

## Exercises

### Chapter 7

1. a) Consider network activities  $v(\theta)$  that are steady-state solutions of equation 7.36, satisfying

$$v(\theta) = \left[ h(\theta) + \int_{-\pi/2}^{\pi/2} \frac{d\theta'}{\pi} (-\lambda_0 + \lambda_1 \cos(2(\theta - \theta'))) v(\theta') \right]_+, \quad (1)$$

in response to input  $h(\theta) = Ac(1 - \epsilon + \epsilon \cos(2\theta))$  as in equation 7.37. Assuming that  $v(\theta)$  is symmetric about  $\theta = 0$ , show that  $v(\theta)$  takes either the form

$$v(\theta) = \alpha [\cos(2\theta) - \cos(2\theta_C)]_+ \quad (2)$$

or the form

$$v(\theta) = \alpha \cos(2\theta) + v_0. \quad (3)$$

In the case of equation 2, which applies when  $\theta_C < \pi/2$  and for which  $\theta_C$  defines the width of the orientation tuning curve, by calculating the integral

$$\int_{-\pi/2}^{\pi/2} \frac{d\theta'}{\pi} (-\lambda_0 + \lambda_1 \cos(2(\theta - \theta'))) v(\theta'),$$

show that  $\alpha$  and  $\theta_C$  must satisfy the consistency conditions

$$\begin{aligned} \alpha &= \frac{Ac\epsilon}{1 - \lambda_1 (\theta_C - \sin(4\theta_C)/4) / \pi} \\ \cos(2\theta_C) &= \frac{\lambda_0}{\pi} (\sin(2\theta_C) - 2\theta_C \cos(2\theta_C)) - \\ &\quad \frac{(1 - \epsilon)}{\epsilon} \left( 1 - \frac{\lambda_1}{\pi} \left( \theta_C - \frac{\sin(4\theta_C)}{4} \right) \right). \end{aligned} \quad (4)$$

- b) In the case of equation 3, calculate  $\alpha$  and  $v_0$ .

c) For values  $\lambda_0 = 7.3$ ,  $\lambda_1 = 11$ ,  $c = 1$ , and  $A = 40$  Hz, use the MATLAB® function `fzero` to find the value of  $\theta_C$  that satisfies the consistency condition in equation 4 as a function of  $\epsilon$  for  $0 < \epsilon \leq 1$ . For  $\epsilon = 0.1$  and  $c = 0.1, 0.2, 0.4$ , and  $0.8$ , solve for  $\alpha$ , and thereby reproduce figure 7.10B. Repeat the plots for  $\lambda_1 = 0$ . At what value of  $\epsilon$  does  $\theta_C$  fall below  $\pi/2$ . This corresponds to a model in which feedforward orientation tuning is sharpened only by inhibition, and the model lacks contrast invariant tuning.

d) Numerically integrate equation 7.36 for the sets of parameters in (c) to confirm your results. Use 100 neurons with preferred values evenly spaced between  $-\pi/2$  and  $\pi/2$ .

- e) Plot  $\theta_C - \sin(4\theta_C)/4$  for  $0 \leq \theta_C \leq \pi/2$ . What is its maximum value? As  $\epsilon \rightarrow 0$  (so that  $(1 - \epsilon)/\epsilon \rightarrow \infty$ ), calculate (from equation 4) a condition on  $\lambda_1$  that ensures there will always be a solution with  $\theta_C < \pi/2$ . This defines a marginal phase in which the recurrent connections create a tuned output even from untuned input, and it constitutes what is called a continuous attractor.
2. A Hopfield associative memory network has activities for individual units,  $v_a$  for  $a = 1, 2, \dots, N$  (or collectively  $\mathbf{v}$ ), that take values of either  $+1$  or  $-1$ , and are updated at every discrete time step of the network dynamics by the rule

$$v_a(t+1) = \text{sgn} \left( \sum_{a'=1}^N M_{aa'} v_{a'}(t) \right), \quad (5)$$

where

$$\text{sgn}(z) = \begin{cases} +1 & \text{if } z \geq 0 \\ -1 & \text{if } z < 0. \end{cases}$$

Here  $\mathbf{M}$  is a matrix constructed from  $P$  “memory” vectors  $\mathbf{v}^m$  ( $m = 1, 2, \dots, P$ ), also composed of elements that are either  $+1$  or  $-1$ , through the sum of outer products

