F-I curve will be stochastic and the results will vary from one trial to another. But will there be any other change compared to the F-I curved measured using DC?

Here's an interactive demo that shows how the F-I curve of a LIF neuron changes for different levels of fluctuation σ.

Make sure you execute this cell to enable the widget!

Make sure you execute this cell to enable the widget.

sig_gwn 3.00

```
---------------------------------------------------------------------------
NotImplementedError                       Traceback (most recent call last)
/opt/hostedtoolcache/Python/3.7.12/x64/lib/python3.7/site-
packages/ipywidgets/widgets/interaction.py in update(self, *args)
    255                     value = widget.get_interact_value()
    256                     self.kwargs[widget._kwarg] = value
--> 257                 self.result = self.f(**self.kwargs)
    258                 show_inline_matplotlib_plots()
    259                 if self.auto_display and self.result is not None:

/tmp/ipykernel_3995/1638264340.py in diff_std_affect_fI(sig_gwn)
     19   for idx in range(len(I_mean)):
     20       I_GWN = my_GWN(pars, mu=I_mean[idx], sig=sig_gwn, myseed=2020)
---> 21       v, rec_spikes = run_LIF(pars, Iinj=I_GWN)
     22       v_dc, rec_sp_dc = run_LIF(pars, Iinj=I_mean[idx])
     23       spk_count[idx] = len(rec_spikes)

/tmp/ipykernel_3995/3866942583.py in run_LIF(pars, Iinj, stop)
     52     ## TODO for students: compute the membrane potential v, spike train sp #
     53     # Fill out function and remove
---> 54     raise NotImplementedError('Student Exercise: calculate the dv/dt and the
update step!')
     55     ##########################################################################
     56

NotImplementedError: Student Exercise: calculate the dv/dt and the update step!
```

Click for solution

Coding Exercise 3: Compute CV_{ISI} values

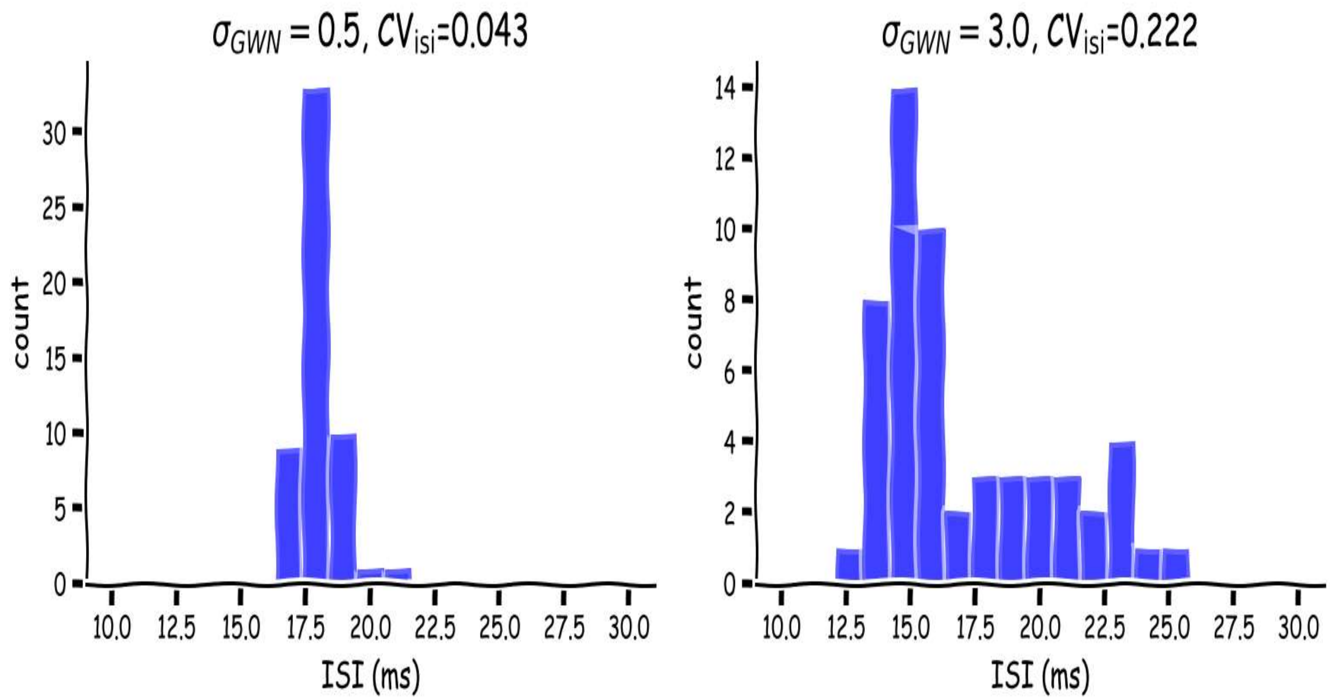
As shown above, the F-I curve becomes smoother while increasing the amplitude of the fluctuation (σ). In addition, the fluctuation can also change the irregularity of the spikes. Let's investigate the effect of $\mu = 250$ with $\sigma = 0.5$ vs $\sigma = 3$.

