JΛN0 & Natalia

AI tools have been used to review parts of this solution.

In [156…

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

In [157…

```
from cycler import cycler
plt.rcParams['axes.prop_cycle'] = cycler(color=['teal', 'purple', 'orange
```

1. Synaptic current

(a) & (b)

In [158…

```
def update_pars(old_pars, keys_to_change, new_vals):
    new_pars = old_pars.copy()
    for k, nv in zip(keys_to_change, new_vals):
        new_pars[k] = nv
    return new_pars
```

In [159…

```
# Params

pars_a_1 = {
    'tau_syn': 10 * 10**-3,
    'tau_m'  : 10 * 10**-3,
    'R_m'    : 1  * 10**7,
    'g_star' : 30 * 10**-9,
    'E_m'    : -80 * 10**-3,
    'E_exc'  : 0 * 10**-3,
    'E_inh'  : -100 * 10**-3,
    'E_syn'  : 0 * 10**-3,
    'g_exc'  : 0 * 10**-9,
    'g_inh'  : 0 * 10**-9,
    'I_e'    : 0 * 10**-9,
    'thr'    : -54 * 10**-3
}


pars_a_2 = update_pars(pars_a_1, ['E_syn'], [-100*10**-3])
pars_b = update_pars(pars_a_1, ['g_exc', 'g_inh'], [50*10**-9, 200*10**-9

# initial conditions for dynamic variables

ics = (-80*10**-3, 0, 0, 0)
```

In [160…

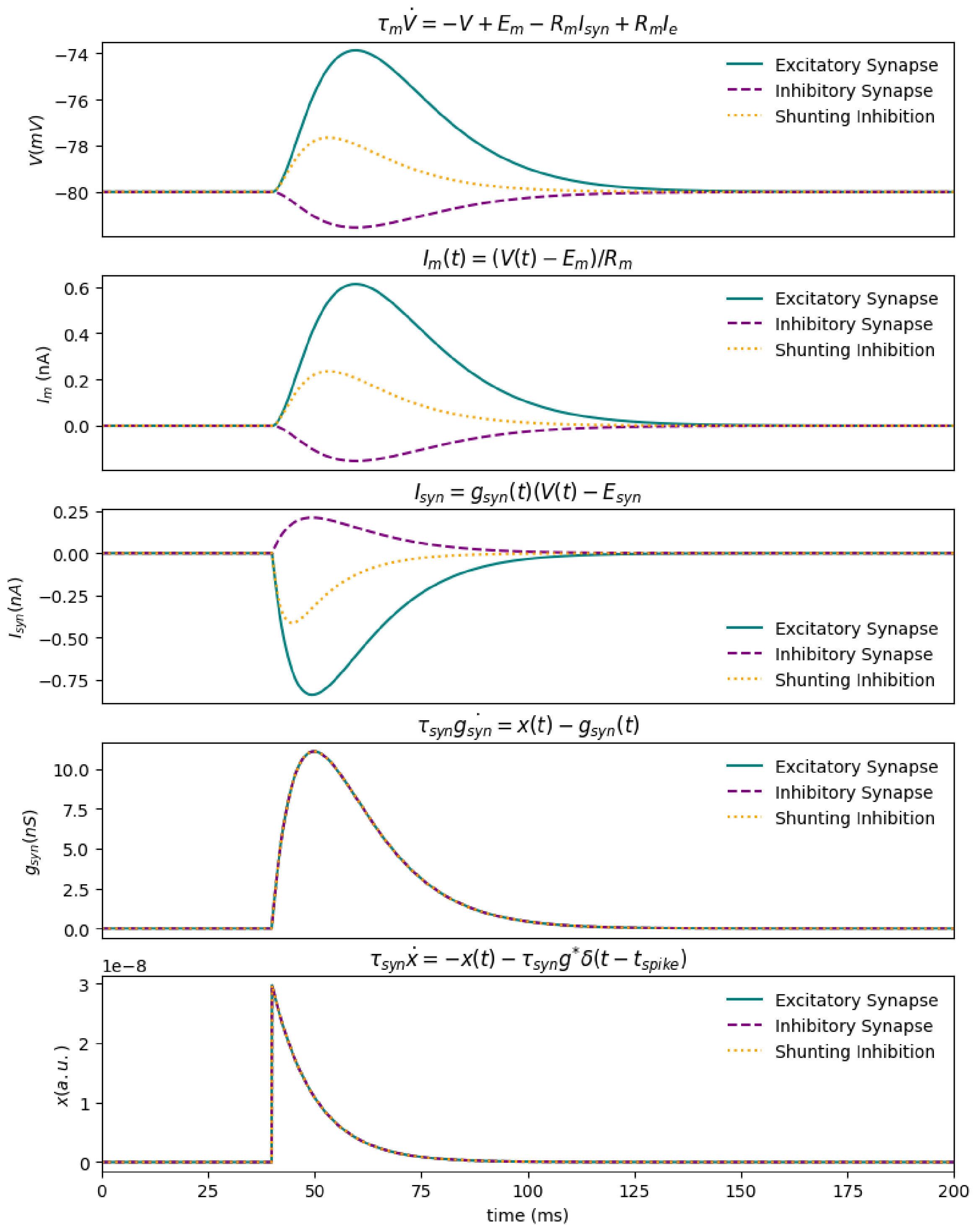
```
def euler_synaptic_if(tmax, dt, pre_spike_times, ics, pars, reset=False):

    tau_syn = pars['tau_syn']
    tau_m   = pars['tau_m']
    R_m     = pars['R_m']
    g_star  = pars['g_star']
    E_m     = pars['E_m']
    E_exc   = pars['E_exc']
    E_inh   = pars['E_inh']
    E_syn   = pars['E_syn']
    g_exc   = pars['g_exc']
    g_inh   = pars['g_inh']
    I_e     = pars['I_e']
    thr     = pars['thr']

    V, x, g, I_syn = ics

    ts = np.arange(0, tmax, dt)
    Vs = np.array([])
    gs = np.array([])
    xs = np.array([])
    I_syns = np.array([])
    spiketimes = np.array([])
    I_m_t = np.array([])

    for t in ts:

        if any(abs(t - ts0) < dt/2 for ts0 in pre_spike_times):
            x += g_star

        dVdt = ( -V + E_m - R_m*I_syn + R_m*I_e ) / tau_m
        dxdt = -x / tau_syn
        dgdt = (x - g) / tau_syn
        I_syn = g*(V - E_syn) + g_exc*(V - E_exc) + g_inh*(V - E_inh)

        V = V + dt*dVdt
        x = x + dt*dxdt
        g = g + dt*dgdt
        I_m = (V - E_m) / R_m

        if reset == True and V >= thr:
            V = E_m
            spiketimes = np.append(spiketimes, t)

        Vs = np.append(Vs, V)
        gs = np.append(gs, g)
        xs = np.append(xs, x)
        I_syns = np.append(I_syns, I_syn)
        I_m_t = np.append(I_m_t, I_m)

    return {
        'ts' : ts / 10**-3,
        'V_t' : Vs / 10**-3,
        'g_syn_t' : gs / 10**-9,
        'x_t' : xs,
        'I_syn_t' : I_syns / 10**-9,
        'I_m_t' : I_m_t / 10 ** -9,
        'spiketimes' : spiketimes / 10**-3
        }
```

