

# Summary

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## 1. Introduction

Multisensory integration and segregation are distinctly important for the survivorship of higher animals. The experimental data shows that the brain process information in a Bayesian way. The model proposed by Wenhao has demonstrate two different neuron groups are relate to the multisensory integration and segregation simultaneously. However, the details of the dynamics of this neuron system remain unknown. In this paper we will discuss the conditions of this neuron network using Bayesian inference to process complementary information.

## 2. Model

The neural circuit consists of two modules, each of them contains two groups of excitatory neurons, congruent and opposite neurons respectively. The synaptic input of congruent groups and opposite groups are denoted as  $\psi_m(y, t)$  and  $\bar{\psi}_m(y, t)$  respectively, where  $m = 1, 2$  is the module index and  $y$  represents the preferred heading direction. The recurrent connections is a von Mises function:  $J_{rc} = \frac{e^{a_0 \cos(y-y')}}{2\pi I_0(a_0)}$ , where  $J_{rc}$  and  $a_0$  represent the strength and width of the connection. There are two types of reciprocal couplings between different modules. For congruent groups, the coupling function is given by  $J_{rp} = \frac{e^{a_0 \cos(y-y')}}{2\pi I_0(a_0)}$ , however, the coupling function of opposite groups ia  $J_{rp} = \frac{e^{a_0 \cos(y-y'+\pi)}}{2\pi I_0(a_0)}$ . The firing rate is determined by synaptic inputs and divisive normalization,  $\frac{[\psi_m(y, t)]_+^2}{1 + \omega D_m}$ , where  $[x]_+ = \max(x, 0)$ .  $D_m$  denotes normalization pool,  $D_m = \sum_{-\pi}^{\pi} ([\psi_m]_+^2 + J_{int}[\bar{\psi}]_+^2)$ . The neuronal dynamics of congruent groups is given by

$$\tau \frac{\partial \psi_m(y, t)}{\partial t} = -\psi_m(y, t) + \frac{J_{rc}}{D_m} \sum_{-\pi}^{\pi} V(y - y', a_0) \psi^2(y') + \frac{J_{rp}}{D_{\bar{m}}} \sum_{-\pi}^{\pi} V(y - y', a_0) \bar{\psi}^2(y') + I_1 V(y - x, a_0/2) + I_b \quad (1)$$

Where  $\bar{m}$  denotes the complementary index. For opposite groups

$$\tau \frac{\partial \bar{\psi}_m(y, t)}{\partial t} = -\bar{\psi}_m(y, t) + \frac{J_{rc}}{\bar{D}_m} \sum_{-\pi}^{\pi} V(y - y', a_0) \bar{\psi}^2(y') + \frac{J_{rp}}{\bar{D}_{\bar{m}}} \sum_{-\pi}^{\pi} V(y - y' + \pi, a_0) \bar{\psi}^2(y') + I_1 V(y - x, a_0/2) + I_b \quad (2)$$

## 3. Basic Functions

Basically we have an intuition to construct a set of von Mises basic functions. First we define  $N_n(k)$

$$N_n(k) = \int_{-\pi}^{\pi} e^{k \cos \theta} \sin^n \theta d\theta$$

Then we integrate by parts and make use of the property of periodical functions, we obtain iterative expression for  $N_n(k)$

$$\begin{aligned}
N_n(k) &= \int_{-\pi}^{\pi} e^{k \cos \theta} \sin^n \theta d\theta \\
&= \frac{n-1}{k} \int_{-\pi}^{\pi} e^{k \cos \theta} \sin^{n-2} \theta \cos \theta d\theta \\
&= \frac{n-1}{k^2} \int_{-\pi}^{\pi} e^{k \cos \theta} [(n-3) \sin^{n-4} \theta \cos^2 \theta - \sin^{n-2} \theta] d\theta \\
&= \frac{(n-1)(n-3)}{k^2} N_{n-4}(k) - \frac{(n-1)(n-2)}{k^2} N_{n-2}(k)
\end{aligned}$$

