

# CAAM 415, Theoretical Neuroscience

Y. Dabaghian

October 10, 2013

## Kicking passive Neurons

### 1 Kicked neuron

Consider the equation 3.1 from Chapter 3, that describes the membrane potential of a passive isopotential neuron,

$$\frac{dv}{dt} = -\frac{1}{\tau}v + f(t). \quad (1)$$

In absence of external stimulating currents, its solution is given by

$$v(t) = v_0 e^{-\frac{t}{\tau}}, \quad (2)$$

in which  $v_0$  is the value of the potential  $v$  at the initial moment. Suppose that, at the moment of time  $t_1$ , the neuron is instantaneously perturbed by an impinging spike, which we will model as a “delta-kick,”

$$\frac{dv}{dt} = -\frac{1}{\tau}v + \eta_1 \delta(t - t_1), \quad (3)$$

where  $\delta(t)$  is Dirac’s delta function and  $\eta_1$  is the amplitude of the kick. The general properties of the delta function are discussed in many textbooks, e.g., [2, 3]. Here we will use one of its main properties, namely that the convolution of any function  $f(t)$  with the delta function centered at  $t = \zeta$  produces the value of  $f(t)$  at that point,

$$f(t) = \int_a^b f(\zeta) \delta(t - \zeta) d\zeta, \quad (4)$$

for any  $a < t$  and any  $b > t$ . By analogy with “ $x \cdot 1 = x$  for any number  $x$ ,” the delta-function may be regarded as a “functional unity” (which is, actually, more than a simple analogy, see [2, 3]).

Since the perturbation in (3) appears only at the moment  $t_1$ , it is possible to evaluate its effect on the solution by integrating the equation (3) from the moment immediately preceding the kick,  $t_1 - \varepsilon$ , to the moment immediately after it,  $t_1 + \varepsilon$ , for an infinitesimally small  $\varepsilon \rightarrow 0$ ,

$$\int_{t_1-\varepsilon}^{t_1+\varepsilon} \frac{dv}{dt} dt = -\frac{1}{\tau} \int_{t_1-\varepsilon}^{t_1+\varepsilon} v dt + \int_{t_1-\varepsilon}^{t_1+\varepsilon} \eta_1 \delta(t - t_1) dt. \quad (5)$$

Integrating the derivative in the left hand side and integrating the delta-term in the right hand side is straightforward,

$$v(t_1 + \varepsilon) - v(t_1 - \varepsilon) = -\frac{1}{\tau} \int_{t_1-\varepsilon}^{t_1+\varepsilon} v dt + \eta_1. \quad (6)$$

Assuming that  $v(t)$  is bounded,  $|v| \leq C$ , the integral in (6) can be estimated as

$$\int_{t_1-\varepsilon}^{t_1+\varepsilon} v dt \leq \lim_{\varepsilon \rightarrow 0} C 2\varepsilon. \quad (7)$$

In the limit  $\varepsilon \rightarrow 0$  this yields

$$v(t_1 + 0) = v(t_1 - 0) + \eta_1, \quad (8)$$

which simply means that, as the result of the kick, the value of the membrane potential jumps by  $\eta_1$  (this is why we refer to  $\eta_1$  as to the “amplitude” of the kick, even though the amplitude of  $\eta_1 \delta(x)$  is infinite). Here and below we use the notation

$$\begin{aligned} f(x \pm 0) &= \lim_{\varepsilon \rightarrow 0} f(x \pm \varepsilon), \\ \int_{a \pm 0}^{b \pm 0} f(x) dx &= \lim_{\varepsilon_1, \varepsilon_2 \rightarrow 0} \int_{a \pm \varepsilon_1}^{b \pm \varepsilon_2} f(x) dx. \end{aligned}$$

The value  $v(t_1 - 0)$  before the kick can be found directly from (2),  $v(t_1 - 0) = v_0 e^{-\frac{1}{\tau} t_1}$ .

