Ch 7. Network Models

Seong Kyun Jung

Seoul National University

May 25, 2023

Outline

Table of Contents

Introduction

- So far we have talked about individual neurons and their behaviors.
- We now wish to talk about models that try to capture the behavior of neural networks.

Motivation

- In Ch 6 we introduced a model of a single neuron model that propagates "Action Potential" along its axon.
- So in theory, by concatenating and connecting multiple neurons, we can construct neural networks!
- But...

Table of Contents

Some Notation

- All firing rate models follow the form of "presynaptic input (firing rate of presynaptic neuron) $\rightarrow$ synaptic input (synaptic current) $->$ postsynaptic output (firing rate of postsynaptic neuron)"
- I_s: total synaptic current (Recall that synaptic current causes ions to flow, thus influencing the spike sequences of neurons)
- u: presynaptic firing rate of a single neuron
- v: postsynaptic firing rate of a single neuron
- We use vector notation for multiple neurons.

The Total Synaptic Current

- (1 action potential, 1 synapse) $w_b K_s(t)$: synaptic weight * synaptic kernel (b: input index, s: synapse index)
- (many action potentials, 1 synapse) Assuming linearity,

$$w_b \Sigma_{t_i < t} K_s(t - t_i) = w_b \int_{-\infty}^{t} d\tau K_s(t - \tau) \rho_b(\tau)$$

  where ρ_b (the neural response function) is a corresponding sum of Dirac deltas.

- (many action potentials, many synapses) Assuming linearity,

$$I_s = \Sigma_{b=1}^{N_u} w_b \int_{-\infty}^{t} d\tau K_s(t - \tau) \rho_b(\tau)$$

Construction of a Firing-Rate model

- Instead of the neural response function, we plug in the firing rate $u_b(\tau)$ to obtain

$$I_s = \Sigma_b w_b \int_{-\infty}^{t} d\tau K_s(t-\tau) u_b(\tau)$$

- A widely used synaptic kernel is given by

$$K_s(t) = exp(-\frac{t}{\tau_r})/\tau_r$$

which expressese decay of the synaptic current in the absence of additional stimuil.

- Taking derivatives with respect to t gives

$$\tau_s \frac{dI_s}{dt} = -I_s + \Sigma_b w_b u_b$$

so we can express I_s as a differential equation.

Completing the Model

- We have u_b and have obtained I_s by integrating u_b
- To conclude the model we need to model the relationship between v and I_s.
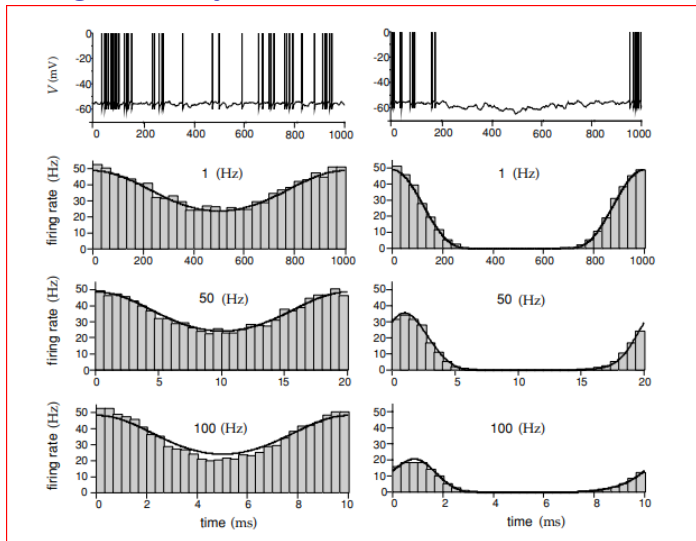- Two possible candidates:

$$\tau_s \frac{dI_s}{dt} = -I_s + w \cdot u, v = F(I_s)$$

where F is the threshold linear function, and

$$\tau_r \frac{dv}{dt} = -v + F(I_s(t))$$

Note that $\tau_r \neq \tau_s$!!

Firing-Rate Dynamics

Does the firing rate instantly trail the input current, or is there a lag? The figures show that both may occur.

Feedforward and Recurrent networks

- Network models may involve many outputs; in this case the w_b becomes a matrix (indexed by input and output) instead of a vector (indexed only by input)

- In case of an interconnection between the output layers, we simply describe the synaptic weights by another matrix M;

- For example, the delayed firing rate adjustment model becomes

$$\tau_r \frac{dv}{dt} = -v + F(Wu + Mv)$$

A Caveat

- We consider some models where M is symmetric.
- However, this actually may be problematic, violating a principle in neuroscience called **Dale's Law**.
- Thus if we wish to use symmetric weights for describing interconnectivity of the output neurons, a specific interpretation of the dynamics must be assumed.

Continuously Labeled Networks

- There is no inherent reason to restrict the input/output neurons to the integers.
- In particular, neurons in the primary visual cortex can be characterized by their preferred orientation angles.

