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Math 6397

Homework 3

10/31/2020

Theoritical Part.

This hand-written part contains only the theoritical part of homework. Experiments and simulations are there in separate python file.

Q.N 1 • Missing steps from Eq:(8.37) to Eq. (8.41)

Let us consider a non linear-Integrate and fire Neuron with index 'i' that is a part of large network.

The following are considered as input:

i) External: $I_i^{ext}(t)$

ii) input spikes $t_j^{(f)}$ from other 'j' neurons

iii) stochastic spikes arrivals $t_k^{(f)}$

The change in membrane potential is given by

$$\frac{du_i}{dt} = \frac{f(u_i)}{\tau_m} + \frac{1}{C} I^{ext}(t) + \sum_j \sum_{t_j^{(f)}} w_{ij}\, \delta(t - t_j^{(f)}) + \sum_K \sum_{t_K^{(f)}} w_{ik}\, \delta(t - t_K^{(f)}), \qquad (A)$$

where δ is Dirac-delta function and w_{ij} is the coupling strength from pre-synaptic neuron 'j' to neuron 'i'.

here we set $f(u) = -u$ and we only assume a single neuron reciving stochastic input

So $$\frac{du}{dt} = -\frac{u}{\tau_m} + \frac{1}{C} I^{ext}(t) + \sum_K \sum_{t_K^{(f)}} w_K \delta(t - t_K^{(f)})$$ (B)

The membrane potential is reset to u_r whenever it reaches threshold ϑ.
Finally we consider $I^{ext} = 0$ (No external current)

The input spikes at synapse K are generated by a Poisson Process and arrive at rate $\nu_K(t)$.

Probability that no spikes arrives in a short time interval Δt

$$\text{Prob}\{\text{No Spikes in } [t, t+\Delta t]\} = 1 - \sum_K \nu_K(t)\,\Delta t$$

* If no spikes arrives, the membrane potential changes from $u(t) = u'$ to $u(t+\Delta t) = u' \exp\left(-\frac{\Delta t}{\tau_m}\right)$

* If spikes arrives at synapse K, the membrane potential change from u' to $u' \exp\left(-\frac{\Delta t}{\tau_m}\right) + w_K$

The probability density of finding a membrane potential 'u' at time $t+\Delta t$ is

$$p^{trans}(u, t+\Delta t \mid u', t) = \left[1 - \Delta t \sum \nu_K(t)\right] \cdot \delta(u - u' e^{-\Delta t/\tau_m}) + \Delta t \sum_K \nu_K(t)\, \delta(u - u' e^{-\Delta t/\tau_m} - w_K) \quad \text{—— (C)}$$

Since the membrane potential is given by differential equation (B) with input spikes generated by Poission distribution

The evolution of membrane potential is Markov process with following.

$$p(u, t+\Delta t) = \int p^{trans}(u, t+\Delta t \mid u', t)\, p(u', t)\, du' \quad \text{—— (D)}$$

From (C) and (D)

$$p(u, t+\Delta t) = \int \Big[\big(1 - \Delta t \sum_K \nu_K(t)\big)\, \delta(u - u' e^{-\Delta t/\tau_m}) + \Delta t \sum_K \nu_K(t)\, \delta(u - u' e^{-\Delta t/\tau_m} - w_K) \Big] p(u', t)\, du'$$

$$= \left[1 - \Delta t \sum_K \nu_K(t)\right] \int \delta(u - u' e^{-\Delta t/\tau_m})\, p(u', t)\, du' + \Delta t \sum_K \nu_K(t) \int \delta(u - u' e^{-\Delta t/\tau_m} - w_K)\, p(u', t)\, du'$$