In [161…

```
sol = []

for pars in [pars_a_1, pars_a_2, pars_b]:
    sol.append(euler_synaptic_if(tmax=0.2, dt=1e-4, pre_spike_times=[0.04
```

In [163…

```
fig, (ax1, ax2, ax3, ax4, ax5) = plt.subplots(5, 1, figsize=(9, 12))


ax1.plot(sol[0]["ts"], sol[0]['V_t'], label="Excitatory Synapse")
ax1.plot(sol[1]["ts"], sol[1]['V_t'], linestyle="--", label="Inhibitory S
ax1.plot(sol[2]["ts"], sol[2]['V_t'], linestyle=":", label="Shunting Inhi

ax2.plot(sol[0]["ts"], sol[0]['I_m_t'], label="Excitatory Synapse")
ax2.plot(sol[1]["ts"], sol[1]['I_m_t'], linestyle="--", label="Inhibitory
ax2.plot(sol[2]["ts"], sol[2]['I_m_t'], linestyle=":", label="Shunting In

ax3.plot(sol[0]["ts"], sol[0]['I_syn_t'], label="Excitatory Synapse")
ax3.plot(sol[1]["ts"], sol[1]['I_syn_t'], linestyle="--", label="Inhibito
ax3.plot(sol[2]["ts"], sol[2]['I_syn_t'], linestyle=":", label="Shunting 

ax4.plot(sol[0]["ts"], sol[0]['g_syn_t'], label="Excitatory Synapse")
ax4.plot(sol[1]["ts"], sol[1]['g_syn_t'], linestyle="--", label="Inhibito
ax4.plot(sol[2]["ts"], sol[2]['g_syn_t'], linestyle=":", label="Shunting 

ax5.plot(sol[0]["ts"], sol[0]['x_t'], label="Excitatory Synapse")
ax5.plot(sol[1]["ts"], sol[1]['x_t'], linestyle="--", label="Inhibitory S
ax5.plot(sol[2]["ts"], sol[2]['x_t'], linestyle=":", label="Shunting Inhi

for ax, title, ylabel in zip(
    [ax1, ax2, ax3, ax4, ax5],
    [
        "$\\tau_{m}\\dot{V} = -V + E_{m} - R_{m}I_{syn} + R_{m}I_{e}$",
        "$I_m (t) = (V(t) - E_m) / R_m$",
        "$I_{syn} = g_{syn}(t)(V(t) - E_{syn}$",
        "$\\tau_{syn} \\dot{g_{syn}} = x(t) - g_{syn}(t)$",
        "$\\tau_{syn} \\dot{x} = -x(t) - \\tau_{syn}g^{*}\\delta(t-t_{spi
    ],
    ["$V (mV)$", "$I_m$ (nA)", "$I_{syn} (nA)$", "$g_{syn} (nS)$", "$x (a

    ax.set_title(title)
    ax.set_ylabel(ylabel)
    ax.legend(frameon=False, loc='best')
    ax.set_xlim([0, 200])

    if ax != ax5:
        ax.set_xticks([])
    else:
        ax.set_xlabel("time (ms)")

plt.show()
```


