Chapter 11

Spiking Network Dynamics: GLM

11.1 Motivation

The number of neurons that can be simultaneously recorded is exponentially growing (Stevenson and Kording 2011). The doubling time is about 7 years. With this growing amount of data it is necessary to design good questions and use good methods.
A particularly interesting question for such a large data set is the encoding) question. How are stimuli encoded in spike trains. If

11.2 Definition of the sSRM0

The stochastic spike response model (sSRM) describes how the input spike trains $x_j(t) = \sum_{t_j^f} \delta(t - t_j^f)$ as well as the external input current I are converted into (delta Dirac) spiking activity $y = \sum_{t^f} \delta(t - t^f)$. Let u denote the neuronal membrane potential which is linear in the input currents:

$$u(t) = u_{\text{rest}} + \sum_j w_j \left(\epsilon_j * x_j\right)(t) + \left(\kappa * I\right)(t) \tag{11.1}$$

where $*$ denotes a convolution, i,e, $\left(\kappa * I\right)(t) = \int_0^\infty k(s) I(t-s) ds$. ϵ_j denotes the PSP kernel from presynaptic neuron j. For simplicity we will assume that synaptic current is represented as a Dirac spike train $x_j = \sum_{t_j^f} \delta(t - t_j^f)$.

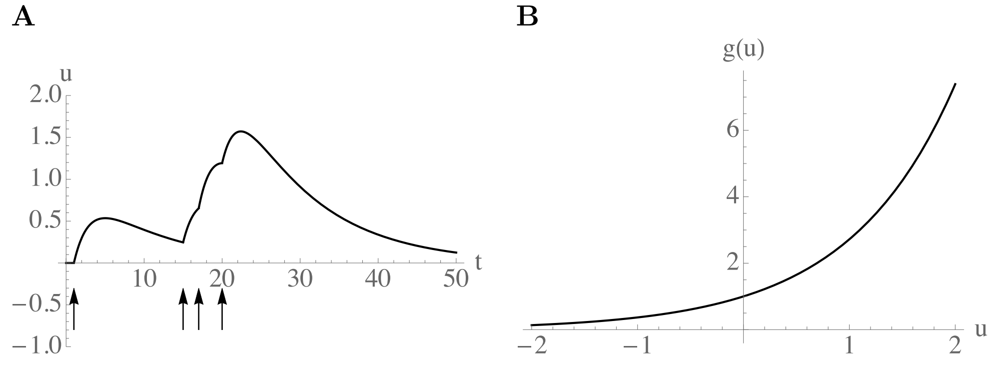

Figure 11.1: **A** Membrane potential trace of the SRM. **B**. In the SRM, the probability of firing is a function of the membrane potential u.

As its name indicate, the spike emission process in the sSRM is not deterministic, but probabilistic. Let $N(t)$ be a counting process associated to the spike train y, i.e. $N(t) = \int_0^t y(s) ds$.

$$dN(t) \sim \text{Poisson}(dN(t); g(u(t))dt) \tag{11.2}$$

where $g(u)$ is a monotonically increasing function. PICTURE. dt is an infinitesimal time step and where the Poisson distribution is given by

$$\text{Poisson}(k; \lambda) = \frac{\lambda^k \mathrm{e}^{-\lambda}}{k!} \tag{11.3}$$

Or written differently, we have

$$p(dN(t)|u(t)) = (g(u(t))dt)^{dN(t)} (1 - g(u(t))dt)^{1-dN(t)} \tag{11.4}$$

In class exercise: convince yourself that this is the case (hint: because dt is small, then $dN(t) \in \{0, 1\}$)

Exercise 11.1. *Check that the Poisson distribution is well normalized*

Solution 11.1.

$$\sum_{k=0}^{\infty} p(k) = \mathrm{e}^{\lambda}\mathrm{e}^{-\lambda} = 1 \tag{11.5}$$