CL Firing Rate Models

- The "matrices" W and M now become functions defined on Cartesian products; e.g. if the neurons are in the primary visual cortex and indexed by their preferred stimulus angle

$$W, M : [0, 2\pi] \times [0, 2\pi] \to \mathbb{R}$$

- The dynamical system describint the evolution of the output firing rate is now dependent on an integral;

$$\tau_r \frac{dv(\theta)}{dt} = -v(\theta) + F(\rho_\theta \int_{-\pi}^{\pi} d\theta' W(\theta, \theta') u(\theta') + M(\theta, \theta') v(\theta'))$$

Table of Contents

Neural Coordinate Transformations 1

- We look at an example of feedforward networks (which don't have recurrence M), by calculating the coordinate transformations in visually guided reaching tasks.
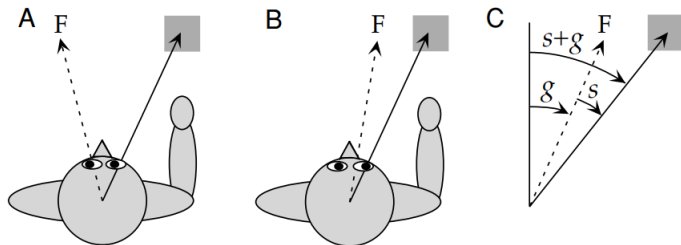
Some experimental data

Figure 7.4 Coordinate transformations during a reaching task. (A, B) The location of the target (the gray square) relative to the body is the same in A and B, and thus the movements required to reach toward it are identical. However, the image of the object falls on different parts of the retina in A and B due to a shift in the gaze direction produced by an eye rotation that shifts the fixation point F. (C) The angles used in the analysis: s is the angle describing the location of the stimulus (the target) in retinal coordinates, that is, relative to a line directed to the fixation point; g is the gaze angle, indicating the direction of gaze relative to an axis straight out from the body. The direction of the target relative to the body is $s + g$.
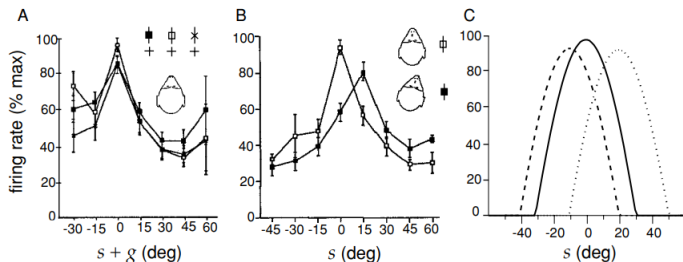
Some experimental data

Figure 7.5 Tuning curves of a visually responsive neuron in the premotor cortex of a monkey. Incoming objects approaching at various angles provided the visual stimulation. (A) When the monkey fixated on the three points denoted by the cross symbols, the response tuning curve did not shift with the eyes. In this panel, unlike B and C, the horizontal axis refers to the stimulus location in body-based, not retinal, coordinates ($s + g$, not s). (B) Turning the monkey's head by $15°$ produced a $15°$ shift in the response tuning curve as a function of retinal location, indicating that this neuron encoded the stimulus direction in a body-based system. (C) Model tuning curves based on equation 7.15 shift their retinal tuning to remain constant in body-based coordinates. The solid, heavy dashed, and light dashed curves refer to $g = 0°$, $10°$, and $-20°$ respectively. The small changes in amplitude arise from the limited range of preferred retinal location and gaze angles in the model. (A, B adapted from Graziano et al., 1997; C adapted from Salinas and Abbott, 1995.)
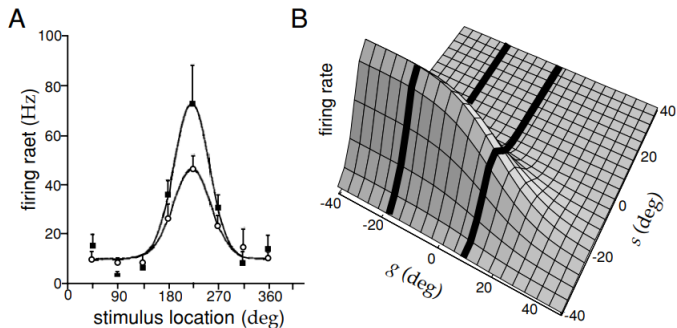
Some experimental data

Figure 7.6 Gaze-dependent gain modulation of visual responses of neurons in posterior parietal cortex. (A) Average firing-rate tuning curves of an area 7a neuron as a function of the location of the spot of light used to evoke the response. Stimulus location is measured as an angle around a circle of possible locations on the screen and is related to, but not equal to, our stimulus variable s. The two curves correspond to the same visual images but with two different gaze directions. (B) A three-dimensional plot of the activity of a model neuron as a function of both retinal position and gaze direction. The striped bands correspond to tuning curves with different gains similar to those shown in A. (A adapted from Brotchie et al., 1995; B adapted from Pouget and Sejnowski, 1995.)