$\tau_m\dot{V} = -V + E_m - R_m I_{syn} + R_m I_e$
$V(mV)$
−74
−76
−78
−80
Excitatory Synapse
Inhibitory Synapse
Shunting Inhibition
$I_m(t) = (V(t) - E_m)/R_m$
I_m (nA)
0.6
0.4
0.2
0.0
$I_{syn} = g_{syn}(t)(V(t) - E_{syn}$
$I_{syn}(nA)$
0.25
0.00
−0.25
−0.50
−0.75
$\tau_{syn}\dot{g_{syn}} = x(t) - g_{syn}(t)$
$g_{syn}(nS)$
10.0
7.5
5.0
2.5
0.0
$\tau_{syn}\dot{x} = -x(t) - \tau_{syn} g^{*}\delta(t - t_{spike})$
1e−8
$x(a.u.)$
3
2
1
0
0
25
50
75
100
125
150
175
200
time (ms)

Explaining the differences

a.) The voltage deflection caused by the inhibtory synapse is much smaller than the one caused by the excitatory synapse due to the differences between the resting membrane potential and the respective reversal potentials (80 mV for the exc. synapse vs. 20 mV for the inh. synapse).

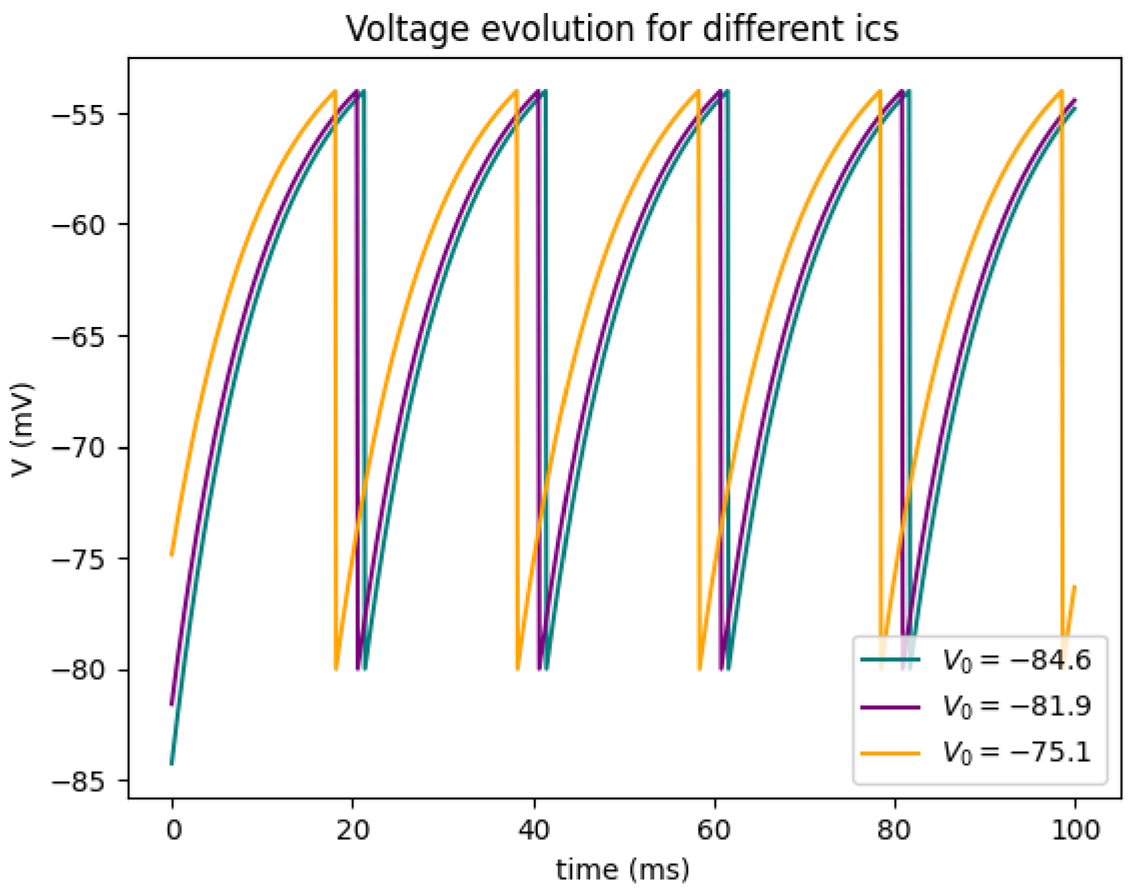
b.) Shunting inhibition introduces additional channels into the membrane, thereby increasing its effective leakiness and in turn decreases the input resistance and the membrane time constant. This leads to decreased integration of the synaptic input current and ultimately results in a smaller voltage defelction.