By the definition of Dirac-Delta function

$$\delta(\alpha x) = \frac{\delta(x)}{|\alpha|}, \quad \delta(-x) = \delta(x)$$

(It is even)

$$x\,\delta(x) = 0$$

and

$$\int_{-\infty}^{\infty} \delta(\alpha x)\,dx = \int_{-\infty}^{\infty} \delta u \,\frac{du}{|\alpha|} = \frac{1}{|\alpha|}$$

$$\left[\text{Also} \quad e^{x} = 1 + x + \frac{x^2}{2!} + \frac{x^3}{3!} + \text{----} \right]$$

$$p(u, t+\Delta t) = \left[1 - \Delta t \sum_k \nu_k(t)\right] e^{\Delta t/\tau_m}\, p(e^{\Delta t/\tau_m} u, t)$$

$$+ \Delta t \sum_k \nu_k(t)\, e^{\Delta t/\tau_m} p(e^{\Delta t/\tau_m} u - w_k, t)$$

$$p(u, t+\Delta t) = \left[1 - \Delta t \sum_k \nu_k(t)\right] \left[1 + \frac{\Delta t}{\tau_m} + \text{---}\right] p\left(u + u\cdot\frac{\Delta t}{\tau_m} + \text{--}, t\right)$$

$$+ \Delta t \sum_k \nu_k(t) \left[1 + \frac{\Delta t}{\tau_m} + \text{---}\right] p\left(u + \frac{\Delta t \cdot u}{\tau_m} - w_k, t\right)$$

taking $\Delta t \to 0$ on R.H.S.

$$p(u, t+\Delta t) = \left[1 + \frac{\Delta t}{\tau_m} - \Delta t \sum \nu_k(t) - \frac{\Delta t^2}{\tau_m} \sum \nu_k(t)\right] p(u, t)$$

$$+ \Delta t \sum \nu_k(t)\, p(u - w_k, t)$$

$$+ \Delta t \sum_k \nu_k \frac{\Delta t}{\tau_m} p(u - w_k, t)$$

$$\frac{p(u, t+\Delta t) - p(u, t)}{\Delta t} = \frac{1}{\tau_m} p(u, t) + \frac{1}{\tau_m} \sum \nu_k \frac{p(u - w_k, t) - p(u, t)}{\Delta t}$$

$$+ \sum_k \nu_k(t) \left[p(u - w_k, t) - p(u, t)\right]$$

P.T.O.

So, $$\frac{P(u,t+\Delta t)-P(u,t)}{\Delta t} = \frac{1}{\tau_m}P(u,t) + \frac{u}{\tau_m}\frac{\partial}{\partial u}P(u,t) + \sum_k \nu_k(t)\left[P(u-w_k,t)-P(u,t)\right]$$

for $\Delta t \to 0$ at L.H.S

also considering w_k small and expanding $P(u-w_k,t)$

$$\frac{\partial}{\partial t}P(u,t) = -\frac{1}{\tau_m}\left[-1+\tau_m\sum_k \nu_k(t)\, w_k\right]P(u,t) + \frac{1}{2\tau_m}\left[\tau_m\sum_k \nu_k(t)\, w_k^2\right]\frac{\partial^2}{\partial u^2}P(u,t)$$

Hence

$$\boxed{\tau_m\frac{\partial}{\partial t}P(u,t) = -\frac{\partial}{\partial u}\left[-u+\tau_m\sum_k \nu_k(t)\, w_k\right]P(u,t) + \frac{1}{2}\left[\tau_m\sum_k \nu_k(t)\, w_k^2\right]\frac{\partial^2}{\partial u^2}P(u,t)}$$

Here I used Linear approximation of multivariable function with Taylor Expansion.

$$\cancel{P(u-w_k,t) = P(w_k,0) + P_u(w_k)}$$

$$\boxed{P(u-w_k,t) = P(u,t) + w_k P_u(w,t) + \frac{w_k^2}{2!}P_{uu}(w,t) + \cdots}$$

Q.N (2) First part:

Expected time for a leaky integrate and fire neuron to fire:-

For this, I use matlab to solve 2nd order differential equation;

$$a\,y'(x) + \frac{1}{2} b\,y''(x) = -1,$$
$$y(c) = 0, \quad y(1) = 0$$

I got the solution as $a = 2.5,\ b = 5,$

$$y(x) = \frac{19e^{20-4c} - 4c + 1}{20(e^{20-4c} - 1)} + \frac{e^{20}(c-5)}{5e^{20-4c-1}} + \frac{1}{20}$$

and when $\lim c \to -\infty$

$$y(x) = 1.$$

Next I will compare this value with the value obtained from simulations in 2nd part.

Conclusion:

The values from simulations also range from 0.2 to 0.9 which are comparable to 1.

