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

We now consider a particular model, the ”ring” model, as a demonstration of how recurrent connections and the threshold in the gain curve can lead to a powerful computation.

5.1 Rate model

We will write our equations for motion over the full range of $2\pi$ radians, which is suitable to describe heading. A similar set of equations can be written for the case of orientation, except that this covers $\pi$ 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, so that

$$\phi_i = \frac{2\pi}{N} i \quad \forall i$$  \hspace{1cm} (5.5)

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

$$\tau \frac{r_i(t)}{dt} + r_i(t) = f \left[ \frac{1}{N} \sum_{j=1}^{N} W(\phi_i, \phi_j) r_j(t) + I^{ext}(\phi_i, \phi_0, t) - \theta \right]$$  \hspace{1cm} (5.6)

where $W(\phi_i, \phi_j)$ is the interaction between cell $i$ and cell $j$, $\phi_0$ is the orientation of the external edge, and $\theta$ is the threshold for spiking. The function $f$ is a nonlinear function that saturates at zero and at a maximum firing rate. One such model is a logistic function. Without loss of generality, we take the maximum rate to be 1.

Motivated by experimental observations in visual systems 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 $W(\phi_i, \phi_j) = W(\phi_i - \phi_j)$ and $I^{ext}(\phi_i, \phi_0, t) = I^{ext}(\phi_i - \phi_0, t)$.

The experimental stimulus can be written in terms of a constant and an orientation dependent term

$$I(\phi_i - \phi_0, t) = \hat{I}_0(t) + \hat{I}_1(t) \cos (\phi_i - \phi_0)$$  \hspace{1cm} (5.7)

The cosine is the leading term for the projection of a long moving bar on a linear array of center-surround detectors. It will be useful to re-express this expression in terms of an overall drive and a modulation, $\epsilon(t)$, of the drive, i.e.,

$$I(\phi_i - \phi_0, t) = I_0(t) [1 + \epsilon(t) (1 + \cos (\phi_i - \phi_0))]$$  \hspace{1cm} (5.8)
where, for completeness, $\hat{I}_0(t) = I_0(t)[1 + \epsilon(t)]$ and $\hat{I}_1(t) = I_0(t)\epsilon(t)$.

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 the reference point, or landmark, and the orientation preference of the neuron, $\phi_i$. Thus

$$W(\phi_i - \phi_j) = W_0 + W_1 \cos(\phi_i - \phi_j) \quad (5.9)$$

where $W_0$ and $W_1$ are constants and we have the interactions follow the form of the stimulus, i.e., we only consider only the cosine term and the connections should be symmetric with respect to the difference in orientation preference. Putting all of this together yields a rate equation as a function of orientation and time

$$\tau \frac{dr(\phi, t)}{dt} + r_i(\phi, t) = f\left\{ \frac{W_0}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) + \frac{W_1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t)\cos(\phi - \phi') + I_0(t)[1 + \epsilon(t)] + I_0(t)\epsilon(t) \cos(\phi - \phi_0) - \theta \right\} \quad (5.10)$$

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.

5.1.1 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
be evaluated in a self consistent manner.

**Mean rate:** We define \( r_0(t) \) as the average firing rate of neurons in the network as
an average over \( \phi \), i.e.,

\[
r_0(t) = \frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t)
\]

(5.11)

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

\[
r_1(t) = |r_1(t)| e^{-i\psi(t)}
\]

(5.12)

This allows us to evaluate the \( W_1 \) term as

\[
\frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) \cos (\phi - \phi') = \Re \{ \frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) e^{i(\phi-\phi')} \}
\]

(5.13)

\[
= \Re \{ e^{i\phi} \frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) e^{-i\phi'} \}
\]

\[
= \Re \{ e^{i\phi} |r_1(t)| e^{-i\psi(t)} \}
\]

\[
= |r_1(t)| \Re \{ e^{i(\phi-\psi(t))} \}
\]

\[
= |r_1(t)| \cos (\phi - \psi(t))
\]

where \( \Re \) means real part.

The mean field rate equation is thus

\[
\tau \frac{dr(\phi, t)}{dt} + r(\phi, t) = f\{ W_0 r_0(t) + W_1 |r_1(t)| \cos (\phi - \psi(t)) + I_0(t) (1 + \epsilon(t)) + I_0(t)\epsilon(t) \cos (\phi - \phi_0) - \theta \}
\]

(5.14)

### 5.2 Steady state

The goal is to understand how the network dynamics can amplify a signal so that
a weak input can drive a full cortical response. This goal can be achieved in steady
state. The rate equation becomes

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

(5.15)
So long as the gain function "$f$" is monotonic, the output will be maximized by maximizing the operant. We make the assumption that $\psi$ is chosen to maximize the firing rate, i.e.,

$$\frac{dr(\phi)}{d\psi}|_{\phi=\phi_0} = W_1 |r_1| \sin(\phi - \psi)$$

$$= 0$$

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

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

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

### 5.2.1 Superthreshold (linear) limit

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

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

The functional dependence of $r(\psi)$ 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.,

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

where

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

$$r_{+1} = \frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) e^{-i\phi'}$$

$$\equiv |r_{+1}| e^{-i\psi(t)}.$$

and

$$r_{-1} = \frac{1}{2\pi} \int_{-\pi}^{\pi} d\phi' r(\phi', t) e^{i\phi'}$$

$$\equiv |r_{+1}| e^{i\psi(t)}.$$

Then

$$\tilde{r}(\phi) = r_0 + |r_{+1}| \left(e^{i\phi'} + e^{-i\phi'}\right)$$

$$= r_0 + 2|r_{+1}| \cos(\phi - \psi)$$

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

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

$$= 0$$

This is the steady state rate equation.
or
\[ r_0 = \frac{I_0(1 + \epsilon) - \theta}{1 - W_0} \] (5.25)

and, recalling that \( \psi \) is chosen to maximize the firing rate so that \( \psi = \phi_0 \),
\[ r_1 = \frac{W_1 r_1 + I_0 \epsilon}{2} \] (5.26)
or
\[ r_1 = \frac{I_0 \epsilon}{2 - W_1} \] (5.27)

We see that, even for the linear case, there is the potential for gain in the modulation term when \( W_1 \rightarrow 2 \). We put all of the above together to write
\[ \tilde{r}(\phi) = I_0 \left( \frac{1 + \epsilon}{1 - W_0} + \frac{2\epsilon}{2 - W_1} \cos(\phi - \phi_0) \right) \] (5.28)

where we took \( \theta = 0 \) in the last step solely for clarity. How does this gain help in altering the output of the network? To make a bit more progress, we can write the selectivity of the input for modulated activity as
\[ \text{Selectivity of input} \equiv \frac{\hat{I}_1}{I_0} = \frac{\epsilon}{1 + \epsilon} \] (5.29)

and note that we can write the selectivity of the output as
\[ \text{Selectivity of output} \equiv \frac{|r_1|}{r_0} = \frac{I_0}{2 - W_1} \frac{1 - W_0}{I_0(1 + \epsilon)} \] (5.30)
\[ = \frac{1 - W_0}{2 - W_1} \times \text{Selectivity of input.} \]

This is as far as linearity gets you. Gain, and potentially very large gain, but no invariance! we will encounter this kind of relation again when we discuss another 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 \( \phi \), by allowing for nonlinearity in the gain functions and the \( W_1 > 2 \).