The first few terms are derived below

$$\begin{aligned}
N_0(k) &= 2\pi I_0(k) \\
N_2(k) &= \frac{2\pi I_1(k)}{k} \\
N_4(k) &= \frac{6\pi}{k^2} \left[ I_0(k) - \frac{2I_1(k)}{k} \right] \\
N_6(k) &= \frac{30\pi}{k^3} \left[ -\frac{4}{k} I_0(k) + \left(1 + \frac{8}{k^2}\right) I_1(k) \right]
\end{aligned}$$

Where  $I_n(k)$  is the modified Bessel function of the first kind.  $N'_n(k)$  denotes the differential coefficient of  $N_n(k)$ .

### 3.1. Recursive Relation

We define  $u_0 = C_0 e^{k \cos \theta}$  as the zeroth order normalized basic function, and we notice the inner production

$$\langle u_0, u_0 \sin \theta \rangle = 0$$

Hence we obtain the first order basic function  $u_1 = C_1 u_0 \sin \theta$ , where  $C_1$  is a normalization factor. Furthermore, we define the second order basic function

$$u_2 = C_2 (u_1 \sin \theta - u_0 \langle u_0, u_1 \sin \theta \rangle)$$

Since  $u_2$  is an even function,  $u_2$  is orthogonal to  $u_1$ . We can prove  $\langle u_2, u_0 \rangle$ .

Suppose we have a set of basic functions satisfying the following conditions

$$\begin{aligned}
\langle u_i, u_j \rangle &= \delta_{i,j} \\
\langle u_i, u_j \sin \theta \rangle &= r_{j-1} \delta_{i,j-1} + r_j \delta_{i,j+1}
\end{aligned}$$

Where  $i, j = 0, 1, 2, \dots, N-1$ , we define  $r_i = \langle u_i, u_{i+1} \sin \theta \rangle$ .  $u_n$  is given by

$$u_n = C_N (u_{N-1} \sin \theta - u_{N-2} \langle u_{N-2}, u_{N-1} \sin \theta \rangle)$$

When  $i < N$ , we can prove

$$\begin{aligned}
\langle u_i, u_N \rangle &= C_N [\langle u_i, u_{N-1} \sin \theta \rangle - \langle u_i, u_{N-2} \rangle \langle u_{N-2}, u_{N-1} \sin \theta \rangle] \\
&= C_N [r_{N-2} \delta_{i,N-2} + r_{N-2} \delta_{i,N} - r_{N-2} \delta_{i,N-2}] \\
&= 0
\end{aligned}$$

We have recursive relation

$$u_i \sin \theta = r_{i-1} u_{i-1} + r_i u_{i+1}$$

Refer to Completeness of Fourier Expansion by Jeremy Orloff, the completeness of this set of basic function is easy to be proved. We can construct a delta function in this way

$$h(\theta) = c_k e^{k_0(\cos \theta - 1)} (1 - \sin^2 \theta)^k \text{ when } k \rightarrow \infty$$

Where  $c_k$  is chosen to make sure  $\int_{-\pi}^{\pi} h(\theta) d\theta = 1$ . Note that the delta function  $h(\theta)$  is a linear combination of  $e^{k_0 \cos \theta} \sin^n \theta$ , and  $e^{k_0 \cos \theta} \sin^n \theta$  could be written by a linear combination of our basic functions.

The first few terms are derived below

$$\begin{aligned} u_0 &= c_0 e^{k \cos \theta} \\ u_1 &= c_1 e^{k \cos \theta} \sin \theta \\ u_2 &= c_2 e^{k \cos \theta} \left[ \sin^2 \theta - \frac{N_2(2k)}{N_0(2k)} \right] \\ u_3 &= c_3 e^{k \cos \theta} \left[ \sin^3 \theta - \frac{N_4(2k)}{N_2(2k)} \sin \theta \right] \end{aligned}$$