2. Integrate-and-fire neuron

(a), (b) & (c)

In [ ]:
```
pars_2_b = {
    'tau_syn': 10 * 10**-3,
    'tau_m'  : 10 * 10**-3,
    'R_m'    : 1  * 10**7,
    'g_star' : 30 * 10**-9,
    'E_m'    : -80 * 10**-3,
    'E_exc'  : 0 * 10**-3,
    'E_inh'  : -100 * 10**-3,
    'E_syn'  : 0 * 10**-3,
    'g_exc'  : 0 * 10**-9,
    'g_inh'  : 0 * 10**-9,
    'I_e'    : 3 * 10**-9,
    'thr'    : -54 * 10**-3
}
```

In [165…
```
for k in range(3):
    initial_V = np.random.choice(np.arange(-85, -75, 0.1) * 10**-3)
    ics = (initial_V, 0, 0, 0)
    sol = euler_synaptic_if(tmax=0.1, dt=1e-4, pre_spike_times=[], pars=p
    plt.plot(sol['ts'], sol['V_t'], label=f"$V_0 = {np.round(initial_V /
plt.legend()
plt.title('Voltage evolution for different ics')
plt.xlabel('time (ms)')
plt.ylabel('V (mV)')
plt.show()
```



Interpretation

Initialising with different V_0's introduces a phase delay in the firing of the different neurons. Since the firing thresholds are the same in all cases and the voltage evolves deterministically, this phase delay is persistent.

In [ ]:
```
def get_fr_ISI(spiketimes):
    spiketimes *= 10**-3
    if len(spiketimes) > 1:
        mean_isi = np.mean([spiketimes[i+1] - spiketimes[i] for i in rang
        fr = 1 / mean_isi
    else:
        fr = 0
    return fr
```

In [ ]:
```
def get_fr_num(spiketimes, simtime):
    if len(spiketimes) > 1:
        fr = len(spiketimes) / simtime
    else:
        fr = 0
    return fr
```

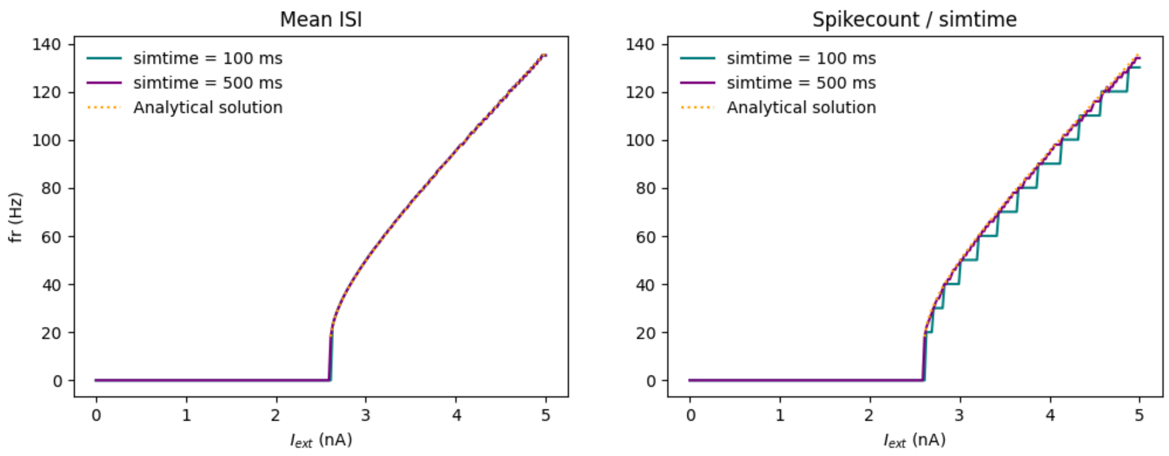
In [ ]:
```
def analytical_fr(pars):

    tau_syn = pars['tau_syn']
    tau_m   = pars['tau_m']
    R_m     = pars['R_m']
    g_star  = pars['g_star']
    E_m     = pars['E_m']
    E_exc   = pars['E_exc']
    E_inh   = pars['E_inh']
    E_syn   = pars['E_syn']
    g_exc   = pars['g_exc']
    g_inh   = pars['g_inh']
    I_e     = pars['I_e']
    thr     = pars['thr']
    V_reset = pars['E_m']

    fr = (tau_m * np.log( (R_m*I_e + E_m - V_reset) / (R_m*I_e + E_m - th

    return fr
```

