

Final Exam of Computational Neuroscience

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Poisson Spike-Train Statistics

1.

$$\begin{aligned}\langle n \rangle &= \sum_{n=0}^{\infty} np(n) = \sum_{n=1}^{\infty} \frac{(rT)^n}{(n-1)!} \exp(-rT) \\ &= \exp(-rT) rT \sum_{n=0}^{\infty} \frac{(rT)^n}{n!} \\ &= \exp(-rT) rT \exp(rT) \\ &= rT\end{aligned}\tag{1}$$

$$\begin{aligned}\langle n^2 \rangle &= \sum_{n=0}^{\infty} n^2 p(n) = rT \exp(-rT) \sum_{n=0}^{\infty} \frac{(rT)^n}{n!} (n+1) \\ &= rT \exp(-rT) \left[\sum_{n=0}^{\infty} n \frac{(rT)^n}{n!} + \sum_{n=0}^{\infty} \frac{(rT)^n}{n!} \right] \\ &= rT \exp(-rT) [rT \exp(rT) + \exp(rT)] \\ &= (rT)^2 + rT\end{aligned}\tag{2}$$

$$Var(n) = \langle n^2 \rangle - \langle n \rangle^2 = rT\tag{3}$$

$$Fano\ factor : \frac{Var(n)}{\langle n \rangle} = 1\tag{4}$$

$$\langle n^4 \rangle = (rT)^4 + 6(rT)^3 + 7(rT)^2 + rT\tag{5}$$

$$k = \langle n^4 \rangle - 3\langle n^2 \rangle^2 = -2(rT)^4 + (rT)^2 + rT\tag{6}$$

if we replace $\langle n^4 \rangle$ with central moments, the result may look more beautiful:

$$\mu_4 = \langle (n - tT)^4 \rangle = 3(rT)^2 + rT\tag{7}$$

$$k = \mu_4 - 3(rT)^2 = rT\tag{8}$$

2. when it comes to inhomogeneous Poisson process:
 we divide time interval $[t_i, t_{i+1}]$ into M time bins of size Δt and setting $M\Delta t = t_{i+1} - t_i$. we will ultimately take limit $\Delta t \rightarrow 0$. The firing rate during bin m within this interval is $r(t_i + m\Delta t)$, the firing probability of firing a spike in this bin is $r(t_i + m\Delta t)\Delta t$, the probability of not firing a spike is $1 - r(t_i + m\Delta t)\Delta t$. So, to have no spike during the entire interval, we need string together the whole M bins, because the probability in each bin is independent, we just need to product them together. Denote entire spike numbers between initial time and time t $N(t)$

$$P[N(t_{i+1}) - N(t_i) = 0] = \prod_{m=1}^M (1 - r(t_i + m\Delta t)\Delta t) \quad (9)$$

$$\begin{aligned} \ln P[N(t_{i+1}) - N(t_i) = 0] &= \sum_{m=1}^M \ln(1 - r(t_i + m\Delta t)\Delta t) \\ &\xrightarrow{t \rightarrow 0} - \sum_{m=1}^M r(t_i + m\Delta t)\Delta t \\ &= - \int_{t_i}^{t_{i+1}} r(t)dt \end{aligned} \quad (10)$$

the probability density $p(t_1, t_2, \dots, t_n)$ is the product of the densities for the individual spikes and the probabilities of not generating spikes during the interspike intervals, between time 0 and the first spike, and between the time of the last spike and the end of the trial period:

$$\begin{aligned} &p(t_1, t_2, \dots, t_n) \\ &= P[N(t_1) - N(0) = 0] \cdot P[N(T) - N(t_n) = 0] \cdot \\ &\quad \prod_{i=1}^{n-1} P[N(t_{i+1}) - N(t_i) = 0] \cdot \prod_{i=1}^n r(t_i) \\ &= \exp\left(-\int_0^T r(t)dt\right) \prod_{i=1}^n r(t_i) \end{aligned} \quad (11)$$