Q.N ③ Suppose that the time between spikes are distributed according to Gamma distribution: $\Gamma(\alpha, \beta)$

- Compute the coefficient of variation of the inter-spike interval.

In Gamma distribution; we use the generalization of the factorial function for $r > 0$,

$$\Gamma(r) = \int_0^\infty x^{r-1} e^{-x} \, dx \quad \text{for } r > 0,$$

The random variable with probability density function

$$f(x) = \frac{\lambda^r x^{r-1} e^{-\lambda x}}{\Gamma(r)}, \quad \text{for } x > 0$$

has gamma distribution with parameters $\lambda > 0, r > 0$

- The terms r and λ are called 'shape' and 'scale'.
- When r increases, the distribution becomes more symmetric.
- $1/\lambda$ can be use as scaling parameter.

here we need to compute coefficient of variation for gamma distribution.

CV is defined as the ratio of standard deviation to mean.

Hence

$$\mu = E(X) = \frac{\alpha}{\beta}$$

$$\sigma^2 = V(X) = \frac{\alpha}{\beta^2}$$

$$CV = \frac{\sigma}{E(X)} = \frac{\sqrt{\frac{\alpha}{\beta^2}}}{\frac{\alpha}{\beta}} = \frac{1}{\sqrt{\beta}}$$

- Next, if X is an Erlang with parameters K' a positive integer, and positive real number λ

Erlang distribution is special case of Gamma distribution where we take integer value of K.

When $K=1$, exponential distribution.
When we sum K-independent variable with mean $1/\lambda$ each, we get Erlang distribution.

Hence CV of Erlang distribution with fixed λ and increasing K is given in the "code file".

Q.N (4)

Two Moran process with to alleles, a and A, with mutation but without selection has the transition rates

$$T(n+1|n) = (1-u)\left(\frac{n}{N}\right)\left(1-\frac{n}{N}\right) + v\left(1-\frac{n}{N}\right)^2$$

$$T(n-1|n) = (1-v)\left(1-\frac{n}{N}\right)\left(\frac{n}{N}\right) + u\left(\frac{n}{N}\right)^2$$

Given master equation is;

$$\frac{dP(n,t)}{dt} = -P(n,t)\left(T(n+1|n) + T(n-1|n)\right) + P(n+1,t)\,T(n|n+1) + P(n-1,t)\,T(n|n-1)$$

Mutation from a to A $= u$.

Mutation from A to a $= v$

Let total population is N and u, v are very small.

we take $x = \frac{n}{N}$

then above transition probabilities change to

$$T\left(x+\frac{1}{N}\Big|x\right) = (1-u)\,x\,(1-x) + v(1-x)^2$$

$$T\left(x-\frac{1}{N}\Big|x\right) = (1-v)(1-x)x + ux^2$$

Also from Lecture (15 page 9)

Transition probabilities in terms of $1/N$ are.

$$T(x|x+\tfrac{1}{N}) = (1-v)(x+\tfrac{1}{N})(1-x-\tfrac{1}{N}) + v(1-x+\tfrac{1}{N})^2$$

$$T(x|x-\tfrac{1}{N}) = (1-u)(1-x+\tfrac{1}{N})(x-\tfrac{1}{N}) + v(1-x+\tfrac{1}{N})^2$$

(from Lecture 15 Note page 9)

We use Taylor Expansion for P as

$$P(x-\tfrac{1}{N},t) = P(x,t) - \frac{1}{N}P_x + \frac{1}{2N^2}P_{xx} + O(\tfrac{1}{N})^3$$

$$P(x+\tfrac{1}{N},t) = P(x,t) + \frac{1}{N}P_x + \frac{1}{2N^2}P_{xx} + O(\tfrac{1}{N})^3$$