$$M_{aa'} = (1 - \delta_{aa'}) \sum_{m=1}^P v_a^m v_{a'}^m. \quad (6)$$

Note that the diagonal elements of  $\mathbf{M}$  are set to zero by this equation. Consider a 100-element network ( $N = 100$ ). Construct  $P$  memory states by randomly assigning  $+1$  and  $-1$  values with equal probabilities to the  $N$  elements of each  $\mathbf{v}^m$ . Using these memory vectors, set the matrix of synaptic weights according to equation 6. Then, study the behavior of the network by iterating equation 5. To measure how close the state of the network at time  $t$ ,  $\mathbf{v}(t)$ , is to a particular memory state, define the overlap function  $q(t) = \mathbf{v}(t) \cdot \mathbf{v}^m / N$ . This is equal to 1 if  $\mathbf{v}(t) = \mathbf{v}^m$ , is near zero if  $\mathbf{v}(t)$  is unrelated to  $\mathbf{v}^m$ , and is equal to  $-1$  if  $\mathbf{v}(t) = -\mathbf{v}^m$ . Set the initial state  $\mathbf{v}(0)$  so that it has a positive overlap,  $q(0)$ , with memory state  $\mathbf{v}^1$ . Plot  $q(t)$  as the network evolves from this state according to equation 5. Final values of  $q(t)$  near one indicate successful recovery of the memory. Do the same starting from  $\mathbf{v}(0)$  close to the inverse of the memory state  $-\mathbf{v}^1$ . What accounts for this behavior? Determine the range of  $q(0)$  values (about  $\mathbf{v}^1$ ) that assures successful memory recovery for different values of  $P$ . Start with  $P = 1$  and increase it until memory recovery fails even for  $q(0) = 1$ . At what  $P$  value does this occur?

3. Repeat exercise 2 with the matrix  $\mathbf{M}$  replaced by

$$M_{aa'} = (1 - \delta_{aa'}) \sum_{m,m'=1}^P v_a^m C_{mm'} v_{a'}^{m'},$$

where  $C_{mm'}$  is the  $m, m'$  element of the inverse of the matrix

$$\sum_{a=1}^N v_a^m v_a^{m'}.$$

Compare the performance and capacity of the associative memory constructed using this matrix with that of the associative memory in exercise 2.

4. Build and study a simple model of oscillations arising from the interaction of excitatory and inhibitory populations of neurons. The firing rate of the excitatory neurons is  $r_E$ , and that of the inhibitory neurons is  $r_I$  and these are characterized by equations 7.50 and 7.51. Set  $M_{EE} = 1.25$ ,  $M_{IE} = 1$ ,  $M_{II} = M_{EI} = -1$ ,  $\gamma_E = -10$  Hz,  $\gamma_I = 10$  Hz,  $\tau_E = 10$  ms, and vary the value of  $\tau_I$ . The negative value of  $\gamma_E$  means that this parameter serves as a source of background activity (activity in the absence of excitatory input) rather than as a threshold. Show what happens for  $\tau_I = 30$  ms and for  $\tau_I = 50$  ms. Find the value of  $\tau_I$  for which there is a transition between fixed-point and oscillatory behavior, thereby verifying the results obtained analytically in chapter 7 on the basis of equation 7.53.
5. MATLAB® files `c7p5.m` and `c7p5sub.m` perform a numerical integration of a two-unit, nonlinear, symmetric recurrent network with a threshold linear activation function  $F(I) = \beta[I]_+$  and plot the results. Here, the dynamics come from

$$\frac{d\mathbf{v}}{dt} = -\mathbf{v} + \mathbf{F}(\mathbf{M} \cdot \mathbf{v} + \mathbf{h})$$

with  $\mathbf{v} = (v_1, v_2)$  and  $h_1 = h_2$ . The weight matrix in this example is  $\mathbf{M} = [0 \ -1; -1 \ 0]$ , which tends to make  $v_1$  and  $v_2$  compete. Execute `c7p5.m` to see the consequences of regimes of high ( $\beta = 2$ ) and low ( $\beta = 0.5$ ) activation (which is equivalent to large and small recurrent weights). For these two values of  $\beta$ , plot the nullclines (the locations in the  $v_1$ - $v_2$  phase plane where  $dv_1/dt = 0$  and  $dv_2/dt = 0$ ). You should find one fixed point for  $\beta = 0.5$  and three for  $\beta = 2$ . Linearize the network about the fixed point with  $v_1 = v_2$  and derive a condition on  $\beta$  for this fixed point to be stable. (Based on a problem from Dawei Dong.)

6. Plot the results of exercise 5 for the inputs  $\mathbf{h} = (0.75, 1.25)$  and  $\mathbf{h} = (0.5, 1.5)$ . By plotting nullclines for these values of  $\mathbf{h}$ , explain the resulting behavior. (Based on a problem from Dawei Dong.)
7. Use the expression

$$f_u(s - \xi, g - \gamma) = A \exp\left(-\frac{(s - \xi)^2}{2\sigma_s^2}\right) N\left(\frac{g - \gamma}{\sigma_g}\right),$$

where  $A$ ,  $\xi$ ,  $\sigma_s$ ,  $\gamma$ , and  $\sigma_g$  are parameters and  $N$  is the (sigmoidal) cumulative normal function

$$N(z) = \int_{-\infty}^z dx \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{x^2}{2}\right) = 1 - \frac{1}{2} \operatorname{erfc}\left(\frac{z}{\sqrt{2}}\right).$$

Plot  $f_u(s - \xi, g - \gamma)$  and find values of the parameters that make it roughly match the gain-modulated response of figure 7.6B. Using  $w(\xi, \gamma) = \exp(-(\xi + \gamma)^2/2\sigma_w^2)$ , evaluate the integral in equation 7.15 in terms of a single cumulative normal function to show that the resulting tuning curves are functions of  $s + g$ , and assess how the tuning width depends on  $\sigma_s$ ,  $\sigma_g$  and  $\sigma_w$ .