$$\begin{aligned} &p[N(T) - N(0) = n] \\ &= \int_0^T dt_1 \cdots \int_0^T dt_n p(t_1, t_2, \dots, t_n) / n! \\ &= \exp\left(-\int_0^T r(t)dt\right) \int_0^T r(t_1)dt_1 \cdots \int_0^T r(t_n)dt_n / n! \\ &= \left(\int_0^T r(t)dt\right)^n \exp\left(-\int_0^T r(t)dt\right) / n! \\ &n = 0, 1, 2, \dots \end{aligned} \quad (12)$$

it is very similar to homogeneous situation, when $r(t) = r(\text{const})$, this expression returns to homogeneous result

$$\langle n \rangle = \int_0^T r(t) dt \quad (13)$$

$$\text{Var}(n) = \int_0^T r(t) dt \quad (14)$$

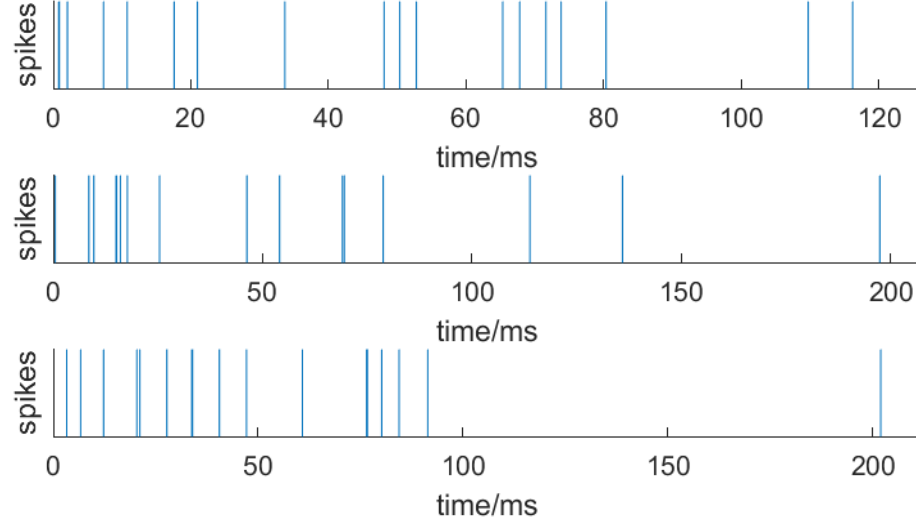
$$\text{Fano factor} : \frac{\text{Var}(n)}{\langle n \rangle} = 1 \quad (15)$$

the result is the same as homogeneous's

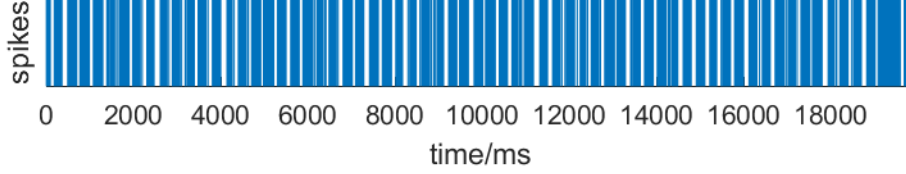
3. Reference the **poisson spike generator** on page 30 of the theoretical Neuroscience book. First, generate the interspike intervals from an exponential probability density. Then extend it to time-dependent rates by using rejection sampling. Rejection sampling requires a bound r_{max} on the estimated firing rate such that $r_{est}(t) \leq r_{max}$ at all times. We first generate a spike sequence corresponding to the constant rate r_{max} by iterating the rule $t_{i+1} = t_i - \ln(x_{rand})/r_{max}$. The spikes are then thinned by generating another x_{rand} for each i and removing the spike at time t_i from the train if $r_{est}(t_i)/r_{max} < x_{rand}$. If $r_{est}(t_i)/r_{max} \geq x_{rand}$, spike i is retained. Thinning corrects for the difference between the estimated time-dependent rate and the maximum rate.

main code is in `poisson_spike_generator.m`.