Since the speed decays exponentially both before and after the kick, the solution after  $t_1$  has the same “decaying exponential” form as (2),

$$v(t \geq t_1) = v_0' e^{-\frac{t}{\tau}}, \quad (9)$$

for some amplitude  $v'_0$ , so the “boundary condition” (8) yields,

$$v'_0 e^{-\frac{1}{\tau} t_1} = v_0 e^{-\frac{1}{\tau} t_1} + \eta_1, \quad (10)$$

from where

$$v'_0 = v_0 + \eta_1 e^{\frac{1}{\tau} t_1}, \quad (11)$$

and hence

$$v(t > t_1) = v_0 e^{-\frac{1}{\tau} t} + \eta_1 e^{-\frac{1}{\tau}(t-t_1)}. \quad (12)$$

Notice, that the potential  $v(t)$  is indeed bounded, so the estimate (7) is justified. Overall, the total solution in this case is

$$v(t) = \begin{cases} v_0 e^{-\frac{1}{\tau} t} & \text{for } t < t_1 \\ v_0 e^{-\frac{1}{\tau} t} + \eta_1 e^{-\frac{1}{\tau}(t-t_1)} & \text{for } t > t_1 \end{cases} \quad (13)$$

If the neuron is perturbed by another kick at the moment  $t_2$ ,

$$\frac{dv}{dt} = -\frac{1}{\tau} v + \eta_1 \delta(t - t_1) + \eta_2 \delta(t - t_2), \quad (14)$$

then the solution up to the moment  $t_2$  is described by (8), and at  $t_2$  the speed changes according to

$$v(t_2 + 0) - v(t_2 - 0) = \eta_2. \quad (15)$$

After  $t_2$ , the solution will again decay exponentially,  $v' = v''_0 e^{-\frac{1}{\tau} t}$ , and the boundary condition at  $t_2$  yields

$$v''_0 e^{-\frac{1}{\tau} t_2} = v_0 e^{-\frac{1}{\tau} t_2} + \eta_1 e^{-\frac{1}{\tau}(t_2-t_1)} + \eta_2, \quad (16)$$

from where

$$v''_0 = v_0 + \eta_1 e^{\frac{t_1}{\tau}} + \eta_2 e^{\frac{t_2}{\tau}}, \quad (17)$$

and hence

$$v(t > t_2) = v_0 e^{-\frac{1}{\tau} t} + \eta_1 e^{-\frac{1}{\tau}(t-t_1)} + \eta_2 e^{-\frac{1}{\tau}(t-t_2)}. \quad (18)$$

This, the total solution for two kicks is

$$v(t) = \begin{cases} v_0 e^{-\frac{1}{\tau} t} & \text{for } t < t_1 \\ v_0 e^{-\frac{1}{\tau} t} + \eta_1 e^{-\frac{1}{\tau}(t-t_1)} & \text{for } t_1 \leq t < t_2 \\ v_0 e^{-\frac{1}{\tau} t} + \eta_1 e^{-\frac{1}{\tau}(t-t_1)} + \eta_2 e^{-\frac{1}{\tau}(t-t_2)} & \text{for } t > t_2 \end{cases} \quad (19)$$

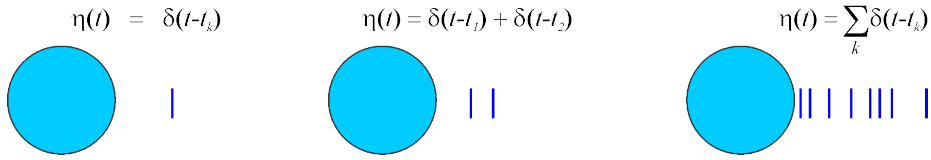


Figure 1: A schematic representation of a neuron and an incoming spike train, Eqs. 3, 14 and 20.

The generalization to many-kick ( $K$  kicks) case,

$$\frac{dv}{dt} = -\frac{1}{\tau}v + \sum_{k=1}^K \eta_k \delta(t - t_k), \quad (20)$$

should now be obvious.

For a mechanical analogy of the passive isopotential neuron discussion see [1].