In [ ]:
```
input_stimuli = np.linspace(0, 5, 250)

firing_rates_100_a = np.empty(len(input_stimuli))
firing_rates_500_a = np.empty(len(input_stimuli))

firing_rates_100_b = np.empty(len(input_stimuli))
firing_rates_500_b = np.empty(len(input_stimuli))

analytical_frs =  np.empty(len(input_stimuli))

for k, I_ext in enumerate(input_stimuli):

    initial_V = np.random.choice(np.arange(-85, -75, 0.1) * 10**-3)
    ics = (initial_V, 0, 0, 0)

    pars = update_pars(pars_2_b, ['I_e'], [I_ext * 10**-9])

    sol_1 = euler_synaptic_if(tmax=0.1, dt=1e-4, pre_spike_times=[], pars
    firing_rates_100_a[k] = get_fr_ISI(sol_1['spiketimes'])
    firing_rates_100_b[k] = get_fr_num(sol_1['spiketimes'], np.max(sol_1[

    sol_2 = euler_synaptic_if(tmax=0.5, dt=1e-4, pre_spike_times=[], pars
    firing_rates_500_a[k] = get_fr_ISI(sol_2['spiketimes'])
    firing_rates_500_b[k] = get_fr_num(sol_2['spiketimes'], np.max(sol_2[

    analytical_frs[k] = analytical_fr(pars)
```

```
/tmp/ipykernel_20119/1782649956.py:17: RuntimeWarning: divide by zero enco
untered in log
  fr = (tau_m * np.log( (R_m*I_e + E_m - V_reset) / (R_m*I_e + E_m - thr)
)) ** -1
/tmp/ipykernel_20119/1782649956.py:17: RuntimeWarning: invalid value encou
ntered in log
  fr = (tau_m * np.log( (R_m*I_e + E_m - V_reset) / (R_m*I_e + E_m - thr)
)) ** -1
```

In [ ]:
```
fig, (ax1, ax2) = plt.subplots(1, 2, figsize=(12, 4))

ax1.plot(input_stimuli, firing_rates_100_a, label="simtime = 100 ms")
ax1.plot(input_stimuli, firing_rates_500_a, label="simtime = 500 ms")
ax1.plot(input_stimuli, analytical_frs, linestyle=":", label="Analytical
ax1.set_title('Mean ISI')
ax1.set_ylabel('fr (Hz)')
ax1.set_xlabel('$I_{ext}$ (nA)')
ax1.legend(frameon=False)
```

```
ax2.plot(input_stimuli, firing_rates_100_b, label="simtime = 100 ms")
ax2.plot(input_stimuli, firing_rates_500_b, label="simtime = 500 ms")
ax2.plot(input_stimuli, analytical_frs, linestyle=":", label="Analytical
ax2.set_title('Spikecount / simtime')
ax2.set_xlabel('$I_{ext}$ (nA)')
ax2.legend(frameon=False)

plt.show()
```



Interpretation

Mean ISI (w/o noise):

Using the (mean) ISI yields an estimate of the firing rate that seems to align quite well with the theoretical expression, even for very short simulations with only a few spikes. Since we are not adding a stochastic term to our ODE,the ISI is indeed the inverse of the firing rate. Hence, we can easily caculate the firing rate to numeric precision as soon as we measure on ISI.

Spikecount / simtime:

This method yields an approximation of the firing rate that is highly dependent on the simulation time and gets better if we simulate longer. This is because the total number of spikes is a discrete measure where the simulation sometimes stops right before the next spike would be elicited. Hence, this approximation becomes better if we simulate longer, as the effects of this will become smaller.