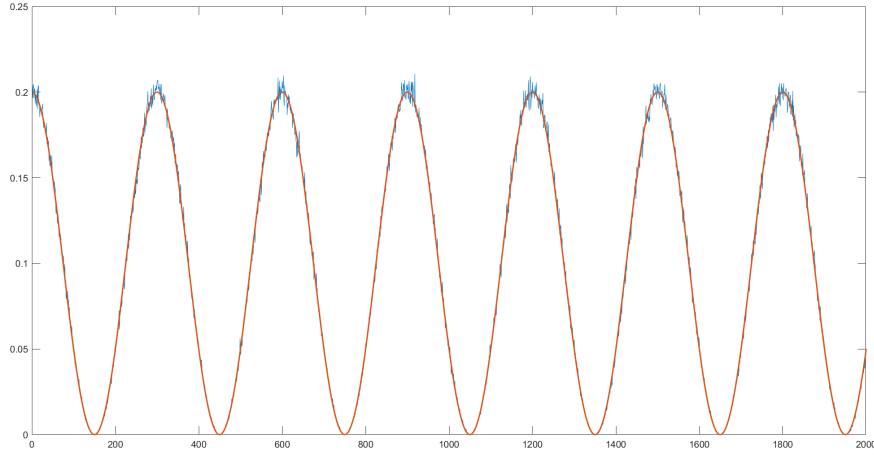
The following is 3 spike examples generated in 200 ms.



Next is a spike train in 20s:



Then, I did a mento carlo silmulation to test whether the sampling is right. Rerun the code I have used above s times, s is a large number, each s represents a trial. I roughly calculate $r(t)$ using sampling result in a discrete way. $r(\text{ith time-bin}) \approx \langle n \rangle$, $\langle \rangle$ is mean from different trial, n is spike numbers in ith time-bin. $i = 1, 2, 3 \dots$ we could see from the following pic, the result is satisfactory, blue line is sample result, red line is real $r(t)$, code is in `sample_test.m`



4. In this problem, we need to use conditional expectation, use formula of total expectation twice

$$\begin{aligned}
 \langle n \rangle &= E[E(n|\theta)] = E \left[\int_0^T (r_0 + r_1 \sin(\omega t + \theta)) dt \right] \\
 &= \frac{1}{2\pi} \int_0^{2\pi} d\theta \int_0^T dt (r_0 + r_1 \sin(\omega t + \theta)) \\
 &= r_0 T
 \end{aligned} \tag{16}$$

$$\begin{aligned}
 \langle n^2 \rangle &= E[E(n^2|\theta)] \\
 &= \frac{1}{2\pi} \int_0^{2\pi} d\theta \left[\left(\int_0^T (r_0 + r_1 \sin(\omega t + \theta)) dt \right)^2 + \int_0^T (r_0 + r_1 \sin(\omega t + \theta))^2 dt \right] \\
 &= (r_0 T)^2 + \left(\frac{r_1}{\omega} \right)^2 - \left(\frac{r_1}{\omega} \right)^2 \cos \omega T + r_0 T
 \end{aligned} \tag{17}$$

$$Var(n) = \langle n^2 \rangle - \langle n \rangle^2 = r_0 T + 2 \left(\frac{r_1}{w} \sin \frac{\omega T}{2} \right)^2 \quad (18)$$

$$Fano \ factor : \frac{Var(n)}{\langle n \rangle} = 1 + \frac{2 \left(\frac{r_1}{w} \sin \frac{\omega T}{2} \right)^2}{r_0 T} \quad (19)$$

Sensory Neuron from an Electric Fish

We consider times that are interger multiples of a basic unit of duration Δt , that is times $t = m\Delta t$ for $m = 1, 2, \dots, M$ where $M\Delta t = T$. The function $s(t)$ is then constructed as a discrete sequence of stimulus values. This produce a steplike stimulus waveform, with a constant stimulus value s_m presented during time bin m . In terms of white-noise stimuli definition, each s_m is uncorrelated means