## 2 Green's function

Let us introduce the function

$$G(t, \zeta) = \begin{cases} 0 & \text{for } t < \zeta \\ e^{-(t-\zeta)} & \text{for } t \geq \zeta \end{cases}, \quad (21)$$

known as the Green's function of the equation (1). It is more convenient to write (21) as

$$G(t, \zeta) = \Theta(t - \zeta) e^{-(t-\zeta)}, \quad (22)$$

where  $\Theta(t - \zeta)$  is the Heaviside theta function:

$$\Theta(x - x_0) = \begin{cases} 0 & \text{for } x < x_0 \\ 1 & \text{for } x \geq x_0. \end{cases} \quad (23)$$

The theta function is related to the delta function via

$$\Theta'(x) = \delta(x), \quad (24)$$

which has a great practical value.

**Comment** Any idea how to prove (24)?

• **Problem** Using (23), rewrite the one-kick and two kick solutions in terms of the theta function.

• **Problem** Using (24), show that

$$v(t) = v_0 e^{-\frac{1}{\tau}t} + \Theta(t - t_1) \eta_1 e^{-\frac{1}{\tau}(t-t_1)} \quad (25)$$

is the solution of (3).

• **Problem** Using (24), show that (22) is the solution of the equation (3) with  $v_0 = 0$  and  $\eta_1 = 1$ ,

$$\frac{dG}{dt} = -\frac{1}{\tau}G + \delta(t - \zeta). \quad (26)$$

Thus, the Green's function describes the response of an unsuspecting neuron ( $v_0 = 0$ ) to a sudden, ideally sharp kick with unit amplitude ( $\eta_1 = 1$ ) and hence serves as a convenient building block for constructing more complex solutions of perturbed equation (1). For example, in terms of  $G(t, \zeta)$ , the solution to the equation (1) with two kicks looks like

$$v(t) = v_0 e^{-\frac{1}{\tau}t} + \eta_1 G(t, t_1) + \eta_2 G(t, t_2). \quad (27)$$

For  $K$  kicks, the solution will then be

$$v(t) = v_0 e^{-\frac{1}{\tau}t} + \sum_{k=1}^K \eta_k G(t, t_k). \quad (28)$$

Thus far, the change from (13) and (19) to (25) and (27) may look just as a formal change of notations. However, the solution of *any* linear differential equation perturbed by delta-kicks, in terms of the corresponding Green's function, looks exactly as (28). In other words, the equation (28) captures the general structure of the “kicked” solutions of linear differential equations.

• **Problem** Consider the cable equation ([4], Chapter 6) with no driving force,

$$\tau \frac{\partial v}{\partial t} + v - \lambda^2 \frac{\partial^2 v}{\partial x^2} = 0 \quad (29)$$

Show by direct substitution that the functions

$$\phi_n(x, t) = Ce^{-(\lambda^2 \vartheta_n^2 + 1) \frac{t}{\tau}} \cos(\vartheta_n x), \quad (30)$$

where  $n$  is any integer,  $C$  is a constant and

$$\vartheta_n = \frac{\pi n}{l}, \quad (31)$$

are the solutions of the equation (29) with the boundary conditions

$$v'(0) = v'(l) = 0. \quad (32)$$

• **Problem** Using the fact that the set  $q_n(x) = \sqrt{\frac{2}{l}} \cos(\vartheta_n x)$  forms a complete orthonormal basis of functions satisfying (32) (see Chapter 6 of [4]), show that the sum

$$\Delta_c(x, x_0) \equiv \sum_n q_n(x) q_n(x_0) = \delta(x - x_0) \quad (33)$$

works as delta function for functions of  $x$ , i.e.,

$$\int_0^l \Delta_c(x, x_0) f(x) dx = f(x_0). \quad (34)$$

• **Problem** Show by direct substitution that the functions

$$\varphi_n(x, t) = Ce^{-(\lambda^2 \vartheta_n^2 - 1) \frac{t}{\tau}} \cos(\vartheta_n x), \quad (35)$$

satisfy the equation

$$\tau \frac{\partial \varphi_n}{\partial t} + \varphi_n - \lambda^2 \frac{\partial^2 \varphi_n}{\partial x^2} = 2\varphi_n. \quad (36)$$