The coefficient  $c_i$   $i = 0, 1, 2, \dots$  are listed

$$\begin{aligned} c_0 &= \frac{1}{\sqrt{N_0(2k)}} \\ c_1 &= \frac{1}{\sqrt{N_2(2k)}} \\ c_2 &= \frac{1}{\sqrt{N_4(2k) - \frac{N_2^2(2k)}{N_0(2k)}}} \\ c_3 &= \frac{1}{\sqrt{N_6(2k) - \frac{N_4^2(2k)}{N_2(2k)}}} \end{aligned}$$

Furthermore, we have

$$r_i = \frac{c_i}{c_{i+1}} \quad i = 0, 1, 2, \dots$$

### 3.2. Convolution

However, the convolution of two basic functions is hard to calculate. First we define

$$\begin{aligned} M_{m,n}(\theta, k_1, k_2) &= \int_{-\pi}^{\pi} e^{k_1 \cos(\theta - \theta')} \sin^m(\theta - \theta') e^{k_2 \sin \theta'} \sin^n \theta' d\theta' \\ T_{m,n}(\theta, k_1, k_2) &= \int_{-\pi}^{\pi} e^{k_1 \cos(\theta - \theta')} e^{k_2 \sin \theta'} \sin^m(\theta - \theta') \cos(\theta - \theta') \sin^n \theta' d\theta' \end{aligned}$$

Our calculation base on the approximation

$$M_{0,0}(\theta, k_1, k_2) = \int_{-\pi}^{\pi} e^{k_1 \cos(\theta - \theta')} e^{k_2 \sin \theta'} d\theta' \approx \frac{2\pi I_0(k_1) I_0(k_2)}{I_0(k_3)} e^{k_3 \cos \theta}$$

Where  $A(k) = \frac{I_1(k)}{I_0(k)}$ ,  $k_3 = A^{-1}(A(k_1)A(k_2))$ . Take derivative of  $M_{0,0}$  with respect to  $k_1$ , we have  $T_{0,0} \approx e^{k_3 \cos \theta} \left[ F'(k_1) + F \frac{\partial k_3}{\partial k_1} \cos \theta \right]$ , where  $F(k_1, k_2) = \frac{2\pi I_0(k_1)I_0(k_2)}{I_0(k_3)}$ ,  $\frac{\partial k_3}{\partial k_1} = \frac{A'(k_1)A(k_2)}{A'(k_3)}$ . We can derive convolution systematically. Take derivative of  $M_{m,0}$

$$\frac{\partial M_{m,n}}{\partial \theta} = mT_{m-1,n} - k_1 M_{m+1,n}$$

That allow us to find  $M_{m+1,n}$ . We take derivative of  $T_{m,n}$  with respect to  $\theta$ , we obtain

$$\frac{\partial T_{m,n}}{\partial \theta} = -k_1 T_{m+1,n} + m M_{m-1,n} - (m+1) M_{m+1,n}$$

We will find  $T_{m+1,n}$ . We start from  $T_{0,0}$  and  $M_{0,0}$ , consider the symmetry we have

$$M_{m,n}(\theta, k_1, k_2) = M_{n,m}(\theta, k_2, k_1)$$

For  $T_{m,n}$ , we have

$$\begin{aligned} T_{m,n}(k_1, k_2) &= \int_{-\pi}^{\pi} e^{k_1 \cos(\theta - \theta')} e^{k_2 \sin \theta'} \sin^m(\theta - \theta') \cos(\theta - \theta') \sin^n \theta' d\theta' \\ &= \cos \theta T_{n,m}(k_2, k_1) + \sin \theta M_{m,n+1}(k_1, k_2) \end{aligned}$$

That allow us to find  $T_{0,n}$   $n = 1, 2, \dots$  starting from  $T_{0,0}$ .

### 3.3. Approximation

Actually this approximation of von Mises convolution may not as accurate as we expect. For instance

$$Solution = \int_{-\pi}^{\pi} e^{2k \cos \theta} \sin^2 \theta d\theta = N_2(2k) = \frac{\pi I_1(2k)}{k}$$

$$Approximation \approx -M_{1,1}(0, k, k) = \frac{2\pi k_3 I_0^2(k) e^{k_3}}{k^2 I_0(k_3)}$$

Where  $k_3 = A^{-1}[A(k)^2]$ . The percentage error is close to 40% when  $2 < k < 3$ . It works perfectly when  $k$  is approaching infinity.

