Inference On Probablistic Models of Neural Signals

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COMMUNICATION OF NEURAL SIGNALS.

Neurons communicate with each other by transmitting sequences of action potentials. Shape of action potential apparently carries no information. Assumed, information is represented in the occurrence of action potentials.

Coding scheme: unclear.

Spiking Activity of a collection of Neurons indexed by the elements of a set S

= Collection of strictly increasing sequences

$\{t_n^s\}_{s \in S}$

Assuming probability of two or more neurons firing an action potential at any time t is zero,(1) the spiking activity of a collection of neurons can be modelled by a marked point process and its associated collection of counting process. If rate process can be defined then spike coding can be analysed using Filtering Theory.

(1) See recent theses of Demba at M.I.T.

Population Coding Scheme

Population Coding = Information Representation scheme in which an external variable such as

(a) orientation of a bar of light at some location in the visual field

(b) direction of movement of a limb.

represented in the spiking activity of neurons such that

→ Each neuron in the ensemble has a preferred value = value of the external variable for which its expected response = expected number of action potentials generated in a fixed time window divided by the length of the window is <u>maximal</u>

→ For a given value of the external variable, expected response of each neuron is an increasing function of the <u>similarity</u> between its preferred value and the value of the external variable.

$x \longmapsto f(x)$: Value of External Variable → Expected response

Tuning Curve.

Information Representation Scheme of Hubel & Wiesel

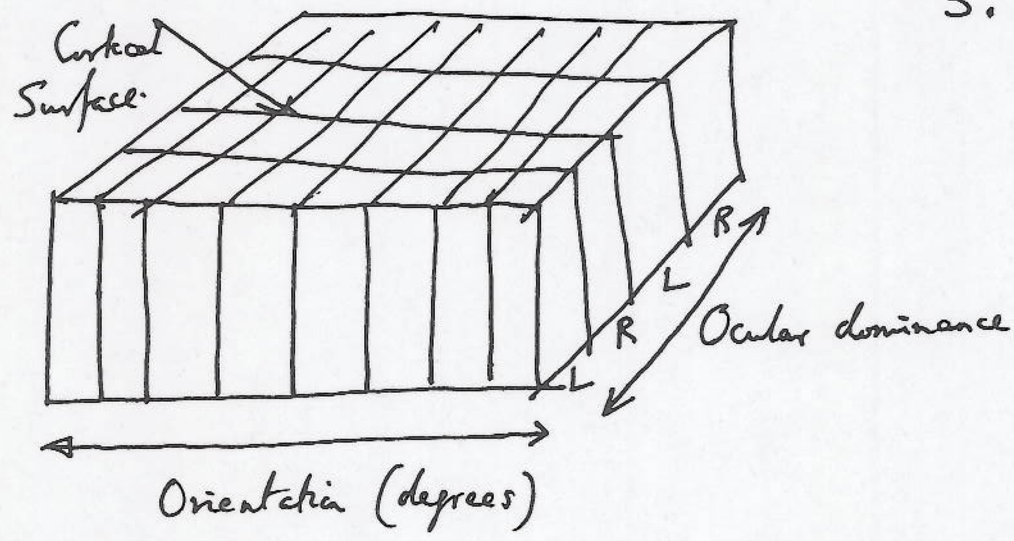
Primary Visual Cortex: Organized into Columns.

Column = Vol. of Cortical tissue formed from a roughly 2mm. x 2mm. area of cortical surface extending towards the white matter.

Cells in each column are responsive to stimulus in roughly the same region of the visual field

Each cell has a preferred orientation and a particular ocular dominance.

Cells close together have similar preferred orientations and ocular dominance.