### 3 Rate model

The solution (28) gives the exact description of our test neuron's membrane potential as a function of the incoming spike times. However, for many practical purposes, this information may be too detailed. Rather than describing

our neuron’s response to every individual kick, it would be more useful for a better *qualitative* understanding of the entire system, to describe the *average* dynamics. One way to do this is to look at the mere *frequency* of spikes’ arrivals instead of the exact times,  $t_k$ , i.e., at the *instantaneous spiking rates*. Given a spike train

$$\eta(t) = \sum_{k=1}^K \eta_k \delta(t - t_k), \quad (37)$$

it is sometimes possible to average over the  $t_k$ ’s and to obtain the firing rate – a “bird’s eye view” characteristics of its activity,

$$\bar{\eta}(t) = \left\langle \sum_k \eta_k \delta(t - t_k) \right\rangle \equiv r(t), \quad (38)$$

where the bar over  $\eta$  and the brackets  $\langle *, * \rangle$  mean “average”.

The precise meaning of the averaging operation is subtle in most cases, but we do not need to go deeply into this problem. Just think of the brackets (38) as of a black box that takes a spike train at the input and produces the instantaneous spiking rate at the output. Notice that the rate  $r(t)$  is time dependent: at different periods of time, the spikes may arrive more or less frequently.

We now need to solve a pretty interesting task: how to average the solution (28) so that it describes the instantaneous spiking rate of our test neuron? First, let us rewrite the formula (28) in the integral form,

$$v(t) = v_0 e^{-\frac{t}{\tau}} + \int_{t_0}^t G(t, \zeta) \eta(\zeta) d\zeta. \quad (39)$$

We would immediately get the (28) back, if we would substitute the delta-train (37) into (39), but this is not our goal. The point is that using (39), we can make a qualitative generalization of (28). In fact, we already made it, since the function  $\eta(t)$  in (39) does not have to be a sequence of delta peaks. The formula (39) will actually work for *any* reasonable function, e.g., for smooth functions of  $t$ , or combinations of smooth functions and delta peaks.

**Comment:** In the continuous case, we basically regard  $\eta(t)$  as a superposition of a continuum amount of delta kicks (remember (4)? just a

generalization of (37)!). Due to the “ $d\zeta$ ” factor, the amplitudes  $\eta_\zeta = \eta(\zeta)d\zeta$  of the kicks are infinitesimally small – if the kicks would not be infinitesimal in the continuous case, the function  $v(t)$  would be immediately kicked to infinity. Thus, using the Green’s function corresponds to a rather curious way of interpreting inhomogeneous linear differential equations: the “inhomogeneous term,”  $\eta(t)$ , is decomposed into a continuous amount of infinitesimal delta-peaks, continuously arranged on the time axis. The Green’s function then incorporates these kicks into the solution, point by point.

• **Problem** Using (36) and (33), show that the function

$$G_c(x, x_0|t, s) = \frac{1}{2} \sum_n \varphi_n(x, -t) \varphi_n(x_0, s) \quad (40)$$

is the Green’s function of the cable equation (29), i.e., that

$$\tau \frac{\partial G_c}{\partial t} + G_c - \lambda^2 \frac{\partial^2 G_c}{\partial x^2} = \delta(x - x_0). \quad (41)$$

The solution of the cable equation with stimulating current,

$$\tau \frac{\partial v}{\partial t} + v - \lambda^2 \frac{\partial^2 v}{\partial x^2} = I_{stim}(x, t), \quad (42)$$

will then be given by (39), with the Green’s function give by (40). Use (40) to write out the solution to (42) and compare the result to the equation (6.45) in Chapter 6 of [4].

Back to our goal of transitioning from the spike times to spiking rates. We will do this in a few steps.