There are two way to solve the problem. One is to modified this approximation. We know the integration

$$\int_{-\pi}^{\pi} e^{k_1 \cos(\theta - \theta')} e^{k_2 \cos \theta'} d\theta' = 2\pi I_0(\sqrt{k_1^2 + k_2^2 + 2k_1 k_2 \cos \theta})$$

Previously, the Bessel function is approximated by

$$I_0(\sqrt{k_1^2 + k_2^2 + 2k_1 k_2 \cos \theta}) \approx \frac{I_0(k_1)I_0(k_2)}{I_0(k_3)} e^{k_3 \cos \theta} \text{ where } k_3 = A^{-1}[A(k_1)A(k_2)]$$

For convenience, we take the log of both sides. Note  $k = \sqrt{k_1^2 + k_2^2 + 2k_1 k_2 \cos \theta}$ . The following paragraph will compare our approximation with  $\ln(I_0(k))$ .

In order to have a von Mises form approximation, suppose  $\ln(I_0(k))$  could be approximated by  $d + h \cos(f\theta)$ .

We expand  $\ln(I_0(k))$ , consider first three terms only

$$\ln(I_0(k)) \approx \frac{b_0}{2} + b_1 \cos \theta + b_2 \cos 2\theta$$

Where  $b_i = \frac{1}{\pi} \langle \ln(I_0(k)), \cos(i\theta) \rangle$   $i = 0, 1, 2$

$$\frac{b_0}{2} + b_1 \cos \theta + b_2 \cos 2\theta \approx d + h \cos(f\theta)$$

Multiply both sides by  $\cos(i\theta)$ , integrate over  $\theta$ , we get the solution

$$\begin{aligned} f &= \sqrt{\frac{4b_2 + b_1}{b_2 + b_1}} \\ h &= \frac{\pi b_1 (1 - f^2)}{2f \sin(\pi f)} \\ d &= \frac{b_0}{2} - \frac{b_1 (1 - f^2)}{2f^2} \end{aligned}$$

This approximation is more accurate than previous one if we still want a von Mises form basic functions. Given  $k_1$  and  $k_2$ , we calculate  $f$   $h$   $d$  respectively.  $F = \frac{e^d}{2\pi I_0(k_1) I_0(k_2)}$  and  $k_3 = h$  represent the coefficient and concentration. So the convolution of two von Mises functions is still a von Mises function.

$$\int_{-\pi}^{\pi} V(\theta - \theta', k_1) V(\theta', k_2) d\theta' \approx F(k_1, k_2) V(f\theta, k_3)$$

The other way is to switch to Fourier basic functions. We are handling the case when concentration is comparatively small ( $k \leq 3$ ), it's more suitable for us to choose Fourier series when applying projection method.

#### 4. Projection Method

Suppose the solution to steady state equations is a linear combination of Fourier series

$$\psi_{1c} = u_0 + u_1 \cos(y_1 - s_1) + u_2 \cos 2(y_1 - s_1) + u_3 \sin 2(y_1 - s_1)$$

For congruent groups, the steady state equation is given by

$$\begin{aligned} \psi(y_1) &= \frac{\rho J_{rc}}{D_1} \int dy_2 V(y_1 - y_2, a_0) \psi^2(y_2) + \frac{\rho J_{rp}}{D_2} \int dy_2 V(y_1 - y_2, a_0) \bar{\psi}^2(y_2) \\ &\quad + I_1 V(y_1 - x_1, \frac{a_0}{2}) + I_b \end{aligned} \quad (3)$$