Real neurons

Real neurons should have a similar onset point, i.e. a value of the input current at which it starts spiking, but effects that casue a saturation of the firing rate might be more prominent in real neurons than in our simulations.

3. Synaptically coupled IF neurons

In [ ]:
```
def euler_synaptic_coupling(tmax, dt, ics1, ics2, pars1, pars2, reset=Fal

    tau_syn1 = pars1['tau_syn']
    tau_m1   = pars1['tau_m']
    R_m1     = pars1['R_m']
    g_star1 = pars1['g_star']
    E_m1     = pars1['E_m']
    E_syn1   = pars1['E_syn']
    I_e1     = pars1['I_e']
    thr1     = pars1['thr']

    V1, x1, g1, I_syn1 = ics1

    ts = np.arange(0, tmax, dt)

    Vs1 = np.array([])
    gs1 = np.array([])
    xs1 = np.array([])
    I_syns1 = np.array([])

    tau_syn2 = pars2['tau_syn']
    tau_m2   = pars2['tau_m']
    R_m2     = pars2['R_m']
    g_star2  = pars2['g_star']
    E_m2     = pars2['E_m']
    E_syn2   = pars2['E_syn']
    I_e2     = pars2['I_e']
    thr2     = pars2['thr']

    V2, x2, g2, I_syn2 = ics2

    Vs2 = np.array([])
    gs2 = np.array([])
    xs2 = np.array([])
    I_syns2 = np.array([])

    for t in ts:

        dV1dt = ( -V1 + E_m1 - R_m1*I_syn1 + R_m1*I_e1) / tau_m1
        dx1dt = -x1 / tau_syn1
        dg1dt = (x1 - g1) / tau_syn1
        I_syn1 = g1*(V1 - E_syn1)

        V1 = V1 + dt*dV1dt
        x1 = x1 + dt*dx1dt
        g1 = g1 + dt*dg1dt

        dV2dt = ( -V2 + E_m2 - R_m2*I_syn2 + R_m2*I_e2) / tau_m2
        dx2dt = -x2 / tau_syn2
        dg2dt = (x2 - g2) / tau_syn2
        I_syn2 = g2*(V2 - E_syn2)

        V2 = V2 + dt*dV2dt
        x2 = x2 + dt*dx2dt
        g2 = g2 + dt*dg2dt

        if reset == True and V1 >= thr1:
            V1 = E_m1
            x2 += g_star2
```

```python
        if reset == True and V2 >= thr2:
            V2 = E_m2
            x1 += g_star1

        Vs1 = np.append(Vs1, V1)
        gs1 = np.append(gs1, g1)
        xs1 = np.append(xs1, x1)
        I_syns1 = np.append(I_syns1, I_syn1)

        Vs2 = np.append(Vs2, V2)
        gs2 = np.append(gs2, g2)
        xs2 = np.append(xs2, x2)
        I_syns2 = np.append(I_syns2, I_syn2)

    return {
        'ts' : ts / 10**-3,

        'V_t1' : Vs1 / 10**-3,
        'g_syn_t1' : gs1 / 10**-9,
        'x_t1' : xs1,
        'I_syn_t1' : I_syns1 / 10**-9,

        'V_t2' : Vs2 / 10**-3,
        'g_syn_t2' : gs2 / 10**-9,
        'x_t2' : xs2,
        'I_syn_t2' : I_syns2 / 10**-9,
        }
```

In [ ]:

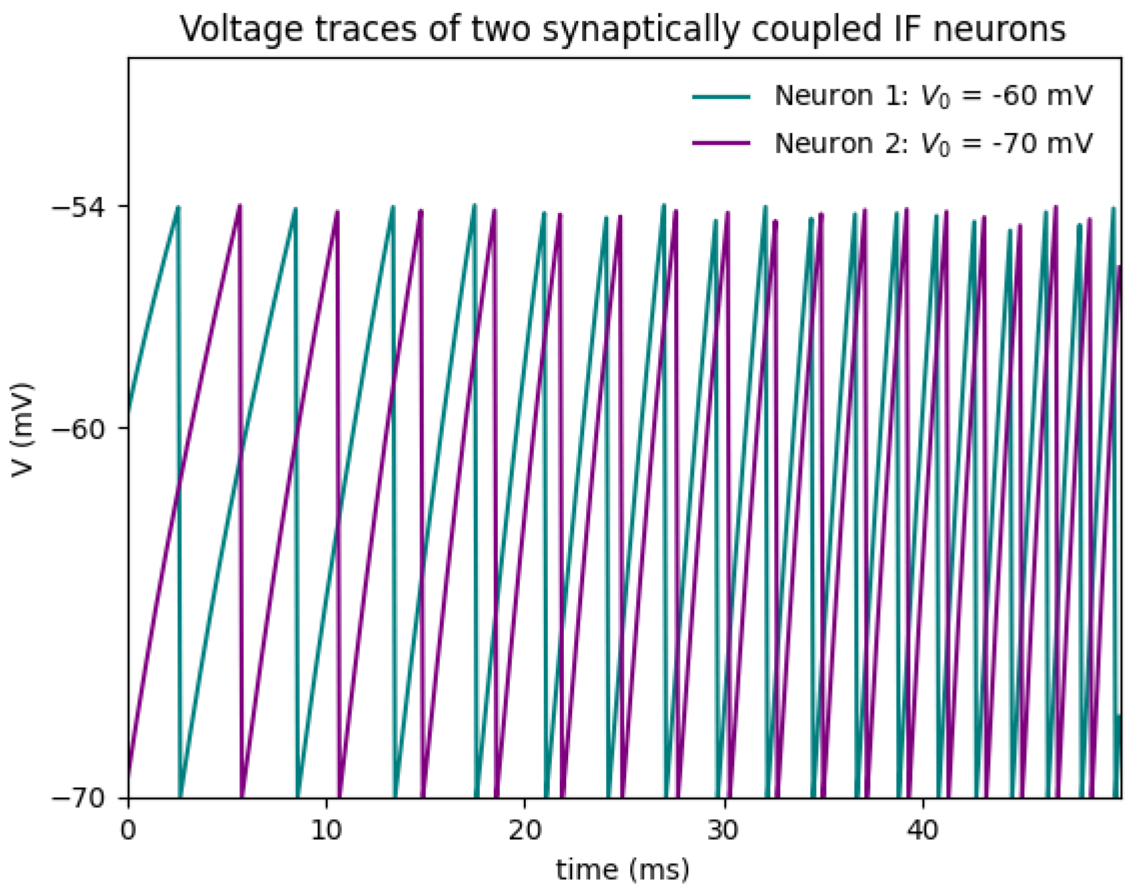
```python
pars_1 = {
    'E_m' : -70*10**-3,
    'R_m' : 1*10**7,
    'g_star' : 30*10**-9,
    'I_e' : 3.5*10**-9,
    'tau_syn' : 10*10**-3,
    'tau_m' : 10*10**-3,
    'thr' : -54*10**-3,
    'E_syn' : 0*10**-3,
}

pars_2 = pars_1.copy()

ics1 = [-60*10**-3, 0, 0, 0]
ics2 = [-70*10**-3, 0, 0, 0]
```

In [ ]:

```python
result = euler_synaptic_coupling(tmax=0.05, dt=1e-4, ics1=ics1, ics2=ics2
```

In [ ]:

```python
plt.plot(result['ts'], result['V_t1'], label="Neuron 1: $V_0$ = -60 mV")
plt.plot(result['ts'], result['V_t2'], label="Neuron 2: $V_0$ = -70 mV")
plt.legend(frameon=False)
plt.xlim(min(result['ts']), max(result['ts']))
plt.ylim([-70, -50])
plt.yticks([-70, -60, -54])
plt.ylabel('V (mV)')
plt.xlabel('time (ms)')
plt.title('Voltage traces of two synaptically coupled IF neurons')
plt.show()
```