1. Since the rate,  $r(t)$ , is obtained by averaging of  $\eta(t)$  (think of (38)), we can formally average both sides of the equation (39),

$$\langle v(t) \rangle = \left\langle v_0 e^{-\frac{t}{\tau}} \right\rangle + \left\langle \int G(t, \zeta) \eta(\zeta) d\zeta \right\rangle. \quad (43)$$

Since the homogeneous term and the Green’s function do not depend on spikes, we have

$$\langle v(t) \rangle = v_0 e^{-\frac{t}{\tau}} + \int G(t, \zeta) \langle \eta(\zeta) \rangle d\zeta, \quad (44)$$



or, in simpler “bar” notations

$$\bar{v}(t) = v_0 e^{-\frac{t}{\tau}} + \int G(t, \zeta) \bar{\eta}(\zeta) d\zeta. \quad (45)$$

2. Since averaging’ implies describing the system over large time scales, we will integrate in (45) over the entire time axis and assume that the potential was zero at the beginning of times,  $v|_{t=-\infty} = 0$ , which gives

$$\bar{v}(t) = \int_{-\infty}^{\infty} G(t, \zeta) \bar{\eta}(\zeta) d\zeta. \quad (46)$$

3. Since the Green’s function  $G(t, \zeta)$  contains the  $\Theta(t - \zeta)$  factor,  $\zeta$ ’s higher than  $t$  do not contribute to (46). As a result, the integral (46) reduces to

$$\bar{v}(t) = \int_{-\infty}^t K(t, \zeta) \bar{\eta}(\zeta) d\zeta, \quad (47)$$

where the kernel

$$K(t, \zeta) = e^{-\frac{1}{\tau}(t-\zeta)} \quad (48)$$

is commonly used in neuroscience literature (typically without a derivation, and now you know where it comes from!).

4. To make the “spiking rate” language self-contained, notice that the mean membrane potential,  $\bar{v}$ , of our test neuron must be proportional to its own mean firing rate,  $r_{test}$ . The higher, on average, is  $\bar{v}$ , the more frequently it fires. Therefore, we may write

$$r_{test} \approx \rho + w \bar{v}, \quad (49)$$

where  $w$  is a proportionality coefficient and  $\rho$  is a constant.

**Comment** A connection with a Taylor expansion, perhaps?

5. Using (49), the expression (46) can be written as relationship between the incoming rate,  $r(t)$ , and the outcome rate of our test neuron,  $r_{test}(t)$ :

$$r_{test}(t) = \rho + w \int_{-\infty}^t K(t, \zeta) r(\zeta) d\zeta. \quad (50)$$

6. To complete the logical loop, notice that, after averaging, the rate function,  $r_{test}(t)$ , is not the solution to (20) anymore, because the right hand side of (20) has changed from a sum of deltas to a continuous function. In other words, in the process of averaging, we lost our dynamical equation, which is a pretty serious loss. So let us now ask the reverse question: which differential equation does the function  $r_{test}(t)$  satisfy?

• **Problem** Using the explicit form of the kernel  $K(t, \zeta)$ , verify that  $\bar{v}$  defined by (47) satisfies the equation

$$\frac{d\bar{v}}{dt} = -\frac{1}{\tau}\bar{v} + \eta(t), \quad (51)$$

the equation 3.1 of [4].

• **Problem** To derive the equation for  $r_{test}(t)$ , write (50) as

$$r_{test}(t) = \rho + w e^{-\frac{t}{\tau}} \int_{-\infty}^t e^{\frac{1}{\tau}\zeta} r(\zeta) d\zeta, \quad (52)$$

and show that the function (52) satisfies the differential equation

$$\tau \frac{d}{dt} r_{test} = -r_{test} + \rho + w r(t). \quad (53)$$

• **Problem** Find the solution to (51) using your favorite standard ODE solving method (e.g., the method of variation of constants) and compare the result to the solution obtained via Green's function approach.