Referring to inhibition pool,  $D_m$  could be replace by integration

$$D_m = 1 + \omega \int \rho [u_m^2(x, k) + J_{int} \bar{u}_m^2(x, k)] dx$$

$D_m = 1 + \pi \omega \rho [2u_0^2 + u_1^2 + u_2^2 + u_3^2 + J_{int} (2\bar{u}_0^2 + \bar{u}_1^2 + \bar{u}_2^2 + \bar{u}_3^2)]$ . Furthermore we define  $B(n, k) = \frac{I_n(k)}{I_0(k)}$ . Multiply the steady state equation's both sides by  $1 \cos(y_1 - s_1) \sin(y_1 - s_1) \cos 2(y_1 - s_1) \sin 2(y_1 - s_1)$  and integrate over  $y_1$ , we obtain different dynamic equations of each mode respectively.

$$\begin{aligned}
u_{10} &= \frac{\rho J_{rc}}{D_1} \left[ u_{10}^2 + \frac{u_{11}^2}{2} + \frac{u_{12}^2}{2} + \frac{u_{13}^2}{2} \right] + \frac{\rho J_{rp}}{D_2} \left[ u_{20}^2 + \frac{u_{21}^2}{2} + \frac{u_{22}^2}{2} + \frac{u_{23}^2}{2} \right] + \frac{I_1}{2\pi} + I_b \\
u_{11} &= \frac{\rho J_{rc}}{D_1} B(1, a_0) [2u_{10}u_{11} + u_{11}u_{12}] + \frac{I_1 B(1, a_0/2)}{\pi} \cos(x_1 - s_1) \\
&\quad + \frac{\rho J_{rp}}{D_2} B(1, a_0) [(2u_{20}u_{21} + u_{21}u_{22}) \cos(s_2 - s_1) - u_{21}u_{23} \sin(s_2 - s_1)] \\
0 &= \frac{\rho J_{rc}}{D_1} B(1, a_0) u_{11}u_{13} + \frac{I_1 B(1, a_0/2)}{\pi} \sin(x_1 - s_1) \\
&\quad + \frac{\rho J_{rp}}{D_2} B(1, a_0) [(2u_{20}u_{21} + u_{21}u_{22}) \sin(s_2 - s_1) + u_{21}u_{23} \cos(s_2 - s_1)] \\
u_{12} &= \frac{\rho J_{rc}}{D_1} B(2, a_0) \left[ 2u_{10}u_{12} + \frac{u_{11}^2}{2} \right] + \frac{I_1 B(2, a_0/2)}{\pi} \cos 2(x_1 - s_1) \\
&\quad + \frac{\rho J_{rp}}{D_2} B(2, a_0) \left[ (2u_{20}u_{22} + \frac{u_{21}^2}{2}) \cos 2(s_2 - s_1) - 2u_{20}u_{23} \sin 2(s_2 - s_1) \right] \\
u_{13} &= \frac{\rho J_{rc}}{D_1} B(2, a_0) 2u_{10}u_{13} + \frac{I_1 B(2, a_0/2)}{\pi} \sin 2(x_1 - s_1) \\
&\quad + \frac{\rho J_{rp}}{D_2} B(2, a_0) \left[ (2u_{20}u_{22} + \frac{u_{21}^2}{2}) \sin 2(s_2 - s_1) + 2u_{20}u_{23} \cos 2(s_2 - s_1) \right]
\end{aligned}$$

Firing rate  $R_m(s_1, u_0, u_1, u_2, u_3) = \frac{\psi_m^2}{D_m}$ , the definition of  $\hat{s}$  in wenhao's paper is given by

$$\hat{s} = \arg\left(\sum_{-\pi}^{\pi} R_m e^{j\theta}\right)$$

Hence  $\hat{s}$  can be expressed by the coefficients

$$\hat{s} = \text{atan2}[(2u_0u_1 + u_1u_2)\sin(s) + u_1u_3\cos(s), (2u_0u_1 + u_1u_2)\cos(s) - u_1u_3\sin(s)]$$

