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6 Stimulus-Invariant Tuning by Neurons and the 'Ring' Model of Recurrent Interactions. Part 1

We now consider a particular model, the so called "ring" model, as a demonstration of how recurrent connections and the threshold in the (piece-wise linear) gain curve can lead to a powerful computation.

6.1 Rate model

We will write our equations for motion over the full range of 2π radians, which is suitable to describe heading, as described previously. A similar set of equations can be written for the case of orientation, except that this covers π radians. Every neuron is labeled with an index, "i", that refers to the angle of the heading that is most likely to cause the cell to spike. This is the "preferred heading" and we assume that these are uniformly distributed across a sea of neurons, so that

$$\phi_i = \frac{2\pi}{N} i \ \ \forall i \tag{6.1}$$

where N is the total number of neurons. The rate equation for a neuron with preferred heading ϕ_i is

$$\tau \ \frac{dr_i(t)}{dt} + r_i(t) \ = \ f \left[\frac{1}{N} \sum_{j=1}^{N} W(\phi_i, \phi_j) \ r_j(t) \ + \ I^{ext}(\phi_i, \phi_0, t) \ - \ \theta \right] \tag{6.2}$$

where $W(\phi_i, \phi_j)$ is the interaction between cell i and cell j, ϕ_0 is the orientation of a vector to the landmark (for heading) or of an external edge (for coding in vision), and θ is the threshold for spiking. The function $f[\cdot]$ is a nonlinear function that saturates at zero and possibly at a maximum firing rate. One such model is a logistic function.

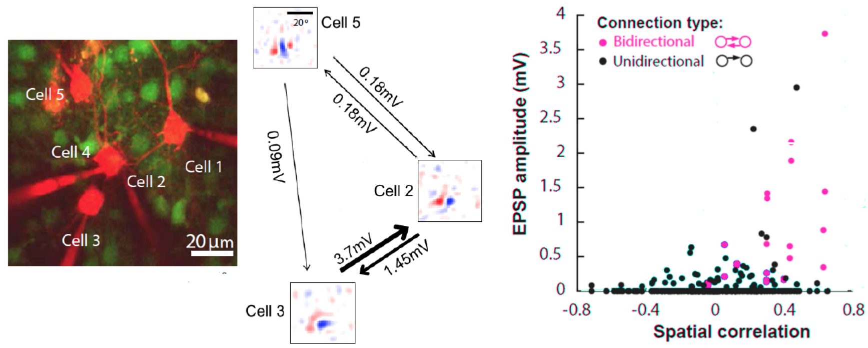
Motivated by experimental observations in visual systems (Figure 1) and heading systems, we take the interactions to be a function of the difference in orientation preference angles, so that neurons with similar orientation preference have relatively stronger connections. Thus

$$W(\phi_i, \phi_j) = W(\phi_i \ - \ \phi_j) \tag{6.3}$$

and

$$I^{ext}(\phi_i, \phi_0, t) = I^{ext}(\phi_i - \phi_0, t). \tag{6.4}$$

Figure 1: Connectivity among neurons in mouse V1 cortex is stronger for cells with overlapping receptive fields. From Cossell, Iacaruso, Muir, Houlton, Sader, Ko, Hofer and Mrsic-Flogel 2015.



We will write the interaction in terms of a constant term plus one term that varies as a function of the in-plane heading preference between two cells. Thus

$$W(\phi_i - \ \phi_j) = W_0 \ + \ W_1 \, cos \, (\phi_i - \phi_j) \tag{6.5}$$

where W_0 and W_1 are constants. We consider only the *cosine* term and thus the connections should be symmetric with respect to the difference in orientation preference (Figure 2). Similarly, the experimental stimulus can be written in terms of a constant and an orientation dependent term

$$I(\phi_i - \phi_0, t) = \hat{I}_0(t) \ + \ \hat{I}_1(t) \, cos \, (\phi_i - \phi_0) \, . \tag{6.6}$$

The *cosine* is the leading term for the projection of a moving bar on a linear array of center-surround detectors. One can add higher order terms, as a Fourier series in $(\phi_i - \phi_0)$ to describe more complicated (and realistic) patterns of connectivity, but the basic lessons will be unchanged.