So $$\frac{dP(x,t)}{dt} = T(x|x+\tfrac{1}{N})P(x+\tfrac{1}{N},t) + T(x|x-\tfrac{1}{N})P(x-\tfrac{1}{N},t)$$

$$- P(x,t)\left[T(x+\tfrac{1}{N}|x) + T(x-\tfrac{1}{N}|x)\right]$$

$$= \left[(1-v)(x+\tfrac{1}{N})(1-x-\tfrac{1}{N}) + u(x+\tfrac{1}{N})^2\right]\left[P(x,t) + \frac{1}{N}P_x + \frac{1}{2N^2}P_{xx}\right]$$

$$+ \left[(1-u)(1-x+\tfrac{1}{N})(x-\tfrac{1}{N}) + v(1-x+\tfrac{1}{N})^2\right]\left[P(x,t) - \frac{1}{N}P_x + \frac{1}{2N^2}P_{xx}\right]$$

$$- \left[(1-u)(1-x)x + v(1-x)^2 + (1-v)x(1-x) + ux^2\right]P(x,t) + O(\tfrac{1}{N})^3$$

$$= \frac{1}{N^2}\Big[P_x(2-u-3v-4x+4ux-4vx) + 2P(u+v-1) + P_{xx}\Big(x-x^2-\frac{ux}{2}-\frac{3vx}{2} + ux^2+vx^2+\frac{u}{2}\Big)\Big]$$

$$+ \frac{1}{N}\Big[P_x(ux+vx-v)+P(u+v)\Big] + O\left(\frac{1}{N}\right)^3$$

Since u and v are small (as of $u, v \in O(\frac{1}{N})$)

So $\frac{u}{N^2}$ and $\frac{v}{N^2}$ become order of $\frac{1}{N^3}$

So, $$\frac{d(P(x,t))}{dt} = \frac{1}{N^2}\Big[P_{xx}(x-x^2)+P_x(2-4x)-2P\Big] + \frac{1}{N}\Big[P_x(ux+vx-v)+P(u+v)\Big] + O\left(\frac{1}{N}\right)^3$$

Hence

$$\frac{dP(x,t)}{dt} = \frac{1}{N^2}\{x(1-x)P\}_{xx} + \frac{1}{N}\{[ux-v(1-x)]P\}_x$$

or, $$\frac{dP(x,t)}{dt} = \frac{1}{N^2}\frac{\partial^2}{\partial x^2}[x(1-x)P] + \frac{1}{N}\frac{\partial}{\partial x}[(ux-v(1-x))P]$$

Q.N (5) Estimation of hitting time via simulation for the two step adaptation process.

Here we initialize the population such that all individual have genotype 1. We assume that genotype 1 mutates to genotype 2 at rate u_{12} and genotype 2 mutates to genotype 3 at rate u_{23}.

let Total Number of individual = N

let n_1, n_2 and n_3 are number of genotypes 1, 2 and 3 respectively.

and $n_1 + n_2 + n_3 = N$ (at any time)

The transition probabilities are;

1) $P(n_1+1, n_2-1, n_3 \mid n_1, n_2, n_3) = (1-u_{12})\left(\frac{n_1}{N}\right)\left(\frac{n_2}{N}\right)$

2) $P(n_1+1, n_2, n_3-1 \mid n_1, n_2, n_3) = (1-u_{12})\left(\frac{n_1}{N}\right)\left(\frac{n_3}{N}\right)$

3) $P(n_1-1, n_2, n_3+1 \mid n_1, n_2, n_3) = \left(\frac{n_3}{N}\right)\left(\frac{n_1}{N}\right)$

4) $P(n_1-1, n_2+1, n_3 \mid n_1, n_2, n_3) = (1-u_{23})\left(\frac{n_2}{N}\right)\left(\frac{n_1}{N}\right) + u_{12}\left(\frac{n_1}{N}\right)\left(\frac{n_1}{N}\right)$

5) $P(n_1, n_2+1, n_3-1 \mid n_1, n_2, n_3) = (1-u_{23})\left(\frac{n_2}{N}\right)\left(\frac{n_3}{N}\right)$

6) $P(n_1, n_2-1, n_3+1 \mid n_1, n_2, n_3) = \left(\frac{n_3}{N}\right)\left(\frac{n_2}{N}\right) + u_{23}\left(\frac{n_2}{N}\right)\left(\frac{n_2}{N}\right)$

In different simulations the arrival of first genotype 3 are recorded.

Since we stop process once n_3 arrives, most of the probabilities are zeros above.

and also, we take (i) $\mu_{12} = \mu_{21} = 0.1/N = \mu$ (say)

(ii) $\mu_{12} = \mu_{21} = \frac{1}{N} = \mu$ (say)

(iii) $\mu_{12} = \mu_{21} = \frac{10}{N} = \mu$ (say)

$N = 1000$