Fill in the code below to compute ISI, then plot the histogram of the ISI and compute the CV_{ISI}. Note that, you can use `np.diff` to calculate ISI.

```python
def isi_cv_LIF(spike_times):
  """
  Calculates the inter-spike intervals (isi) and
  the coefficient of variation (cv) for a given spike_train

  Args:
    spike_times : (n, ) vector with the spike times (ndarray)

  Returns:
    isi         : (n-1,) vector with the inter-spike intervals (ms)
    cv          : coefficient of variation of isi (float)

  """
  ########################################################################
  ## TODO for students: compute the membrane potential v, spike train sp #
  # Fill out function and remove
  raise NotImplementedError('Student Exercise: calculate the isi and the cv!')
  ########################################################################
  if len(spike_times) >= 2:
    # Compute isi
    isi = ...
    # Compute cv
    cv = ...
  else:
    isi = np.nan
    cv = np.nan

  return isi, cv


# Set parameters
pars = default_pars(T=1000.)
mu_gwn = 250
sig_gwn1 = 0.5
sig_gwn2 = 3.0

# Run LIF model for sigma = 0.5
I_GWN1 = my_GWN(pars, mu=mu_gwn, sig=sig_gwn1, myseed=2020)
_, sp1 = run_LIF(pars, Iinj=I_GWN1)

# Run LIF model for sigma = 3
I_GWN2 = my_GWN(pars, mu=mu_gwn, sig=sig_gwn2, myseed=2020)
_, sp2 = run_LIF(pars, Iinj=I_GWN2)

# Compute ISIs/CV
isi1, cv1 = isi_cv_LIF(sp1)
isi2, cv2 = isi_cv_LIF(sp2)

# Visualize
my_hists(isi1, isi2, cv1, cv2, sig_gwn1, sig_gwn2)
```

[*Click for solution*](#)

Example output:



Interactive Demo 3B: Spike irregularity explorer for different `sig_gwn`

In the above illustration, we see that the CV of inter-spike-interval (ISI) distribution depends on σ of GWN. What about the mean of GWN, should that also affect the CV_{ISI}? If yes, how? Does the efficacy of σ in increasing the CV_{ISI} depend on μ?

In the following interactive demo, you will examine how different levels of fluctuation σ affect the CVs for different average injected currents (μ).

1. Does the standard deviation of the injected current affect the F-I curve in any qualitative manner?
2. Why does increasing the mean of GWN reduce the CV_{ISI}?
3. If you plot spike count (or rate) vs. CV_{ISI}, should there be a relationship between the two? Try out yourself.

Make sure you execute this cell to enable the widget!

sig_gwn 0.00

```
---------------------------------------------------------------------------
NotImplementedError                       Traceback (most recent call last)
/opt/hostedtoolcache/Python/3.7.12/x64/lib/python3.7/site-
packages/ipywidgets/widgets/interaction.py in update(self, *args)
    255                     value = widget.get_interact_value()
    256                     self.kwargs[widget._kwarg] = value
--> 257                 self.result = self.f(**self.kwargs)
    258                 show_inline_matplotlib_plots()
    259                 if self.auto_display and self.result is not None:

/tmp/ipykernel_3995/2982391413.py in diff_std_affect_fI(sig_gwn)
     18   for idx in range(len(I_mean)):
     19     I_GWN = my_GWN(pars, mu=I_mean[idx], sig=sig_gwn)
---> 20     v, rec_spikes = run_LIF(pars, Iinj=I_GWN)
     21     spk_count[idx] = len(rec_spikes)
     22     if len(rec_spikes) > 3:

/tmp/ipykernel_3995/3866942583.py in run_LIF(pars, Iinj, stop)
     52     ## TODO for students: compute the membrane potential v, spike train sp #
     53     # Fill out function and remove
---> 54     raise NotImplementedError('Student Exercise: calculate the dv/dt and the
update step!')
     55     ########################################################################
     56 

NotImplementedError: Student Exercise: calculate the dv/dt and the update step!
```