It will be useful to re-express this in terms of an overall drive and a modulation, $\epsilon(t)$, of the drive, i.e.,

$$I(\phi_i - \phi_0, t) = I_0(t) \, (\, 1 \ + \ \epsilon(t) \, [1 \ + \ cos \, (\phi_i \ - \ \phi_0)] \,) \tag{6.7}$$

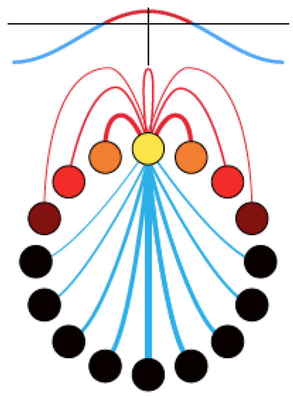
where, for completeness, $\hat{I}_0(t) = I_0(t)[1 + \epsilon(t)]$ and $\hat{I}_1(t) = I_0(t)\epsilon(t)$. Putting all of this together yields a rate equation as a function of orientation and time

$$\tau \, \frac{dr(\phi, t)}{dt} + r(\phi, t) = \quad f \quad \{ \, \frac{W_0}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) \tag{6.8}$$

$$
\begin{aligned}
&+ \frac{W_1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t) cos\,(\phi-\phi') \\
&+ I_0(t)\,[1+\epsilon(t)] \\
&+ I_0(t)\epsilon(t)\; cos\,(\phi-\phi_0) \;-\; \theta \,\}
\end{aligned}
$$

where $\frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi'$ replaces $\frac{1}{N}\sum_{j=1}^{N}$.

Figure 2: Connectivity among neurons from W_0 multiplying a constant term and W_1 multiplying a cosine term.



6.1.1 Mean field approach

We solve the coupled rate equations by introducing two parameters, referred to as "order parameters", that will represent the mean activity of the network and the modulation of the activity of the network. This will allow us to write a single equation for the network in terms of the behavior of one neuron in terms of the mean rate of spiking and the modulation of that rate. These new parameters must evaluated in a self consistent manner.

Mean rate: We define $r_0(t)$ as the average firing rate of neurons in the network. This order parameter is an average over ϕ, i.e.,

$$
r_0(t) \;=\; \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t) \tag{6.9}
$$

Thus the W_0 term is just $r_0(t)$,

Modulated rate: We define $r_1(t)$ as the average modulation of the firing rate of neurons in the network. This order parameter is a complex number, so we write it as:

$$
\begin{aligned}
r_1(t) \;&\equiv\; |r_1(t)|e^{-i\psi(t)} \\
&=\; \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t)\; e^{-i\phi'}
\end{aligned} \tag{6.10}
$$

This allows us to evaluate the W_1 term as

$$\begin{aligned}
\frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t)\ cos\,(\phi-\phi') &= \Re\{\frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t) e^{i(\phi-\phi')}\} \\
&= \Re\{e^{i\phi}\ \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi',t) e^{-i\phi'}\} \\
&= \Re\{e^{i\phi}\ |r_1(t)| e^{-i\psi(t)}\} \\
&= |r_1(t)|\ \Re\{e^{i(\phi-\psi(t))}\} \\
&= |r_1(t)|\ cos\,(\phi-\psi(t)) \qquad (6.11)
\end{aligned}$$

where $\Re$ means real part.

The mean field rate equation is thus

$$\begin{aligned}
\tau\ \frac{dr(\phi,t)}{dt} + r(\phi,t) &= f\{\ W_0 r_0(t)\ +\ W_1|r_1(t)|\ cos\,(\phi-\psi(t)) \qquad (6.12) \\
&\quad +\ I_0(t)\,(1\ +\ \epsilon(t))\ +\ I_0(t)\epsilon(t)\ cos\,(\phi-\phi_0))\ -\ \theta\}.
\end{aligned}$$

Now we have three simpler requations to solve.

6.2 Equilibrium

The goal is to understand how the network dynamics can amplify a signal so that a weak input can drive a full cortical response. Can this goal can be achieved under static conditions?

The rate equation becomes

$$r(\phi) = f\{W_0 r_0 + W_1|r_1| cos\,(\phi-\psi)) + I_0\,(1+\epsilon) + I_0\ \epsilon\ cos(\phi-\phi_0) - \theta\}. \qquad (6.13)$$

So long as the gain function "$f[\cdot]$" is monotonic, the output will be maximized by maximizing the operant. We make the assumption that ψ is chosen to maximize the firing rate, i.e.,

$$\begin{aligned}
\frac{dr(\phi)}{d\psi}|_{\phi=\phi_0} &= W_1|r_1| sin\,(\phi-\psi) \qquad (6.14) \\
&= 0
\end{aligned}$$

This gives $\psi = \phi_0$ and the steady state rate equation becomes

$$r(\phi) = f\{[W_0 r_0 + I_0(1+\epsilon) - \theta]\ +\ [W_1|r_1| + I_0\ \epsilon]\ cos(\phi-\phi_0)\} \qquad (6.15)$$

where we have clustered the input into constant pieces and pieces that are modulated by orientation.