Next we take noise into consideration. The dynamics of congruent groups of neurons in module 1 in the presence of noise can be approximated by

$$\begin{aligned}
\tau \frac{\partial \psi(y_1)}{\partial t} &= -\psi(y_1) + \frac{J_{rc}}{D_1} \int_{-\pi}^{\pi} V(y_1 - y_2, a_0) \psi^2(y_2) + \frac{J_{rp}}{D_2} \int_{-\pi}^{\pi} V(y_1 - y_2, a_0) \psi^2(y_2) \\
&\quad + I_1 V(y - x, a_0/2) + I_b + \sqrt{FI_1 V(y - x, a_0/2)} \xi_1 + \sqrt{FI_b} \epsilon_1
\end{aligned}$$

Consider the dynamics of displacement mode and multiply both sides by  $\sin(y_1 - s_1)$ , integrate over  $y_1$

$$\begin{aligned}
\tau \frac{\partial}{\partial t} \delta s_1 &= -\delta s_1 + \frac{\rho J_{rc}}{D_1 u_{11}} B(1, a_0) [2u_{10}u_{11} + u_{11}u_{12}] \delta s_1 \\
&\quad + \frac{\rho J_{rp}}{D_2 u_{11}} B(1, a_0) [(2u_{20}u_{21} + u_{21}u_{22}) \cos(s_2 - s_1) - u_{21}u_{23} \sin(s_2 - s_1)] \delta s_2 \\
&\quad + \frac{\sqrt{FI_1}}{\pi u_{11}} \int \sqrt{V(y - x, a_0/2)} \sin(y_1 - s_1) \xi_1 dy_1 + \frac{\sqrt{FI_b}}{\pi u_{11}} \int \sin(y_1 - s_1) \epsilon_1 dy_1
\end{aligned}$$

The equivalent noise temperature is given by

$$T_1 = \frac{F}{2\pi^2 \rho u_{11}^2} \left[ I_1 \int V(y_1 - x_1, a_0/2) \sin^2(y_1 - s_1) dy_1 + I_b \int \sin^2(y_1 - s_1) dy_1 \right]$$

$$= \frac{F}{2\pi^2 \rho u_{11}^2} \left[ \left( \frac{I_1}{2} + \pi I_b \right) - \frac{I_1}{2} B(2, a_0/2) \cos 2(x_1 - s_1) \right]$$

And  $T_2$

$$T_2 = \frac{F}{2\pi^2 \rho u_{21}^2} \left[ \left( \frac{I_2}{2} + \pi I_b \right) - \frac{I_2}{2} B(2, a_0/2) \cos 2(x_2 - s_2) \right]$$

Consider the dynamics  $\tau \frac{\partial x_i}{\partial t} = -\sum_j g_{ij} x_j + \xi_j$  where  $\langle \xi_i(t) \xi_j(t') \rangle = 2T_i \delta_{ij} \delta(t - t')$  and  $\langle \xi_i(t) \rangle = 0$ . Diagonalizing the matrix,  $g_{ij} = \sum_k S_{ik} \lambda_k S_{kj}^{-1}$ . Then

$$\tau \frac{\partial}{\partial t} \sum_j S_{ij}^{-1} x_j = -\lambda_i \sum_j S_{ij}^{-1} x_j + \sum_j S_{ij}^{-1} \xi_j$$

The solution is

$$x_i(t) = \sum_j S_{ij} \int_{-\infty}^t \frac{dt'}{\tau} \exp\left[-\frac{\lambda_j}{\tau}(t - t')\right] S_{jk}^{-1} \xi_k(t')$$

Consider the moments of the distribution of  $x_i(t)$

$$\langle x_i^2(t) \rangle = \sum_{j_1 \dots j_{2n} k_1 \dots k_{2n}} S_{ij_1} \dots S_{ij_{2n}} \int_{-\infty}^t \frac{dt_1}{\tau} \exp\left[-\frac{\lambda_{j_1}}{\tau}(t - t_1)\right]$$

$$\dots \int_{-\infty}^t \frac{dt_{2n}}{\tau} \exp\left[-\frac{\lambda_{j_{2n}}}{\tau}(t - t_{2n})\right] S_{j_1 k_1}^{-1} \dots S_{j_{2n} k_{2n}}^{-1} \langle \xi_{k_1}(t_1) \dots \xi_{k_{2n}}(t_{2n}) \rangle$$