## 4 Many spike trains

**Feedforward network case.** A given neuron can receive not just one, but several spike trains, coming from different neurons (Fig. ??). If each presynaptic neuron will spike at a rate  $r_i$  and all these  $r_i$ 's will independently drive our test neuron, then the equation (46) would generalize to

$$r_{test}(t) = \rho + \sum_i w_i \int_{-\infty}^t K(t, \zeta) r_i(\zeta) d\zeta, \quad (54)$$

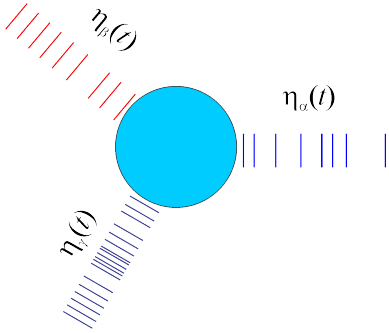


Figure 2: Several spike trains falling onto the same neuron, leading to the equation (54).

in which  $w_i$  describes the connection strength between  $i$ th presynaptic neuron and the test neuron, and  $\rho$  is the net background input,

$$\rho = \sum_i \rho_i, \quad (55)$$

coming from all the presynaptic cells.

• **Problem** Using the explicit form of  $K(t, \zeta)$ , derive the analogue of (52) for this case. By differentiating (54), show that the differential equation for  $r_{test}$  in this case is

$$\tau \frac{d}{dt} r_{test} = -r_{test} + \rho + \sum_i w_i r_i(t), \quad (56)$$

The equation (56) is still of the same type as (51) – although the physical (or the physiological) interpretation of the right hand has changed, the overall mathematical form of (56) remained the same. If, e.g., we introduce a notation

$$\eta(t) = \rho + \sum_i w_i r_i(t), \quad (57)$$

then we get the equation (51) back.

**Recurrent network case.** A fundamental change occurs if we assume that our test neuron does not only receive the spike trains, but also sends its own spikes to other neurons in the network. In other words, suppose that our

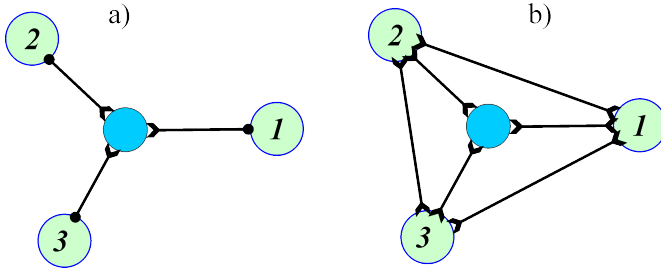


Figure 3: A schematic representation of a feedforward (a) and a recurrent (b) network connectivity. Notice that the connections on a) go from the presynaptic cells 1, 2 and 3 to our test neuron, and on b) all neurons are interconnected.

“test neuron” is not a special “ $r_{test}$ ” anymore, but just another “ $r_i$ ,” where index  $i$  runs over *all* neurons in the ensemble of  $N$  neurons. Each neuron can now connect to an arbitrary set of other neurons, so that the rate equation is now

$$\tau \frac{dr_i}{dt} = -r_i + \rho_i + \sum_j w_{ij} r_j, \quad (58)$$

where  $w_{ij}$  describes the connection strength from a presynaptic neuron  $n_j$  to a postsynaptic neuron  $n_i$ ,  $i, j = 1, \dots, N$ , and  $\rho_i$  is the net background input into the neuron  $n_i$ .

The equation (58) is fundamentally different from (56) because it can produce more types of dynamical behavior. However, it is still just a linear system of ODEs which we should be able to solve. In matrix notations, the equation (58) can be written as

$$\tau \frac{d\vec{r}}{dt} = -\vec{r} + \vec{\rho} + \mathbf{W}\vec{r}, \quad (59)$$

where  $\vec{r}$  is the activity vector with the components  $r_i$ ,  $\mathbf{W} = \|w_{ij}\|$  is the connectivity matrix,  $\vec{\rho}$  is a constant background input vector.