6.2.1 Superthreshold (linear) limit

Lets see what happens when the inputs are sufficiently large so that the neuron operates solely above threshold. We thus take $f[x] = x$. Then

$$r(\phi) = [W_0 r_0 + I_0(1+\epsilon) - \theta] \ + \ [W_1|r_1| + I_0\epsilon]\, cos(\phi - \phi_0). \quad (6.16)$$

The functional dependence of $r(\phi)$ must follow the drive and thus vary as $\phi - \phi_0$. We can expend $r(\phi)$ as a Fourier series with coefficients that are identical to the order parameters, i.e.,

$$\tilde{r}(\phi) = r_0 \ + \ r_{+1}e^{i\phi} \ + \ r_{-1}e^{-i\phi} \quad (6.17)$$

where

$$r_0 \ \equiv \ \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi'), \quad (6.18)$$

$$\begin{aligned} r_{+1} \ &= \ \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi', t)\ e^{-i\phi'} \\ &\equiv \ |r_{+1}|e^{-i\psi(t)}. \end{aligned} \quad (6.19)$$

and

$$\begin{aligned} r_{-1} \ &= \ \frac{1}{2\pi}\int_{-\pi}^{\pi} d\phi' r(\phi', t)\ e^{i\phi'} \\ &\equiv \ |r_{+1}|e^{i\psi(t)}. \end{aligned} \quad (6.20)$$

Then

$$\begin{aligned} \tilde{r}(\phi) \ &= \ r_0 \ + \ |r_{+1}| \left(e^{-i(\psi(t)-\phi)} + e^{i(\psi(t)-\phi)}\right) \\ &= \ r_0 \ + \ 2|r_{+1}|cos(\phi \ - \ \psi) \\ &= \ r_0 \ + \ 2|r_{+1}|cos(\phi \ - \ \phi_0). \end{aligned} \quad (6.21)$$

where we recall that ψ is chosen as $\psi = \phi_0$ to maximize the firing rate.

We now equate terms for the average and for the harmonic, i.e.,

$$r_0 = W_0 r_0 + I_0(1+\epsilon) - \theta \quad (6.22)$$

or

$$r_0 = \frac{I_0(1+\epsilon) - \theta}{1 - W_0} \quad (6.23)$$

and

$$r_1 = \frac{W_1 r_1 + I_0\epsilon}{2}. \quad (6.24)$$

or

$$r_1 = \frac{I_0\epsilon}{2 - W_1}. \quad (6.25)$$

We see that, even for the linear case, there is the potential for gain in the modulation term when $W_1 \to 2$. We put all of the above together to write

$$\tilde{r}(\phi) = I_0 \left[\frac{1+\epsilon}{1-W_0} \; + \; \frac{2\epsilon}{2-W_1} cos(\phi \; - \; \phi_0) \right] \tag{6.26}$$

where we took $\theta = 0$ in the last step solely for clarity.

How does this response help in altering the output of the network? To make a bit more progress, we write the selectivity of the input for modulated activity as

$$\begin{aligned} \textbf{Selectivity of input} \quad &\equiv \quad \frac{\hat{I}_1}{\hat{I}_0} \\ &= \quad \frac{\epsilon}{1+\epsilon} \end{aligned} \tag{6.27}$$

and note that we can write the selectivity of the output as

$$\begin{aligned} \textbf{Selectivity of output} \quad &\equiv \quad \frac{|r_1|}{r_0} \\ &= \quad \frac{I_0 \, \epsilon}{2-W_1} \frac{1-W_0}{I_0(1+\epsilon)} \\ &= \quad \frac{1-W_0}{2-W_1} \times \textbf{Selectivity of input}. \end{aligned} \tag{6.28}$$

This is as far as linearity gets you. There is gain, and potentially very large gain, but *no* invariance! We will encounter this kind of relation again when we discuss the linear circuit for the control of eye position.

In the linear case, the input determines the output. Thus the choice $\epsilon = 0$ will lead to $r_1 = 0$ and no modulation of the neuronal activity, despite the angular dependence of the interactions. In the next lecture we will see how to introduce an angular dependence to the activity, a bump along ϕ, by allowing for nonlinearity in the gain functions and the $W_1 > 2$.