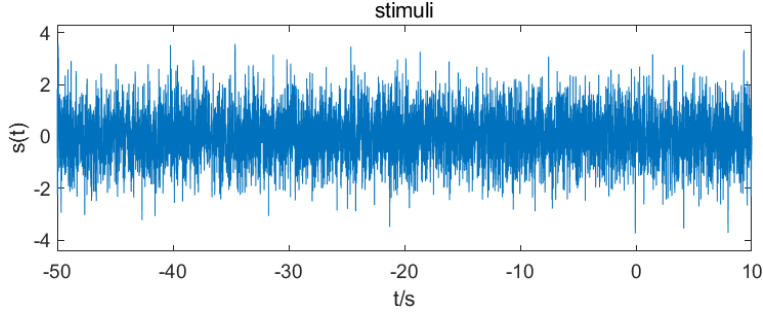
$$\frac{1}{M} \sum_m^M \sum_n^M s_m s_n = \frac{\sigma_s^2}{\Delta t} \delta_{mn} \quad (20)$$

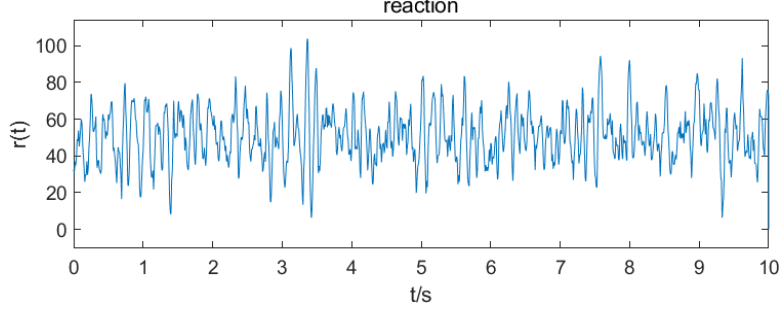
where $\delta_{mn} = 0$, only if $m = n$

1. When $t \in [(n-1)\Delta t, n\Delta t]$, $s = s_n$, during each bin, the value of D could be seen as a constant, for example, when $t - \tau \in [(n-1)\Delta t, n\Delta t]$, $D(\tau) \approx D(t - n\Delta t)$. Then, we can replace integral with limited sum, the following equation could be obtained easily

$$\begin{aligned} r(t) &= R_0 + \int_0^\infty D(\tau) s(t - \tau) d\tau \\ &= R_0 + \sum_{n=-\infty}^{[t/\Delta t]} s_n D(t - n\Delta t) \Delta t \end{aligned} \quad (21)$$

with the equation we have aquired above, we realize it in code `fish.m`. The stimulus and reaction is plotted in the following pictures





2. Same as the previous question, replace the integral with limited sum, when $t + \tau \in [(m-1)\Delta t, m\Delta t]$, $D(t - n\Delta t) \approx D(m\Delta t - \tau - n\Delta t)$

$$\begin{aligned}
Q_{rs}(\tau) &= \frac{1}{T} \int_0^T r(t)s(t+\tau)dt \\
&= \frac{1}{T} \int_0^T (R_0 + \sum_n s_n D(t - n\Delta t)\Delta t)s(t+\tau)dt \\
&= \frac{1}{T} \sum_m (R_0 + \sum_n s_n D(m\Delta t - \tau - n\Delta t)\Delta t)s_m\Delta t \\
&= \frac{1}{T} \sum_m R_0 s_m(\Delta t)^2 + \frac{\Delta t}{T} \sum_m \sum_n s_m s_n D[(m-n)\Delta t - \tau] \\
&= \frac{1}{M} \sum_m \sum_n s_m s_n D[(m-n)\Delta t - \tau]
\end{aligned} \tag{22}$$

omit $\frac{1}{T} \sum_m R_0 s_m(\Delta t)^2$ because it is higher order infinitesimal. Then, with the definition of white noise stimuli (20)