The number of ways the pairing of the noise terms can be done is  $(2n)! / (2!^n n!) = (2n - 1)!!$ . Hence

$$\langle x_i^2(t) \rangle = (2n - 1)!! \left\{ \sum_{j_1 j_2 k_1 k_2} S_{ij_1} S_{ij_2} \int_{-\infty}^t \frac{dt_1}{\tau} \exp\left[-\frac{\lambda_{j_1}}{\tau}(t - t_1)\right] \right.$$

$$\left. \int_{-\infty}^t \frac{dt_2}{\tau} \exp\left[-\frac{\lambda_{j_2}}{\tau}(t - t_2)\right] S_{j_1 k_1}^{-1} S_{j_2 k_2}^{-1} 2T_{k_1} \delta_{k_1 k_2} \delta(t_1 - t_2) \right\}^n$$

After integrating

$$\langle x_i^2(t) \rangle = (2n - 1)!! \left[ \sum_{ijk} S_{ij} S_{ik} \frac{2T_l}{(\lambda_j + \lambda_k) \tau} S_{jl}^{-1} S_{kl}^{-1} \right]^n$$

Hence the distribution of  $x_i(t)$  is a Gaussian with variance

$$\sigma_i^2 = \sum_{ijk} S_{ij} S_{ik} \frac{2T_l}{(\lambda_j + \lambda_k) \tau} S_{jl}^{-1} S_{kl}^{-1}$$

For the matrix  $\begin{bmatrix} G_{11} & G_{12} \\ G_{21} & G_{22} \end{bmatrix}$

Where

$$\begin{aligned}
G_{11} &= 1 - \frac{\rho J_{rc}}{D_1 u_{11}} B(1, a_0) [2u_{10}u_{11} + u_{11}u_{12}] \\
G_{22} &= 1 - \frac{\rho J_{rc}}{D_2 u_{21}} B(1, a_0) [2u_{20}u_{21} + u_{21}u_{22}] \\
G_{12} &= -\frac{\rho J_{rp}}{D_2 u_{11}} B(1, a_0) [(2u_{20}u_{21} + u_{21}u_{22})\cos(s_2 - s_1) - u_{21}u_{23}\sin(s_2 - s_1)] \\
G_{21} &= -\frac{\rho J_{rp}}{D_1 u_{21}} B(1, a_0) [(2u_{10}u_{11} + u_{11}u_{12})\cos(s_1 - s_2) - u_{11}u_{13}\sin(s_1 - s_2)]
\end{aligned}$$

The variance and concentration

$$\begin{aligned}
\sigma_1^2 &= \frac{T_1}{(G_{11} + G_{22})\tau} + \frac{T_1 G_{22}^2 + T_2 G_{12}^2}{(G_{11}G_{22} - G_{12}G_{21})(G_{11} + G_{22})\tau} \\
\kappa_1 &= \frac{1}{\sigma_1^2}
\end{aligned}$$

## 5. Bayesian Inference

However, this network doesn't behave in a Bayesian way. We focus on the case that the stimulus strengths are equal, that is  $I_1 = I_2 = I$ . We consider the competition between congruent and opposite group in module 1. The solution is symmetric with respect to the perception displacement, that is  $s_1 - x_1 = x_2 - s_2$ . The matrix then becomes

$$\begin{aligned}
G_{11} &= 1 - \frac{\rho J_{rc}}{D} B(1, a_0) [2u_0 + u_2] \\
\bar{G}_{11} &= 1 - \frac{\rho J_{rc}}{\bar{D}} B(1, a_0) [2\bar{u}_0 + \bar{u}_2] \\
G_{12} &= -\frac{\rho J_{rp}}{D} B(1, a_0) [(2u_0 + u_2)\cos(s_2 - s_1) - u_3\sin(s_2 - s_1)] \\
\bar{G}_{12} &= -\frac{\rho J_{rp}}{\bar{D}} B(1, a_0) [(2\bar{u}_0 + \bar{u}_2)\cos(\bar{s}_1 - \bar{s}_2) - \bar{u}_3\sin(\bar{s}_1 - \bar{s}_2)]
\end{aligned}$$