Exercise 11.2. *Calculate the mean and variance of the Poisson distribution*

Solution 11.2. *The mean is given by*

$$\sum_{k=0}^{\infty} kp(k) = \sum_{k=0}^{\infty} \frac{k\lambda^k \mathrm{e}^{-\lambda}}{k!} = \lambda \sum_{k=1}^{\infty} \frac{\lambda^{k-1}\mathrm{e}^{-\lambda}}{(k-1)!} = \lambda \tag{11.6}$$

The second order moment is calculated as

$$\begin{aligned} \sum_{k=0}^{\infty} k^2 p(k) &= \sum_{k=0}^{\infty} \frac{k^2\lambda^k \mathrm{e}^{-\lambda}}{k!} = \lambda \sum_{k=1}^{\infty} \frac{k\lambda^{k-1}\mathrm{e}^{-\lambda}}{(k-1)!} \\ &= \lambda \mathrm{e}^{-\lambda} \left(\sum_{k=1}^{\infty} \frac{(k-1)\lambda^{k-1}}{(k-1)!} + \frac{\lambda^{k-1}}{(k-1)!} \right) \\ &= \lambda \mathrm{e}^{-\lambda} \left(\lambda \mathrm{e}^{\lambda} + \mathrm{e}^{\lambda} \right) = \lambda^2 + \lambda \end{aligned} \tag{11.7}$$

So the variance is given by

$$\langle k^2 \rangle - \langle k \rangle^2 = \lambda \tag{11.8}$$

which is the same as the expectation.

11.3 Probability density function

Exercise 11.3. *Calculate the pdf $p(y^T|u^T)$ where $y^T = \{y(t)|t \in [0, T]\}$ and $u^T = \{u(t)|t \in [0, T]\}$*

Solution 11.3. *Let n denote the number of bins, such that $T = ndt$ and let $t_k = kdt$. Let us further denote $y = (y(t_1), \dots, y(t_n))$ and $u = (u(t_1), \dots, u(t_n))$. Then, because of the conditional independence, we have*

$$\begin{aligned} p(y|u) &= \prod_{t_k} \text{Poisson}\left(dN(t_k); g(u(t_k))dt\right) \\ &= \prod_{t_k = t^f} \text{Poisson}\left(1; g(u(t_k))dt\right) \cdot \prod_{t_k \neq t^f} \text{Poisson}\left(0; g(u(t_k))dt\right) \\ &= \prod_{t^f} g(u(t^f))dt \cdot \exp\left(- \sum_{t_k} g(u(t_k))dt \right) \end{aligned}$$

In the limit of small dt, we can replace the sum by an integral and express the log-probability density *(i.e. dividing by $dt^{N(T)}$) as*

$$p(y^T|u^T) = \exp\left(\int_0^T \log\left(g(u(t))\right) y(t) - g(u(t))dt\right) \tag{11.9}$$

11.4 Definition of the sSRM (with spike-afterpotential and adaptation)

PICTURE of the kernels
Two main ingredients were missing in the sSRM0: the spike-afterpotential and the adaptation. The definition of the membrane potential can be extended as

$$u(t) = u_{\text{rest}} + \sum_j w_j \left(\epsilon_j * x_j\right)(t) + \left(\kappa * I\right)(t) + \left(\eta * y\right)(t) \tag{11.10}$$

where the kernel η describes the spike after-potential. So now the membrane potential of a given neuron depends on its past spiking activity. The second important missing part is the refractoriness or adaptation part. This can be included in the spiking mechanism as follows

$$dN(t) \sim \text{Poisson}(dN(t); g(u(t), y^{T^-} dt) \tag{11.11}$$

A convenient choice for this new intensity function g is

$$g(u(t), y^{T^-}) = \tilde{g}(u(t))R(y^{T^-}) \tag{11.12}$$

An absolute refractory period can be expressed as

$$R = \begin{cases} 0 & \text{if} \quad t - \hat{t} < \Delta \\ 1 & \text{else} \end{cases} \tag{11.13}$$

where $\hat{t} = \max\{t^f | dN(t^f) = 1, t^f < t\}$ is the last spike of neuron y before t.
PICT refractory and gain function