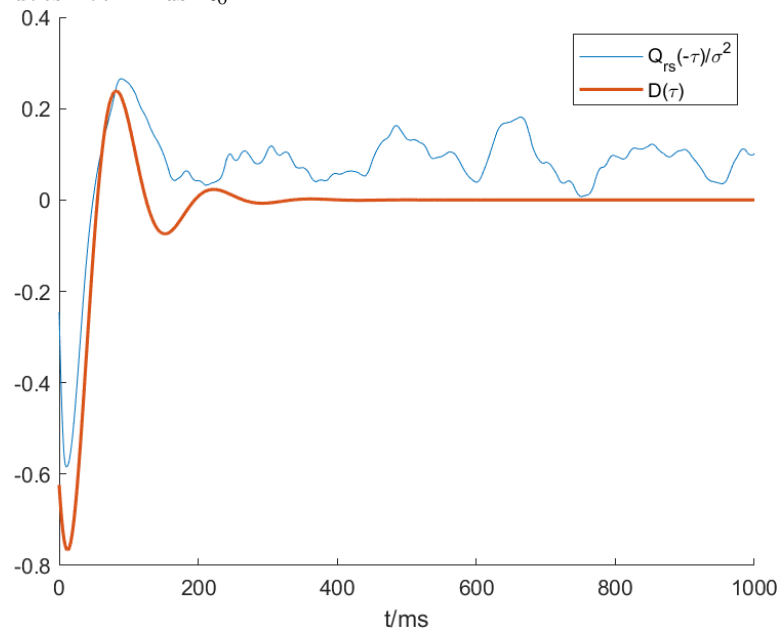
$$Q_{rs}(\tau) = \sigma_s^2 D[(m-n)\Delta t - \tau] \delta_{mn} = \sigma_s^2 D(-\tau) \tag{23}$$

3. From theoretical deduction, it is obvious that

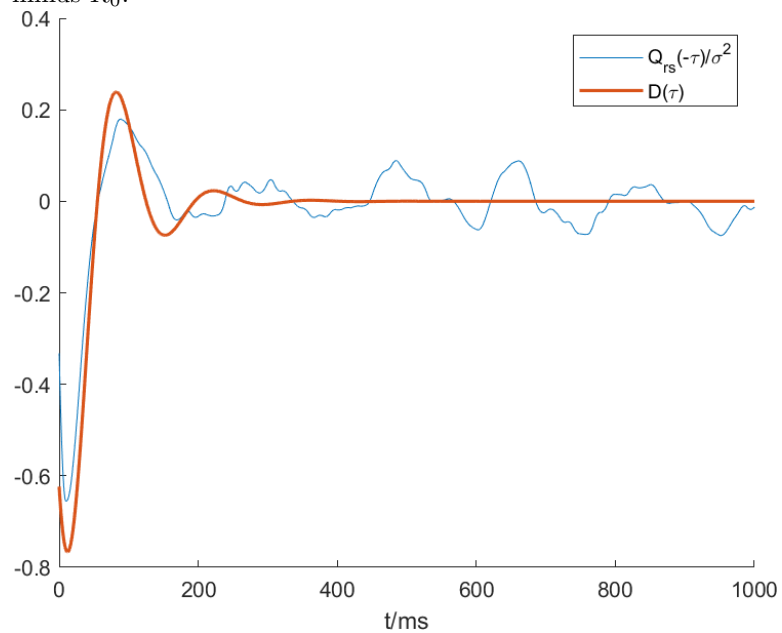
$$Q_{rs}(-\tau)/\sigma^2 = D(\tau) \tag{24}$$

The simulation result could be gotten from code `fish.m` In equation 22, we omit the first term in forth line because when $\Delta t \rightarrow 0$, it is a higher order infinitesimal, but in my calculation, I replace integration with discrete sum, so Δt is not infinitesimal, so when we compute Q_{rs} , if we minus R_0 from R , i.e. omit the first term manually, our result would be much more satisfactory.

does not minus R_0 :



minus R_0 :



Winner Take All Circuit

1. We have known the Lyapunov stability theorem, assume x^* is equilibrium point, the system is globally asymptotically stable if following conditions are satisfied

- $E(x^*) = 0$
- $E(x) > 0, \forall x \neq x^*$
- $E(x)$ is radially unbounded
- $E(x) < 0, \forall x \neq x^*$

the Lyapunov function is

$$E(x) = -\sum_i b_i x_i + \frac{1}{2}(1-\alpha) \sum_i x_i^2 + \frac{\beta}{2} \sum_{i \neq j} x_i x_j \quad (25)$$