Click for solution

Estimated timing of tutorial: 1 hour, 10 min

Congratulations! You've just built a leaky integrate-and-fire (LIF) neuron model from scratch, and studied its dynamics in response to various types of inputs, having:

- simulated the LIF neuron model
- driven the LIF neuron with external inputs, such as direct current and Gaussian white noise
- studied how different inputs affect the LIF neuron's output (firing rate and spike time irregularity),

with a special focus on low rate and irregular firing regime to mimc real cortical neurons. The next tutorial will look at how spiking statistics may be influenced by a neuron's input statistics.

If you have extra time, look at the bonus sections below to explore a different type of noise input and learn about extensions to integrate-and-fire models.

Bonus Section 1: Orenstein-Uhlenbeck Process

When a neuron receives spiking input, the synaptic current is Shot Noise – which is a kind of colored noise and the spectrum of the noise determined by the synaptic kernel time constant. That is, a neuron is driven by **colored noise** and not GWN.

We can model colored noise using the Ohrenstein-Uhlenbeck process - filtered white noise.

We next study if the input current is temporally correlated and is modeled as an Ornstein-Uhlenbeck process $\eta(t)$, i.e., low-pass filtered GWN with a time constant τ_η:

$$\tau_\eta \frac{d}{dt}\eta(t) = \mu - \eta(t) + \sigma_\eta \sqrt{2\tau_\eta}\xi(t).$$

Hint: An OU process as defined above has

$$E[\eta(t)] = \mu$$

and autocovariance

$$[\eta(t)\eta(t+\tau)] = \sigma_\eta^2 e^{-|t-\tau|/\tau_\eta},$$

which can be used to check your code.

Execute this cell to get helper function `my_OU`

```
Help on function my_OU in module __main__:

my_OU(pars, mu, sig, myseed=False)
    Function that produces Ornstein-Uhlenbeck input

    Args:
      pars       : parameter dictionary
      sig        : noise amplitute
      myseed     : random seed. int or boolean

    Returns:
      I_ou       : Ornstein-Uhlenbeck input current
```

Bonus Interactive Demo 1: LIF Explorer with OU input

In the following, we will check how a neuron responds to a noisy current that follows the statistics of an OU process.

- How does the OU type input change neuron responsiveness?
- What do you think will happen to the spike pattern and rate if you increased or decreased the time constant of the OU process?

Remember to enable the widget by running the cell!

tau_ou 10.00

sig_ou 10.00

mu_ou 190.00

```
---------------------------------------------------------------------------
NotImplementedError                       Traceback (most recent call last)
/opt/hostedtoolcache/Python/3.7.12/x64/lib/python3.7/site-
packages/ipywidgets/widgets/interaction.py in update(self, *args)
    255                     value = widget.get_interact_value()
    256                     self.kwargs[widget._kwarg] = value
--> 257                 self.result = self.f(**self.kwargs)
    258                 show_inline_matplotlib_plots()
    259                 if self.auto_display and self.result is not None:

/tmp/ipykernel_3995/867870810.py in LIF_with_OU(tau_ou, sig_ou, mu_ou)
     20   I_ou = my_OU(pars, mu_ou, sig_ou)
     21 
---> 22   v, sp = run_LIF(pars, Iinj=I_ou)
     23 
     24   plt.figure(figsize=(12, 4))

/tmp/ipykernel_3995/3866942583.py in run_LIF(pars, Iinj, stop)
     52     ## TODO for students: compute the membrane potential v, spike train sp #
     53     # Fill out function and remove
---> 54     raise NotImplementedError('Student Exercise: calculate the dv/dt and the
update step!')
     55     ###########################################################################
     56 

NotImplementedError: Student Exercise: calculate the dv/dt and the update step!
```

Click for solution

Bonus Section 2: Generalized Integrate-and-Fire models

LIF model is not the only abstraction of real neurons. If you want to learn about more realistic types of neuronal models, watch the Bonus Video!

Video 3 (Bonus): Extensions to Integrate-and-Fire models

Youtube | Bilibili

```
Video available at https://youtube.com/watch?v=G0b6wLhuQxE
```