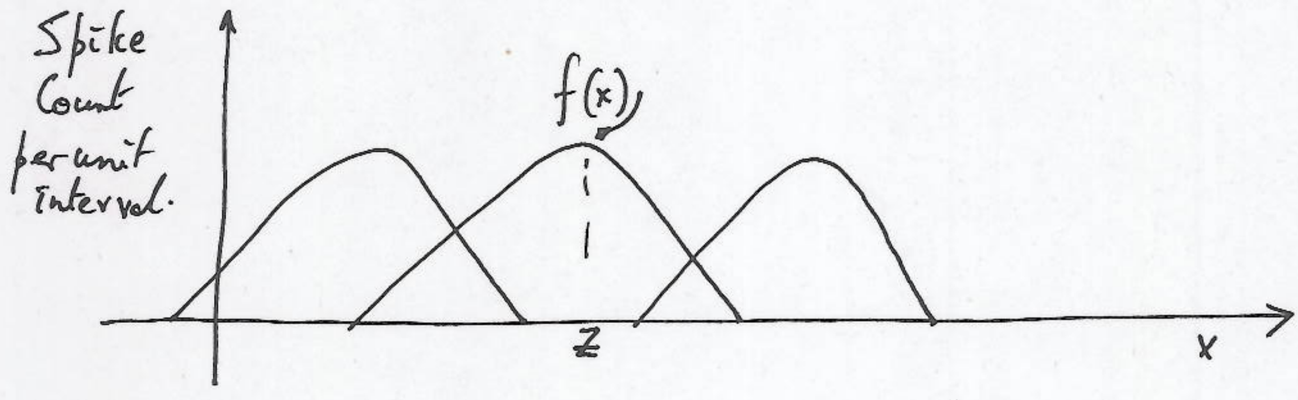


Hubel (1988)

Population Coding Schemes

Direction of arm movements of the monkey encoded by Neurons in the motor cortex (Georgopoulos et al. 1988).

Position of a rat in its environment encoded by place cells in the hippocampus



Models of Population Code

Discrete Population Code

Let $M \subset \mathbb{R}^N$ be a p-dimensional submanifold. $\mathcal{B}(M) = \sigma$-algebra of Borel sets of M. $\|\cdot\|$ = Eucledan norm on $\mathbb{R}^N$. Consider the collection

$$\{z_1, z_2, \ldots, z_d\}, \quad z_i \in M.$$

Let $\{\Lambda_k\}_{k=1}^{d}$ = collection of real-valued functions on $(M, \mathcal{B}(M))$ s.t.

(i) $\Lambda_k \geq 0$, Borel-measurable

(ii) $\exists\ K > 0$, s.t. for $1 \leq k \leq d$.

$$\Lambda_k(x) \leq K \quad \forall x \in M.$$

(iii) For each $1 \leq k \leq d$, $\Lambda_k(x)$ is monotone decreasing in $\|z_k - x\|$

$$\|z_k - x\| < \|z_k - x'\| \Longrightarrow \Lambda_k(x) \geq \Lambda_k(x') \quad \forall x, x' \in M$$

Let $\mathcal{U}$ = set of M-valued Stochastic Processes with left limits.

Discrete Population Code on M = systems which associates with each $(u_t) \in \mathcal{U}$, a d-dimensional counting process (n_t) with rate (λ_t) w.r.t the filtration $\sigma(u_0^\infty, n_0^t)$ where

$$\lambda_{t,k}(\omega) = \Lambda_k(u_{t-}(\omega)).$$

$(\Lambda_k)_{k=1}^d$ = set of tuning curves for population code

$z_k \in M$ = preferred value for tuning curve.

<u>Example</u> $S^1 \subset \mathbb{R}^2$ unit circle

$\{v_1, v_2, \ldots v_d\}$, $v_i \in S^1$

Let b_1 and b_2 be non-negative real numbers such that

$b_2 < \frac{1}{2} b_1$. Consider

$\{\Lambda_k\}_{k=1}^{d}$, $\Lambda_k : S^1 \to \mathbb{R}$ s.t.

$$\Lambda_k(v) = b_1 - b_2 \|v - v_k\|^2 \;:\; \text{monotone decreasing in } \|w - v_k\|.$$

$\mathcal{U}$ = set of S^1-valued stochastic processes

Consider system which associates ~~with~~ each stochastic process $(u_t) \in \mathcal{U}$ with a d-dimensional counting process (n_t) which has rate λ w.r.t. $\{\sigma(u_0^\infty, n_0^t)\}$

$$\lambda_{t,k}(\omega) = \Lambda_k\left(u_t(\omega)\right) = b_1 - b_2 \|u_t(\omega) - v_k\|^2$$

Equivalent model:

$$\nexists \; \lambda_{t,k}(\omega) = c_1 \cos\left(\theta_t(\omega) - \psi_k\right) + c_2$$

Digression. $(\Omega, \mathcal{F}, P)$ complete $(\mathcal{F}_t)_{t\geq 0}$ right continuous filtration.

$(T_k)_{k=0}^{\infty}$ sequence of random variables s.t.

$T_0 = 0$ and $T_k < \infty \Rightarrow T_k < T_{k+1}$ a.s.

$\Big\}$ Point Process.

$\lim_{k\to\infty} T_k = \infty$ a.s. non-explosive. (infinitely many events cannot occur in finite time).

$$n_t(\omega) = \sum_{k\geq 1} \mathbb{1}_{(T_k \leq t)}(\omega)$$ Counting Process.