Then,

$$\begin{aligned} \frac{dE}{dt} &= \frac{dE}{dx} \dot{x} = \sum_i (-b_i + (1-\alpha)x_i + \frac{\beta}{2} \sum_{j \neq i} x_j) (-x_i + [b_i + (Wx)_i]_+) \\ &= -\sum_i (-x_i + b_i + (Wx)_i) (-x_i + [b_i + (Wx)_i]_+) \end{aligned} \quad (26)$$

when $b_i + (Wx)_i > 0$, $\frac{dE}{dt} = -\sum_i (-x_i + b_i + (Wx)_i)^2 \leq 0$, the equality holds when x is at equilibrium point

when $b_i + (Wx)_i < 0$, $\frac{dE}{dt} = \sum_i x_i (-x_i + b_i + (Wx)_i)$, the discussion about this situation is a little complicated

let's consider a suitable linear transformation

$$y_i = b_i + \sum w_{ij} x_j \quad (27)$$

then we could get that the following two equalities are equivalent

$$\begin{aligned} \dot{y} + y = b + W[y]_+ &\xleftrightarrow{y=Wx+b} Wx + b + W\dot{x} = b + W[b + Wx]_+ \\ &\xleftrightarrow{W \text{ invertible}} x + \dot{x} = [b + Wx]_+ \end{aligned} \quad (28)$$

then, E for y is

$$E = \frac{1}{2} \sum_{kj} F_k (\delta_{kj} - w_{kj}) F_j - \sum_k b_k F_k \quad (29)$$

where $F_i = [y_i]_+$ write E in vector form, $E = \frac{1}{2} F^T (\mathbb{I} - W) F - b^T F$, E is lower bounded if $z^T (\mathbb{I} - W) z$ is copositive, i.e. $z^T (\mathbb{I} - W) z > 0 \forall z \neq 0$

with $z_i \geq 0, \forall i$, so, when it comes to the exact W we have, for simplicity, let the size of W is $(n \times n)$:

$$(F_1 \ F_2) \begin{pmatrix} 1-\alpha & \beta \\ \beta & 1-\alpha \end{pmatrix} \begin{pmatrix} F_1 \\ F_2 \end{pmatrix} = (1-\alpha)(F_1^2 + F_2^2) + 2\beta F_1 F_2 > 0 \quad (30)$$

since is inequality has to hold for any $x \geq 0$ (and $\beta > 0$), it has to hold that

$$\begin{aligned} 1 - \alpha &> 0, \\ i.e. \quad \alpha &< 1 \end{aligned} \quad (31)$$

2. Reference the work we done in hw3 about the ring network, replace the **rectified linear network** with **x**, then do calculation and analysis the result.

First try to find the eigenvalue and eigenvector of W. let $n = 3$

$$\begin{vmatrix} \alpha & -\beta & -\beta \\ -\beta & \alpha & -\beta \\ -\beta & -\beta & \alpha \end{vmatrix} \rightarrow \begin{vmatrix} \alpha-2\beta & -\beta & -\beta \\ \alpha-2\beta & \alpha & -\beta \\ \alpha-2\beta & -\beta & \alpha \end{vmatrix} \rightarrow \begin{vmatrix} \alpha-2\beta & -\beta & -\beta \\ 0 & \alpha+\beta & 0 \\ 0 & 0 & \alpha+\beta \end{vmatrix} \quad (32)$$

it is easy to get the eigenvalues are $\{\alpha - (n-1)\beta, \alpha + \beta\}$, the eigenvector for $\alpha - (n-1)\beta$ is $(1, 0, \dots, 0)$, for $\alpha + \beta$ are unit vector in the other dimensions, eg. $e_i = (0, \dots, 1, \dots, 0), i = 2, 3, \dots, n$

let $x = \sum_k c_k e_k$, then the equation $\dot{x} = -x + [b + Wx]_+$ could be written as

$$\begin{aligned} \sum_k \frac{dC_k}{dt} e_k &= \sum_k c_k (\lambda_k - 1) e_k + \vec{b} \\ \frac{dC_m}{dt} &= C_m (\lambda_m - 1) + \vec{b} \cdot e_m = C_m (\lambda_m - 1) + b_m \end{aligned} \quad (33)$$

the solution is

$$c_m(t) = \frac{b_m}{1 - \lambda_m} \{1 - \exp[-t(1 - \lambda_m)]\} + c_m(0) \exp(-t(1 - \lambda_m)) \quad (34)$$

as same, let the exponent term do not explode, we request $\lambda_m < 1$, i.e.