11.5 Further properties of the sSRM

Exercise 11.4. *Show that the PDF in this case is identical to Eq. (11.9) up to the redefinition of g and u.*

Solution 11.4. *Hint: use the fact that $p(x_{1:n}) = \prod_{j=1}^n p(x_j|x_{1:j-1})$ (with the convention that $p(x_1|x_{1:0}) = p(x_1)$).*

Exercise 11.5. *Calculate the inter-spike interval distribution (ISI) for the sSRM with $\eta = 0$ and R is such that there is an absolute refractory period of Δ ms.*

Solution 11.5.

Exercise 11.6. *Calculate the F-I curve for the same conditions as the exercise above.*

Solution 11.6.

Exercise 11.7. *Network model of sSRM. Let us consider a recurrent network of N neurons whose activity is denoted by $\mathbf{y} = (y_1, \ldots, y_N)$. Calculate the expected firing rate $\nu = \langle \mathbf{y} \rangle$ as a function of the input firing rates $\boldsymbol{\rho} = \langle \mathbf{x} \rangle$ where $\mathbf{x} = (x_1, \ldots, x_M)$ denotes the input spiking activity.*

Solution 11.7.

Exercise 11.8. *Calculate the expected firing rate and the correlation matrix $C(\tau)$ (where $C_{ij}(\tau) = \langle x_i(t)x_j(t+\tau)\rangle$) of n independent Poisson neurons. By definition a Poisson neuron is such that its Dirac delta spike train is given by $x_i(t) = dN_i(t)/dt$ where $dN_i(t)$ drawn from*

$$dN_i(t) \sim \text{Poisson}(dN_i(t); \rho_i dt) \tag{11.14}$$

Solution 11.8. *The mean is given by*

$$\langle x_i(t)\rangle \;=\; \frac{\langle dN_i(t)\rangle}{dt} = \frac{\rho_i dt}{dt} = \rho_i \tag{11.15}$$

When $i \neq j$ and $t \neq t'$, then $dN_i(t)$ and $dN_j(t')$ are independent, we therefore have

$$\left\langle x_i(t)x_j(t')\right\rangle = \frac{\langle dN_i(t)dN_j(t')\rangle}{dt^2} = \frac{\langle dN_i(t)\rangle\,\langle dN_j(t')\rangle}{dt^2} = \rho_i\rho_j \tag{11.16}$$

In contrary, when $i = j$ and $t = t'$, we have

$$\left\langle x_i(t)x_j(t')\right\rangle = \left\langle x_i^2(t)\right\rangle = \frac{\left\langle dN_i^2(t)\right\rangle}{dt^2} = \frac{\rho_i^2 dt^2 + \rho_i dt}{dt^2} = \rho_i^2 + \frac{\rho_i}{dt} \tag{11.17}$$

All together we have $\forall i, j$ and $\forall \tau$:

$$C_{ij}(\tau) = \langle x_i(t)x_j(t+\tau)\rangle = \rho_i\rho_j + \delta_{ij}\delta(\tau)\rho_i \tag{11.18}$$

Exercise 11.9. *Calculate the mean and variance of the membrane potential in the SRM_0 model, i.e. assuming $k = 0$ and $\eta = 0$ and assuming that the inputs are n independent Poisson processes with firing rates ρ_i, $i = 1, \ldots, n$.*

Solution 11.9. *The mean is given by*

$$\begin{aligned}\langle u\rangle &= u_{\text{rest}} + \sum_j w_j\left(\langle x_j\rangle * \epsilon\right)(t)\\ &= u_{\text{rest}} + \sum_j w_j\rho_j\bar{\epsilon}\end{aligned} \tag{11.19}$$

where $\bar{\epsilon} = \int_0^\infty \epsilon(s)ds$. Let $\Delta = u - \langle u\rangle$ and $\Delta x_j = x_j - \rho_j$. The variance of the membrane potential is given by

$$\begin{aligned}\left\langle \Delta u^2\right\rangle &= \left\langle\left(\sum_j w_j(\Delta x_j * \epsilon)(t)\right)^2\right\rangle\\ &= \sum_{i,j} w_i w_j\left\langle \Delta x_i * \epsilon)(t)\Delta x_j * \epsilon)(t)\right\rangle\\ &= \sum_{i,j} w_i w_j \int_0^\infty\int_0^\infty \epsilon(s)\epsilon(s')\left\langle \Delta x_i(t-s)\Delta x_j(t-s')\right\rangle\\ &= \sum_i w_i^2\rho_i\bar{\epsilon^2}\end{aligned} \tag{11.20}$$

where $\bar{\epsilon^2} = \int_0^\infty \epsilon^2(s)ds$.

With similar calculations as in Ex. 11.9, we can calculate the covariance of the membrane potential of a neuron that receives N independent Poisson spike trains

$$\langle \Delta u(t) \Delta u(t+\tau) \rangle = \sum_i w_i^2 \rho_i \int_0^\infty \epsilon(s)\epsilon(s+\tau)ds \tag{11.21}$$

Note that if $\epsilon(s) = \epsilon_0 \exp(-s/\tau_m)\Theta(s)$ and if the number of inputs (which have non-zero weight w_j and non-zero firing rate ρ_j) is large, then from the central limit theorem, the dynamics of the membrane potential is similar to that of an Ornstein-Uhlenbeck process:

$$du = -\frac{u - \bar{u}}{\tau} dt + \sigma dW \tag{11.22}$$

where $\bar{u} = \langle u \rangle$ and $\sigma = \sqrt{2 \langle \Delta u^2 \rangle / \tau}$

11.6 Definition of the GLM

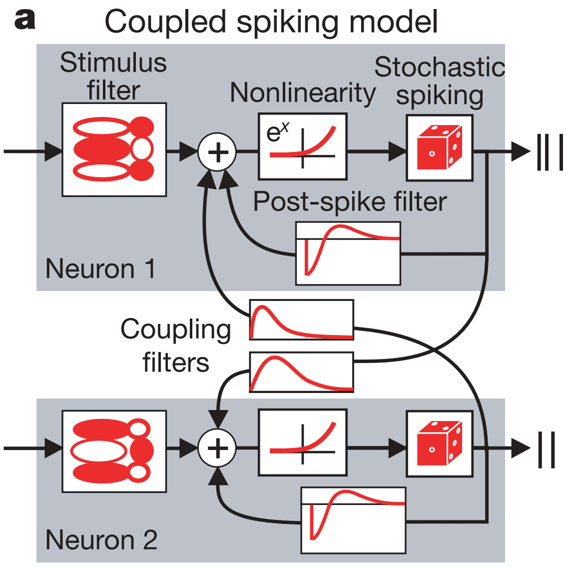

Figure 11.2: .

The Generalized linear model (GLM) is a model that computes the response of a network of spiking neurons to some stimulus. This model is structurally very similar to a network model of sSRM neurons. There are two main conceptual differences

- the input currents defined for the sSRM is replaced by an external stimulus (e.g. movies or sound)
- the variable u in the GLM can be seen as an internal variable and does not need to be identified to the membrane potential

So the GLM defines a set of N internal variables u_i, $i = 1, \ldots, N$ which are given by

$$u_i(t) = \sum_j w_{ij} \left(\epsilon_{ij} * y_j\right)(t) + \left(\kappa_i * I\right)(t) \tag{11.23}$$

and the spiking probability is similar to the one for the sSRM.