(Counts number of events occurring in each interval $[0,t)$)

Poisson Process

Let $\lambda \geq 0$. A counting process $(n_t) = (\mathcal{F}_t)$-Poisson process with parameter $\lambda : [0,\infty) \to [0,\infty)$ if

(i) $\forall\ 0 \leq s < t < \infty$ $(n_t - n_s)$ independent of $\mathcal{F}_s$

$$P(n_t - n_s = k) = \frac{\left(\int_s^t \lambda(u)\,du\right)^k}{k!} e^{-\int_s^t \lambda(u)\,du}$$

Marked Point Process $(\Omega, \mathcal{F}, P)$

$Z \subset \mathbb{R}^d$ $\mathcal{B}(Z)$: σ-alegebra of Borel sets.

$(Z_k)_{k=1}^{\infty}$: Z-valued random variables

$((T_k), (Z_k))$: Marked Point Process.

Counting Process

$$n_{t,z}(\omega) = \sum_{k \geq 1} 1_{(T_k \leq t)}(\omega) \, 1_{\{Z_k = z\}}(\omega)$$

Counts number of events with a mark value z which have occurred in $[0, t]$.

Conditional Poisson Processes

$(\Omega, \mathcal{F}, P)$

Let (λ_t) be a non-negative process on $[0, \infty)$. Let n be a counting process defined on $(\Omega, \mathcal{F}, P)$ adapted to $(\mathcal{G}_t)$

If $\forall \; 0 \leq s < t < \infty$, following holds:

$$P\left(n_t - n_s = k \,\middle|\, \lambda_0^\infty, \mathcal{G}_s\right) = \frac{\left(\int_s^t \lambda_u \, du\right)^k}{k!} e^{-\int_s^t \lambda_u \, du}$$

then n is an $(\mathcal{F}_t)$-conditional Poisson process with rate process λ, $\mathcal{F}_t = \mathcal{G}_t \vee \sigma(\lambda_0^\infty)$. ▨

λ = deterministic $\Rightarrow$ n is an $\mathcal{F}_t$-Poisson Process.

Martingale Approach

Let n be an $(\mathcal{F}_t)$-conditional Poisson Process with rate process (λ_t). Suppose

$$E\left(\int_0^t \lambda_s \, ds\right) < \infty \quad \forall t \geq 0$$

Then

$$m_t = n_t - \int_0^t \lambda_s \, ds$$

is an $\mathcal{F}_t$- martingale.

Integrate and Fire Model

Output of Neuron = increasing sequence (t_n)

= time of occurrence of the action potentials

Membrane potential of the neuron:

$$\left.\begin{array}{l} \dot{x} = -\alpha x + u \quad , \alpha \geq 0 \\ u : \text{input to neuron} \end{array}\right\} \text{may include noise}$$

v_0 : threshhold

When x crosses threshhold at time τ, x reset to zero

τ : part of sequence (t_n) as a spike occurrence time

and the whole process is repeated.

Stochastic Model.

(m) : d-dimensional counting process

$(\tilde{m}_t)$: Poisson Process with rate λ

$$dX_t = -\alpha X_t\,dt + \sum_{k=1}^{d} \beta\, \underbrace{dm_{t,k}}_{\text{Input}} - X_t\,dn_t$$

$$\text{Output} \longrightarrow dn_t = f(X_{t-})\,d\tilde{m}_t \qquad m_0 = 0$$

$f : \mathbb{R} \longrightarrow \{0,1\}$ is given by

$$f(x) = \begin{cases} 1, & x \geq v_0 \\ 0, & x < v_0 \end{cases}$$

$\alpha \geq 0$, $0 < \beta < v_0$, $X_0 \geq 0$ r.v.

$(m, \tilde{m}, X_0)$: independent.

Parameters : β determines how much X increases when a jump occurs on one of the input counting processes