Modeling the Neuron

- The stimulus of the visual cortex neurons seems to depend on the "body coordinates" rather than the "retinal coordinates"

- We model this situation as a feedforward network with one output neuron and a continuously indexed layer of input neurons

- In particular, the steady-state firing rate is given by

$$v_\infty = F(\rho_\xi \rho_\gamma \int d\xi d\gamma w(\xi, \gamma) f_u(s - \xi, g - \gamma))$$

where ξ is the preferred retinal location and γ is the preferred gaze direction.

- The problem remains whether this integral can become a function of $s + g$, which holds if $w(\xi, \gamma) = w(\xi - g, \gamma + g)$.

Table of Contents

Linear Recurrent Networks

- We begin by investigating the simplest recurrent network, the linear network:

$$F(Wu + Mv) = Wu + Mv$$

- The recurrent model becomes

$$\tau_r \frac{dv}{dt} = -v + Wu + Mv$$

and since the model is linear, we can simply solve it as a system of first-order linear ODEs (diagonalization and eigenvectors)

- Suppose the eigenvectors of M are $e_\mu, \mu = 1, ..., N_v$ with respective eigenvalues λ_μ.

- Since M is assumed to be symmetric, we can choose e_μ to be orthonormal, thus giving a coordinate system to express $v(t)$.

LRN - Analytic Solution

- If Wu (the input) is time-independent, doing some ODE things we get

$$c_v(t) = \frac{e_v \cdot Wu}{1 - \lambda_v}(1 - exp(-\frac{t(1 - \lambda_v)}{\tau_r})) + c_v(0)exp(-\frac{t(1 - \lambda_v)}{\tau_r})$$

- Some characteristics of the steady-state values:
  (1) Highly explosive - may blow up
  (2) If not, approaches the value exponentially
  (3) The value depends on the projection of the input onto the eigenvector
  (4) τ_r (which dictates the lag) slows down convergence linearly

LRN - Selective Amplification

- If some eigenvalues are very close to 1 while others are not, the firing rate vector will depend only on some coordinates and not others; eg. if only λ_1 is close to 1

$$v_\infty \approx \frac{(e_1 \cdot h)e_1}{1 - \lambda_1}$$

- The network only amplifies certain input (firing rate) patterns while discarding others.
- Note that mathematically this is just elementary linear algebra...

LRN - Input Integration

- Some neurons seem to maintain activity in the absence of additional stimulus (eg. neurons that maintain eye position); these neurons are called "integrators".

- Integrators can be modelled by LRNs where Wu is time-dependent and one eigenvalue is exactly 1;

$$v(t) \approx \frac{e_1}{\tau_r} \int_0^t dt' e_1 \cdot (W(t')u(t'))$$

LRN - Continuous networks

- Recall that now, M becomes a function, and instead of summation we need to integrate:

$$\tau_r \frac{dv(\theta)}{dt} = -v(\theta) + h(\theta) + \rho_\theta \int_{-\pi}^{\pi} d\theta' M(\theta - \theta') v(\theta')$$

where $h(\theta)$ is the feedforward input and ρ_θ is density (which we assume constant).

- If we assume M is 2π-periodic and even, under some regularity conditions we would be able to write M as a trigonometric series; thus the eigenfunctions would become cosine and sine functions.

LRN - Continuous Networks

- The steady-state firing rate becomes

$$v_\infty(\theta) = \frac{1}{1-\lambda_0} \int_{-\pi}^{\pi} \frac{d\theta'}{2\pi} h(\theta') + \Sigma \frac{\cos(\mu\theta)}{1-\lambda_\mu} \int_{-\pi}^{\pi} \frac{d\theta'}{\pi} h(\theta') \cos(\mu\theta')$$

$$+ \Sigma \frac{\sin(\mu\theta)}{1-\lambda_\mu} \int_{-\pi}^{\pi} \frac{d\theta'}{\pi} h(\theta') \sin(\mu\theta')$$
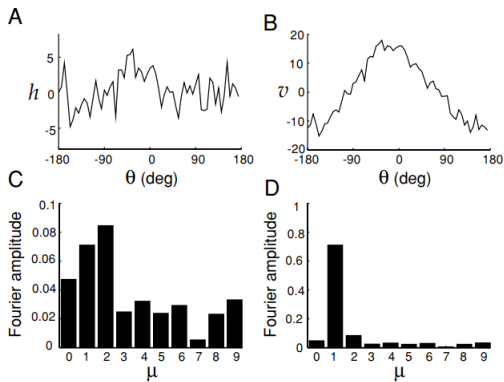
LRN - Continuous Networks

Figure 7.8 Selective amplification in a linear network. (A) The input to the neurons of the network as a function of their preferred stimulus angle. (B) The activity of the network neurons plotted as a function of their preferred stimulus angle in response to the input of panel A. (C) The Fourier transform amplitudes of the input shown in panel A. (D) The Fourier transform amplitudes of the output shown in panel B. The recurrent coupling of this network model took the form of equation 7.33 with $\lambda_1 = 0.9$. (This figure, and figures 7.9, 7.12, 7.13, and 7.14, were generated using software from Carandini and Ringach, 1997.)

Thank You