The behavior of the system (59) depends primarily on the structure of the matrix  $\mathbf{W}$ . Let us consider the symmetric case,

$$w_{ij} = w_{ji}. \quad (60)$$

In this case, as you have seen in the Exercises 2-6 from Chapter 6 of [4], the eigenvectors of the matrix  $W$  are orthogonal to one another. In other words,

if  $\vec{e}_k$  is an eigenvector,

$$\mathbf{W} \vec{e}_k = \lambda_k \vec{e}_k, \quad (61)$$

then

$$\vec{e}_k \cdot \vec{e}_l = \delta_{kl} \equiv \begin{cases} 0 & \text{for } k \neq l \\ 1 & \text{for } k = l \end{cases}, \quad (62)$$

(we assume that  $\vec{e}_k$ 's are already normalized).

**Comment** Is  $\delta_{kl}$  a discrete analogue of the  $\Theta(x)$  or of the  $\delta(x)$ ?

Now we can handle the equation (58) just as we handled the equation (6.7) from Chapter 6 of [4]. Let us expand the activity vector  $\vec{r}$  from (58) using the basis vectors  $e_k$ ,

$$\vec{r} = \sum_k c_k(t) \vec{e}_k. \quad (63)$$

Since  $\mathbf{W}$  is a constant matrix ( $w_{ij}$ 's do not depend on time), its eigenvectors and eigenvalues are also time independent. Therefore, all the time dependence of  $\vec{r}(t)$  now hides in the  $c_k(t)$ 's. Let us now substitute (63) in (59):

$$\tau \frac{d}{dt} \left( \sum_k c_k(t) \vec{e}_k \right) = - \sum_k c_k(t) \vec{e}_k + \vec{\rho} + \mathbf{W} \sum_k c_k(t) \vec{e}_k. \quad (64)$$

Due to (61), the last term in (64) gives

$$\tau \frac{d}{dt} \left( \sum_k c_k(t) \vec{e}_k \right) = - \sum_k c_k(t) \vec{e}_k + \vec{\rho} + \sum_k c_k(t) \lambda_k \vec{e}_k. \quad (65)$$

Now we can use the orthogonality condition (62) and multiply both sides of the equation (65) by an eigenvector  $\vec{e}_l$ .

• **Problem** In the case when  $\vec{\rho} = 0$ , perform the multiplication of (65) by  $\vec{e}_l$  and obtain

$$\tau \frac{d}{dt} c_k(t) = (\lambda_k - 1) c_k(t). \quad (66)$$

• **Problem** The solution to (66) is obviously

$$c_k(t) = c_k(0) e^{\frac{\lambda_k - 1}{\tau} t}. \quad (67)$$

What does this solution tell us about what the eigenvalues of  $\mathbf{W}$  can do to our system?

- **Problem** Consider the full equation

$$\tau \frac{d\vec{r}}{dt} = -\vec{r} + \vec{\rho} + \mathbf{W}\vec{r}, \quad (68)$$

with  $\vec{\rho} \neq 0$ . Follow the previous steps to derive the equation for the individual  $c_k(t)$ 's and show that the solution in this case is

$$c_k(t) = \frac{h_k}{1 - \lambda_k} + \left( c_k(0) - \frac{h_k}{1 - \lambda_k} \right) e^{\frac{\lambda_k - 1}{\tau} t}, \quad (69)$$

where  $h_k = \vec{\rho} \cdot \vec{e}_k$ .

- **Problem** What happens to the solution (69) if  $\lambda_k < 1$  ? if  $\lambda_k = 0$ ? if  $\lambda_k > 1$ ?

- **Problem** Think of a conceptual question that involves spiking networks or rate networks that is not covered by this discussion.

## 5 References

### References

- [1] H. Haken, *Brain Dynamics: An Introduction to Models and Simulations*, Springer (2008).
- [2] D. Duff, *Green's Functions with Applications*, Chapman and Hall, (2001).
- [3] I. Gel'fand and G. Shilov, *Generalized functions, Vol. I: Properties and operations*, Academic Press (1964).
- [4] F. Gabbiani and S. Cox, *Mathematics for Neuroscientists*, Academic Press (2010).