$$\begin{cases} \alpha - (n-1)\beta < 1 \\ \alpha + \beta < 1 \end{cases} \quad (35)$$

but given that $\beta > 1 - \alpha$, i.e. $\alpha + \beta > 1$, the second inequality cannot be satisfied, so when $m = 2, 3, \dots, n$, the corresponding term will explode. Then, we replace **x** with **rectified linear network**, the corresponding terms will converge to zero.

Consider the leftover term ,

$$\alpha - (n-1)\beta < \alpha - (n-1)(1 - \alpha) = 1 + n * (\alpha - 1) < 1$$

so this term will converge to a steady state

all in all, only a single neuron is active

3. If just pick the neuron with largest b_{max} , when the system meets the steady state, $x_i^* = [b_i + (Wx)_i]_+ = b_i + \alpha x_i$, let $x_i = \max_i b_i$, we could get $\alpha = 0$

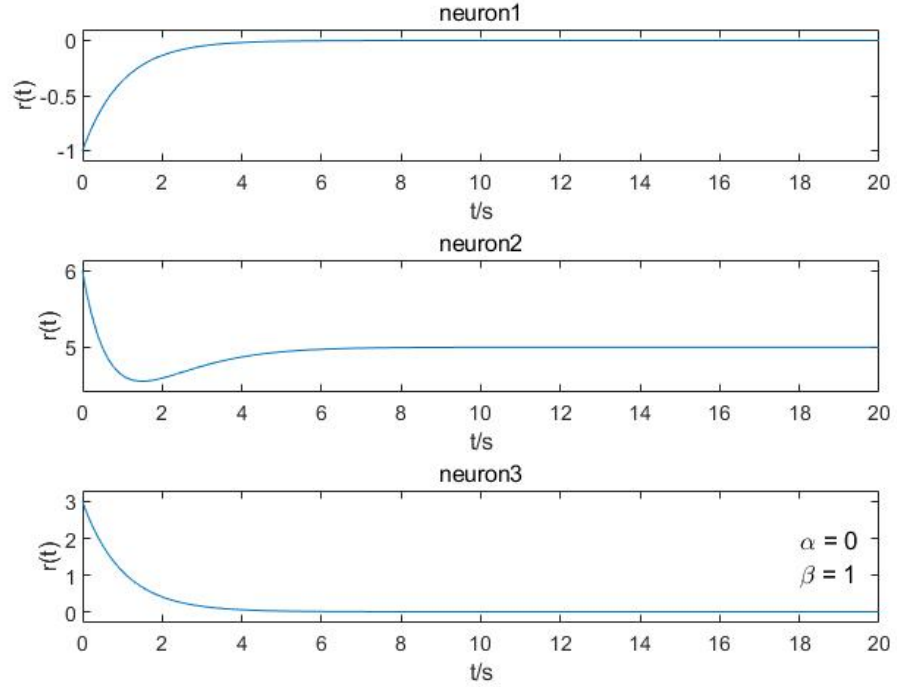
Further, consider the transformation 27 we have taken in the first question. if $x_j = 0$ for all j except $j = \operatorname{argmax}(b_j) = m$, this means $y_j = b_j + (Wx)_j = b_j - \beta b_m \leq 0, \forall j \neq m$, thus, $\beta \geq \frac{\max_{j \neq m} b_j}{b_m} \rightarrow 1$

all in all,

$$\alpha = 0, \beta = 1 \quad (36)$$

the following is some simulation results with code `winner_take_all.m` for simplicity, there are only 3 neurons, vector b is set to $\{4, 5, 0.5\}$. We can get more results by changing the initial conditions

the situation in question 3, network picks the winner neuron:



not only one neuron is excited:

