Homework (03) Stochastic Process in Biology

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Pb # (01).

(a) The probability density of finding a membrane potential u @ time $t+\Delta t$ is

$$\cancel{P^{trans}(u, t+\Delta t / u', t) = \left[1 - \Delta t \sum_k \nu_k(t)\right]}$$

$$P^{trans}(u, t+\Delta t | u', t) = \left[1 - \Delta t \sum_k \nu_k(t)\right] \delta\left(u - u' e^{-\Delta t/\tau_m}\right) +$$

$$+ \Delta t \sum_k \nu_k(t)\, \delta\left(u - u' e^{-\Delta t/\tau_m} - w_k\right) \quad \ldots (8.37)$$

Now using van Kampen's (1992)[2] model, we describe the evolution of the membrane potential u by.

$$(8.38) \ldots \boxed{P(u, t+\Delta t) = \int P^{trans}(u, t+\Delta t | u', t)\, p(u', t)\, du'}$$

$$\Rightarrow P(u, t+\Delta t) = \left[1 - \Delta t \sum_k \nu_k(t)\right] \int \delta\left(u - u' e^{-\Delta t/\tau_m}\right) p(u', t)\, du' +$$

$$+ \left(\Delta t \sum_k \nu_k(t)\right) \int \delta\left(u - u' e^{-\Delta t/\tau_m} - w_k\right) p(u', t)\, du'$$

Using $\delta(a u) = a^{-1} \delta(u)$, thus

$$\delta\left(u - u' e^{-\Delta t/\tau_m}\right) = \delta\left(e^{-\Delta t/\tau_m}\left(e^{\Delta t/\tau_m} u - u'\right)\right)$$

$$\boxed{= e^{\Delta t/\tau_m}\, \delta\left(e^{\Delta t/\tau_m} u - u'\right)}$$

$$\delta\left(u - u' e^{-\Delta t/\tau_m} - w_k\right) = \delta\left(e^{-\Delta t/\tau_m}\left(e^{\Delta t/\tau_m} u - u' - w_k e^{\Delta t/\tau_m}\right)\right)$$

Therefore,

$$\delta(u - u' e^{-\Delta t/2m} - w_h) = e^{\Delta t/2m} \{ \delta(e^{\Delta t/2m} u - u' - w_h e^{\Delta t/2m})$$

Then,

$$p(u, t+\Delta t) = \left[1 - \Delta t \sum_h v_h(t)\right] e^{\Delta t/2m} J_1 + \Delta t \sum_h v_h(t) e^{\Delta t/2m} J_2$$

Where, $\begin{cases} J_1 = \int \delta(e^{\Delta t/2m} u - u') \, p(u', t) \, du' \\ J_2 = \int \delta(e^{\Delta t/2m} u - u' - w_h e^{\Delta t/2m}) \, p(u', t) \, du' \end{cases}$

Strating by developping J_1,

$$J_1 = \int \delta(e^{\Delta t/2m} u - u') \, p(u', t) \, du'$$

We know that "Dirac delta function" $\delta(.)$ has the following properties

$\boxed{1}$ $\delta(t-a) = 0, \quad t \neq a$

$\boxed{2}$ $\int_{a-\varepsilon}^{a+\varepsilon} \delta(t-a) \, dt = 1, \quad \varepsilon > 0$

$\boxed{3}$ $\int_{a+\varepsilon}^{a+\varepsilon} f(t) \, \delta(t-a) \, dt = f(a), \quad \varepsilon > 0$

Put $a = e^{\Delta t/2m} u$, then

$$J_1 = \int_{-\infty}^{\infty} \delta(a - u') \, p(u', t) \, du' = \lim_{\varepsilon \to \infty} \int_{-\varepsilon}^{\varepsilon} \delta(a - u') \, p(u', t) \, du'$$

$$= \lim_{\varepsilon \to \infty} - \int_{a+\varepsilon}^{a-\varepsilon} \delta(u' - a) \, p(u', t) \, du'$$

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$$\Rightarrow J_1 = \lim_{\varepsilon \to 0} \int_{a-\varepsilon}^{a+\varepsilon} \delta(u'-a)\, p(u',t)\, du' = p(a,t)$$

$\boxed{3}$

Therefore $\quad J_1 = p(e^{\Delta t/2m} u, t)$

Similarly $\quad J_2 = p(e^{\Delta t/2m}(u-w_k)\}, t)$

Therefore,

(8.39) $$\boxed{\begin{aligned} p(u, t+\Delta t) = {} & \left[1 - \Delta t \sum_k v_k(t)\right] p\left(e^{\Delta t/2m} u, t\right) + \\ & + \left(\Delta t \sum_k v_k(t)\right) p\left(e^{\Delta t/2m}(u-w_k)\}, t\right) \end{aligned}}$$

~~For $\Delta t \to 0$ $p(u,t) \to$~~

We expand around $\Delta t = 0$ $\quad (i.e. \; 0 < \Delta t \ll 1)$

Around $\Delta t = 0$ using (8.37)

$$p(u, t+\Delta t) = p(u,t) + \Delta t \Big[-\sum_h v_h(t) e^{\Delta t/\tau_m} p(e^{\Delta t/\tau_m} u, t)$$

$$+ \frac{1}{\tau_m} e^{\Delta t/\tau_m} \left(1 - \Delta t \sum_h v_h(t)\right) p\left(e^{\Delta t/\tau_m} u, t\right)$$

$$+ \frac{1}{\tau_m} e^{\Delta t/\tau_m} u \frac{\partial p}{\partial u}\left(e^{\Delta t/\tau_m} u, t\right) + \sum_h v_h(t) e^{\Delta t/\tau_m} \Big($$

$$p\left(e^{\Delta t/\tau_m}(u - w_h), t\right)\Big) + \Delta t \left(\cdots \right) \Big]_{\Delta t = 0} + O(\Delta t)$$

$$= p(u,t) + \Delta t \Big[-\left(\sum_h v_h(t)\right) p(u,t) +$$

$$+ \frac{1}{\tau_m} p(u,t) + \frac{1}{\tau_m} u \frac{\partial p}{\partial u}(u,t) + \left(\sum_h v_h(t)\right) p(u - w_h, t) \Big]$$

$$+ O(\Delta t)$$

Thus,

$$\boxed{\begin{aligned} \frac{p(u, t+\Delta t) - p(u,t)}{\Delta t} &= \frac{1}{\tau_m} p(u,t) + \frac{u}{\tau_m} \frac{\partial p}{\partial u}(u,t) \\ &\quad + \sum_h v_h(t) \left[p(u - w_h, t) - p(u,t) \right] \\ &\quad + O(\Delta t)/\Delta t \end{aligned}}$$

(8.40)

When $\Delta t \to 0$: $\frac{O(\Delta t)}{\Delta t} \to 0$

$$\tau_m \frac{\partial p}{\partial t}(u,t) = p(u,t) + u \frac{\partial p}{\partial u}(u,t) + \tau_m \sum_h v_h(t) \Big[p(u - w_h, t)$$

$$- p(u,t) \Big]$$

We have

$$p(u-w_k, t) = p(u,t) - w_k \frac{\partial p}{\partial u} + \frac{1}{2} w_k^2 \frac{\partial^2 p}{\partial u^2} + O(w_k^3)$$

$O(w_k^3) \sim 0$ for $w_k \sim 0$

$$\Rightarrow p(u-w_k, t) - p(u,t) = -w_k \frac{\partial p}{\partial u} + \frac{1}{2} w_k^2 \frac{\partial^2 p}{\partial u^2}(u,t)$$

Therefore,

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

Since:

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

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

Hence,

$$\boxed{\tau_m \frac{\partial p}{\partial t}(u,t) = -\frac{\partial}{\partial u}\left\{\left[-u + \tau_m \sum_k \nu_k(t) w_k\right] p(u,t)\right\} + \frac{1}{2}\left[\tau_m \sum_k \nu_k(t) w_k^2\right] \frac{\partial^2 p}{\partial u^2}(u,t) \quad \ldots (8.41)}$$

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(b)

From (a) we get

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

(8.41)

And (8.45) gives:

$$p(u,t) = \frac{1}{\sqrt{2\pi \langle \Delta u^2(t) \rangle}} \exp\left(-\frac{[u(t|\hat{t}) - u_0(t)]^2}{2\langle \Delta u^2(t) \rangle}\right)$$

Pb# 04

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

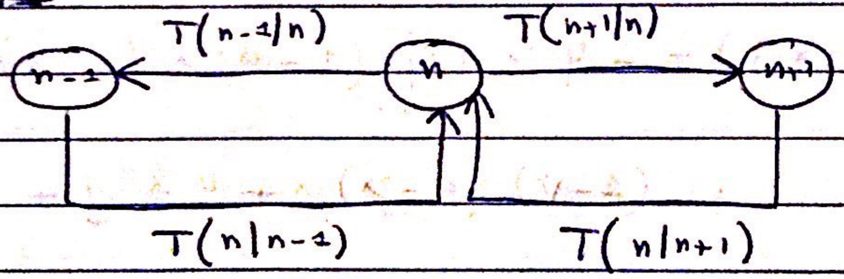
$$T(n-1|n) = (1-v)\left(1-\frac{n}{N}\right)\left(\frac{n}{N}\right) + u\left(\frac{n}{N}\right)^2$$

Set $x = \frac{n}{N}$, thus

$$T(n+1|n) = (1-u)\,x\,(1-x) + v(1-x)^2$$
$$T(n-1|n) = (1-v)\,x\,(1-x) + u\,x^2$$

$\cancel{n = Nx \Rightarrow \frac{d}{dt} f(n,t) = \frac{\partial}{\partial t} f(Nx,t)}$

$\cancel{\frac{\partial f}{\partial t}(x,t) =}$



$$\Rightarrow \begin{cases} T(n|n+1) = (1-v)\left(1-x-\frac{1}{N}\right)\left(x+\frac{1}{N}\right) + \\ \qquad + u\left(x+\frac{1}{N}\right)^2 \\ T(n|n-1) = (1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right) + \\ \qquad + v\left(1-x+\frac{1}{N}\right)^2 \end{cases}$$

Set $P(n,t) = P(Nx,t) = \varphi(x,t)$

$x = \frac{n}{N} \rightarrow n = Nx \quad , \quad n+1 = Nx + 1 \Rightarrow \boxed{x + \frac{1}{N} = \frac{n}{N} + \frac{1}{N}}$

Therefore, $\frac{dP(n,t)}{dt} = \frac{\partial \varphi}{\partial t}(x,t)$

Hence,

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

$$= \frac{\partial \varphi}{\partial t}(x,t)$$

$$\Rightarrow \frac{\partial \varphi}{\partial t}(x,t) = -\varphi(x,t)\left[(1-u)\,x\,(1-x) + v\,(1-x)^2 + (1-v)(1-x)\,x + u\,x^2\right] +$$

$$+ \varphi\left(x+\frac{1}{N},t\right)\left[(1-v)\left(1-x-\frac{1}{N}\right)\left(x+\frac{1}{N}\right) + u\left(x+\frac{1}{N}\right)^2\right] +$$

$$+ \varphi\left(x-\frac{1}{N},t\right)\left[(1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right) + v\left(1-x+\frac{1}{N}\right)^2\right]$$

Hence

$$\Rightarrow \varphi(x+\tfrac{1}{N},t) = \varphi(x,t) + \frac{1}{N}\frac{\partial\varphi}{\partial x}(x,t) + \frac{1}{2}\frac{1}{N^2}\frac{\partial^2\varphi}{\partial x^2}(x,t) + O\left(\frac{1}{N^3}\right)$$

$$\varphi(x-\tfrac{1}{N},t) = \varphi(x,t) - \frac{1}{N}\frac{\partial\varphi}{\partial x}(x,t) + \frac{1}{2}\frac{1}{N^2}\frac{\partial^2\varphi}{\partial x^2}(x,t) + O\left(\frac{1}{N^3}\right)$$

$O\left(\frac{1}{N^3}\right) \sim 0$

$$\Rightarrow \frac{\partial\varphi}{\partial t}(x,t) = \varphi(x,t)\Big[-(1-u)x(1-x) - v(1-x)^2 - (1-v)(1-x)x - ux^2 + (1-v)\left(1-x-\tfrac{1}{N}\right)\left(x+\tfrac{1}{N}\right)$$

$$+ u\left(x+\tfrac{1}{N}\right)^2 + (1-u)\left(x-\tfrac{1}{N}\right)\left(1-x+\tfrac{1}{N}\right) +$$

$$+ v\left(1-x+\tfrac{1}{N^2}\right)\Big] + \Big[(1-v)\left(1-x-\tfrac{1}{N}\right)\left(x+\tfrac{1}{N}\right)$$

$$+ u\left(x+\tfrac{1}{N}\right)^2 - (1-u)\left(x-\tfrac{1}{N}\right)\left(1-x+\tfrac{1}{N}\right)$$

$$- v\left(1-x+\tfrac{1}{N}\right)^2\Big]\frac{1}{N}\frac{\partial\varphi}{\partial x}(x,t) +$$

$$+ \Big[(1-v)\left(1-x-\tfrac{1}{N}\right)\left(x+\tfrac{1}{N}\right) + u\left(x+\tfrac{1}{N}\right)^2 +$$

$$+ (1-u)\left(x-\tfrac{1}{N}\right)\left(1-x+\tfrac{1}{N}\right) + v\left(1-x+\tfrac{1}{N}\right)^2\Big]\Big(\frac{1}{2}\Big(\frac{1}{N^2}\frac{\partial^2\varphi}{\partial x^2}(x,t)\Big)$$

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$$\cancel{\to \frac{\partial \varphi}{\partial t}(x,t) =}$$

Denote: $A(x) = -(\cancel{1-u})x(1-x) - v(1-x)^2 -$

$$- (1-v)\cancel{(1-x)}x - ux^2 + \cancel{(1-v)}\left(1-x-\frac{1}{N}\right)\left(\right.$$

$$\left. x+\frac{1}{N}\right) + u\left(x+\frac{1}{N}\right)^2 + (1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right)$$

$$+ v\,\cancel{\left(1-x+\frac{1}{N^2}\right)}$$

$$\cancel{A(x) = -x(1-x)(-2+u+v) + v\left(x \ldots \frac{1}{N} \ldots \frac{1}{N}\right)}$$

$$A(x) = -x(1-x)(-2+u+v) - v(1-x)^2 - ux^2 +$$

$$+ (1-v)\left(1-x-\frac{1}{N}\right)\left(x+\frac{1}{N}\right) + u\left(x+\frac{1}{N}\right)^2 +$$

$$+ (1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right) + v\left(1-x+\frac{1}{N^2}\right)$$

$$B(x) = (1-v)\left(1-x-\frac{1}{N}\right)\left(x+\frac{1}{N}\right) + u\left(x+\frac{1}{N}\right)^2$$

$$- (1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right)$$

$$- v\left(1-x+\frac{1}{N}\right)^2$$

$$C(x) = (1-v)\left(1-x-\frac{1}{N}\right)\left(x+\frac{1}{N}\right) +$$

$$+ u\left(x+\frac{1}{N}\right)^2 + (1-u)\left(x-\frac{1}{N}\right)\left(1-x+\frac{1}{N}\right) + v\left(1-x+\frac{1}{N}\right)^2$$

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Hence,

$$\frac{\partial \varphi}{\partial t}(x,t) = A(x)\,\varphi(x,t) + \frac{1}{N} B(x) \frac{\partial \varphi}{\partial x}(x,t) + \frac{1}{2N^2} C(x) \frac{\partial^2 \varphi}{\partial x^2}(x,t)$$

FP for the ME given ●, where $x = \frac{n}{N}$

Pb #3.

The ~~spikes~~ times between X spikes are distributed according to a gamma distribution, $\Gamma(\alpha, \beta)$

$$\begin{cases} f(x) = \dfrac{\beta^{\alpha} x^{\alpha-1} e^{-\beta x}}{\Gamma(\alpha)} & \forall x > 0 \\ & \alpha, \beta > 0 \\ Var(X) \overset{(PDP)}{=} \dfrac{\alpha}{\beta^2}, \; E[X] = \alpha/\beta \end{cases}$$

$\boxed{1}$ The coefficient of variation of the inter-spike interval, Coff

$$Coff_{-Var} = \frac{\sqrt{Var(\text{inter-spike interval})}}{E[\text{Inter-Spike interval}]}$$

$$= \frac{\sqrt{\alpha/\beta^2}}{\frac{\alpha}{\beta}} = \frac{\cancel{\beta}}{\alpha} \frac{\sqrt{\alpha}}{\cancel{\beta}} \quad (\alpha, \beta > 0)$$

$$= \frac{1}{\sqrt{\alpha}}$$

$\boxed{2}$ The special case of $\Gamma(\alpha,\beta)$: "The Earlang distribution".

E_dist = $\sum$ k i.i.d exponentially distributed
Erlang dist $\longleftrightarrow$ $E[\,] = \frac{k}{\lambda}$, $Var(\,) = \frac{k}{\lambda^2}$
r.vs with parameter λ.

Coff_var_inter_event_time that follows the

Erlang dist with λ fixed and k $\uparrow$

denoted by Coff_var_Erlang:

$$\text{Coff\_var\_Erlang} = \frac{\sqrt{Var(\text{inter\_Spike\_interval})}}{E[\text{inter\_spike\_interval}]}$$

$$Var\left(\sum_{i=1}^{k} X_i\right) = k\,Var(X_i) = k/\lambda^2$$

$$E\left[\sum_{i=1}^{k} X_i\right] = k\,E[X_i] = \boxed{k/\lambda} \qquad X_i \hookrightarrow \exp(\lambda)$$

$$\Rightarrow \text{Coff\_var\_Erlang} = \frac{\sqrt{k/\lambda^2}}{k/\lambda}$$

$$= \frac{\sqrt{k}\,\cancel{\lambda}}{\cancel{\lambda}\,k} = \boxed{\frac{1}{\sqrt{k}}}$$

$k > 0$

λ The mean of the i.i.d expontial r.vs doesn't

affect the Coff_var_Erlang since this last

one is not ~~…~~ depend to "λ".

Note. Please check the associated simulations in Mathematica and Python in the same Git respiratory.