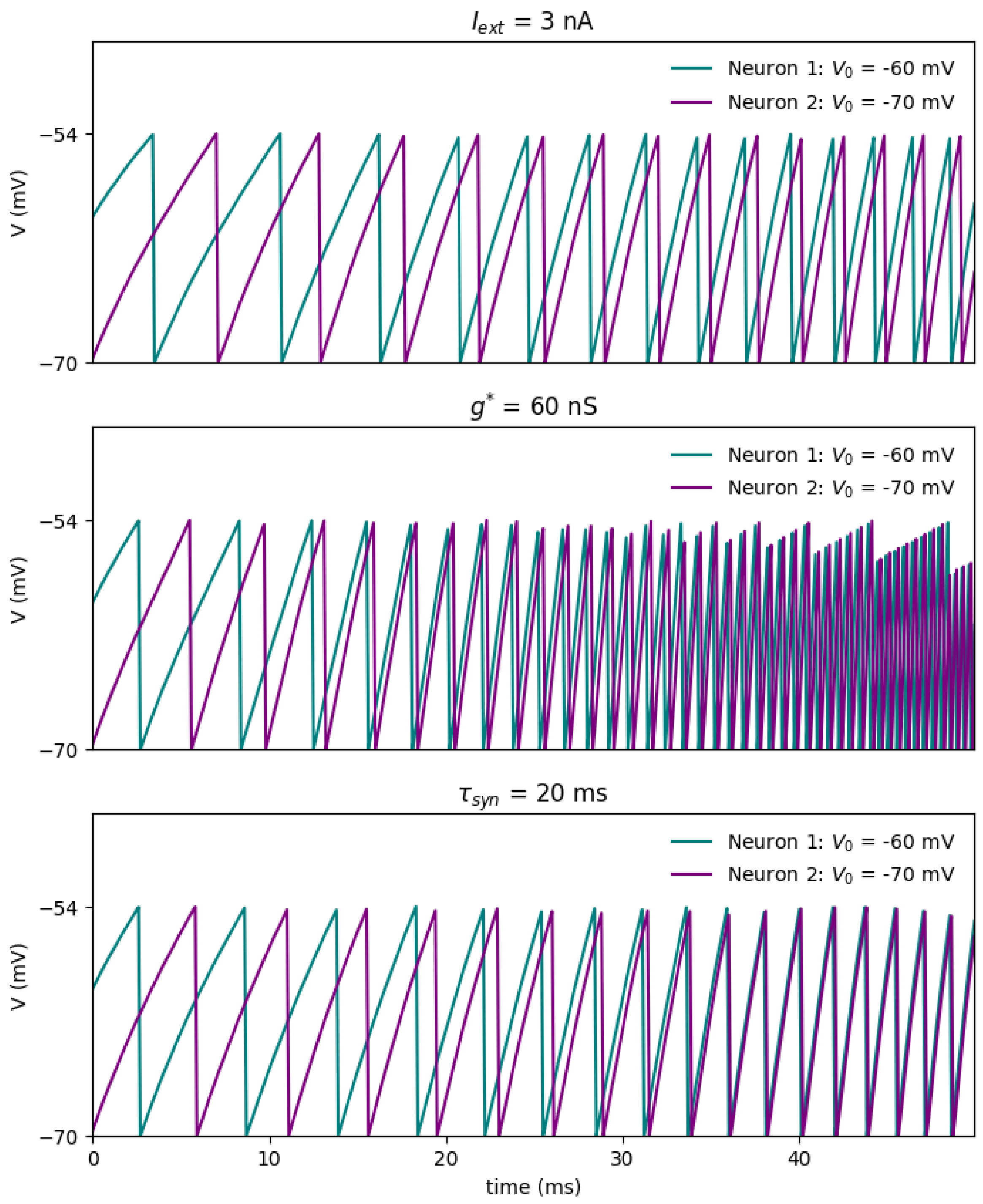


Interpretation

The firing of the two neurons seems to synchronize. This is because they are recurrently coupled which means that each spike will advance the firing of the other neuron until a steady state of synchronous firing is reached.

In [ ]:
```
pars_I = update_pars(pars_1, ['I_e'], [3*10**-9])
pars_g = update_pars(pars_1, ['g_star'], [2 * 30*10**-9])
pars_tau = update_pars(pars_1, ['tau_syn'], [2 * 10*10**-3])
```

In [ ]:
```
fig, (ax1, ax2, ax3) = plt.subplots(3, 1, figsize=(8, 10))

for (pars, title, ax) in zip([pars_I, pars_g, pars_tau], ['$I_{ext}$ = 3
    result = euler_synaptic_coupling(tmax=0.05, dt=1e-4, ics1=ics1, ics2=
    ax.plot(result['ts'], result['V_t1'], label="Neuron 1: $V_0$ = -60 mV
    ax.plot(result['ts'], result['V_t2'], label="Neuron 2: $V_0$ = -70 mV
    ax.legend(frameon=False)
    ax.set_xlim(min(result['ts']), max(result['ts']))
    ax.set_yticks([-70, -54])
    ax.set_ylim([-70, -47.5])
    ax.set_ylabel('V (mV)')
    ax.set_title(title)
    if ax != ax3:
        ax.set_xticks([])
ax3.set_xlabel('time (ms)')

plt.show()
```



Interpretation

I_{ext}

A smaller value of I_{ext} reduces the firing rate. As a result, the neurons start to synchronize much slower.

g^*

A higher value of g^* increases the EPSPS of the neurons and therefore leads to faster synchronization. During the end of the simulation, other effects of this increased synaptic coupling become apparent: The neurons seem to reset before really reaching the firing threshold. Presumably, this is due to our implementation of the reset mechanism, where the membrane voltage is reset once it surpasses the threshold value for the next simulation time step. Since both neurons are super close to the threshold at the same time and strongly coupled, this might cause an "early reset".

τ_{syn}

A bigger synaptic time constant leads to better integration of synaptic inputs and thereby promotes synchronization of the two recurrently coupled neurons.

```
In [ ]:
```