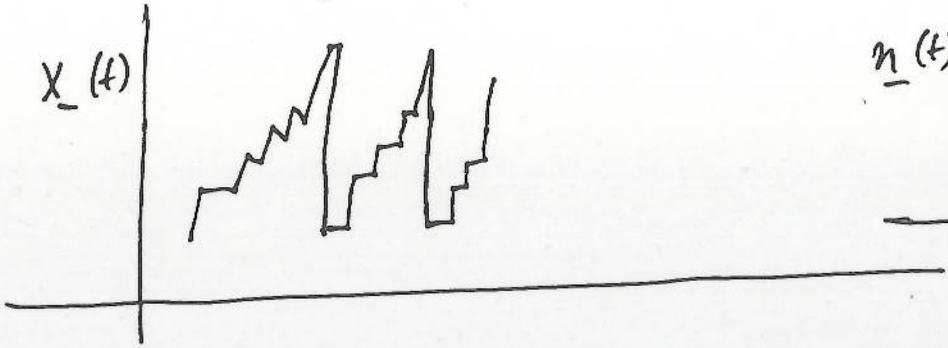
α : rate of decay

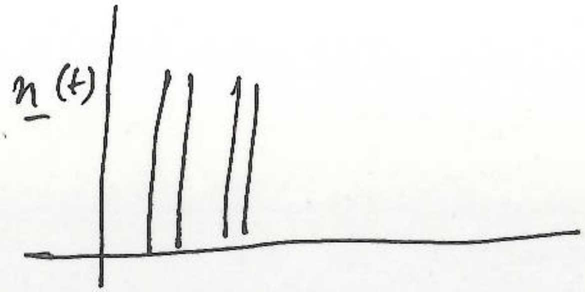
v_0 : threshold.

Rate μ of the Poisson process $\tilde{m}$ characterizes timing jitter in the system. To see this, note that when X_t reaches threshold, n fires at the next jump time of $\tilde{m}$. Now $\tilde{m}$ is Poisson with rate μ

$\Rightarrow$ expected length of the time interval between jump times of $\tilde{m}$ is $\frac{1}{\mu}$

$\Rightarrow$ when X_t reaches v_0, a jump occurs on the output counting process n after $\frac{1}{\mu}$ units of time on average.





Consider related model

$$dx_t = -\alpha x_t dt + \sum_{k=1}^{d} \beta dm_{t,k} - v_0 dn_t$$

$$dn_t = f(x_{t-}) d\tilde{m}_t \ , \ n_0 = 0$$

(When jump occurs on the output (n_t), x_t is decreased by v_0)

$$f(x) = \begin{cases} 1 & \text{if } x \geq v_0 \\ 0 & \text{if } x < v_0 . \end{cases}$$

One can prove:

if $\mathcal{F}_t = \sigma(x_0, \tilde{m}_0^t, u_0^\infty)$

$\sigma(u_0^\infty, n_0^t) \subset \mathcal{F}_t$

n has a rate process $\{\mu f(x_{t-})\}$ w.r.t $(\mathcal{F}_t)$

Filtering with Counting Process Observations.

$(\Omega, \mathcal{F}, P)$ Filtration $(\mathcal{F}_t)$

Processes & Filtrations defined on $[0, T]$.

(X_t) : $\mathcal{F}_t$-adapted Markov Process taking values $S \subset \mathbb{R}^n$

(n_t) : $\mathcal{F}_t$-adapted d-dimensional counting process.

$$\mathbb{E}\, n_{t,k} < \infty \quad \forall t \;,\; 1 \leq k \leq d$$

rate process (λ_t) : $\mathcal{F}_t$-adapted.

Rate process is given by

$$\lambda_{t,k} = \Lambda_k (X_{t-}) \quad \forall t \quad 1 \leq k \leq d$$

$$0 \leq \Lambda_k \leq K \;, \forall k \;, \quad \Lambda_k : S \longrightarrow \mathbb{R}.$$

Estimate X from observations (n_t) on $[0, T]$

Two Cases

1) $dX_t = \sum_{K=1}^{q} g_K(X_{t-})\,dm_{t,K}$

m - q-dimensional $(\mathcal{F}_t)$-Poisson Process with rate vector μ.

2) $dX_t = f(X_t)\,dt + g(X_t)\,dW_t$

Diffusion Process.

→ Evolution of the Distribution of X_t

→ Evolution of the Conditional Distribution $P(X_t \mid n_0^t)$

Filtering for Population Codes

(X_t) diffusion process

$(x_k)_{k=1}^{q} \subset \mathbb{R}^m.$

Tuning Curves

$$\Lambda_k(x) = \phi(x - x_k) \quad : \text{suitable } \phi$$

Evolution of Unnormalized Conditional Density of X_t given n_0^t

$$d\tilde{\rho}_t(x) = \left(L^* - \sum_{k=1}^{q} \phi(x - x_k)\right)\tilde{\rho}_t(x)\,dt + \sum_{k=1}^{q} \phi_k(x - x_k)\tilde{\rho}_{t-}(x)\,dn_{t,k}$$

Mutual Information between Input and Output Processes

$$I\left(x_0^t ; n_0^t\right) = \mathbb{E}_{P_{x,n}} \log \frac{dP_{x,n}}{d(P_x \otimes P_n)}.$$

Synchronized Input Processes

(Abeles 1993) : Nearly synchronized firing activity in the frontal cortex of monkeys.

Maximizes Mutual Information.