We have  $G_{11} = G_{22}$ ,  $G_{12} = G_{21}$ ,  $\bar{G}_{11} = \bar{G}_{22}$ ,  $\bar{G}_{12} = \bar{G}_{21}$  because of symmetry. The noise temperature are given below

$$\begin{aligned}
T &= \frac{F}{2\pi^2 \rho u_1^2} \left[ \frac{I_1}{2} (1 - B(2, a_0/2)\cos 2(x_1 - s_1)) + \pi I_b \right] \\
\bar{T} &= \frac{F}{2\pi^2 \rho \bar{u}_1^2} \left[ \frac{I_1}{2} (1 - B(2, a_0/2)\cos 2(x_1 - \bar{s}_1)) + \pi I_b \right]
\end{aligned}$$

Finally we obtain

$$\begin{aligned}
\sigma_1^2 &= \frac{G_{11}T}{(G_{11}^2 - G_{12}^2)\tau} \\
\kappa_1 &= \frac{1}{\sigma_1^2} = \frac{\tau}{T} (G_{11} - \frac{G_{12}^2}{G_{11}}) \approx \frac{\tau}{T}
\end{aligned}$$

Hence  $\frac{\kappa_1}{\bar{\kappa}_1} \approx \frac{u_1^2}{\bar{u}_1^2}$ . The information of position and variance is decoded from the second and the third equations.



$$1 = HJ_{rc} + HJ_{rp}\cos\Delta s + \frac{F}{u_1}\cos(x_1 - s_1) \quad (4)$$

$$0 = HJ_{rp}\sin\Delta s + \frac{F}{u_1}\sin(x_1 - s_1) \quad (5)$$

Where  $H = \frac{\rho}{D}(2u_0 + u_2)B(1, a_0)$ ,  $F = \frac{IB(1, a_0/2)}{\pi}$ , under the weak input limit  $H$  can be treated as a constant.

When  $\Delta s = \frac{\pi}{2}$

$$\begin{aligned} 1 &= HJ_{rc} + \frac{F}{u_1} \\ 0 &= HJ_{rp} + \frac{F}{u_1}(x_1 - s_1) \end{aligned}$$

Where  $(x_1 - s_1) \rightarrow 0$ . We have  $(s_1 - x_1)_{\Delta s = \frac{\pi}{2}} = \frac{HJ_{rp}}{1 - HJ_{rc}}$ . When  $\Delta x = 0$ , we know  $x_1 = s_1$ ,  $x_2 = s_2$ , the equations become

$$1 = HJ_{rc} + HJ_{rp} + \frac{F}{u_1}$$

Since  $HJ_{rp}$  is small, the ratio of  $u_1$  to  $\bar{u}_1$  can be approximated by

$$\left(\frac{u_1}{\bar{u}_1}\right)_{\Delta x=0} = \frac{1 - HJ_{rc} + HJ_{rp}}{1 - HJ_{rc} - HJ_{rp}} \approx 1 + \frac{2}{1 - HJ_{rc}}HJ_{rp} = 1 + 2(s_1 - x_1)_{\Delta s = \frac{\pi}{2}}$$

$$\left(\frac{\kappa_1 - \bar{\kappa}_1}{\kappa_1 + \bar{\kappa}_1}\right)_{\Delta x=0} = \frac{\left(\frac{u_1^2}{\bar{u}_1^2}\right)_{\Delta x=0} - 1}{\left(\frac{u_1^2}{\bar{u}_1^2}\right)_{\Delta x=0} + 1} \approx 2(s_1 - x_1)_{\Delta s = \frac{\pi}{2}}$$

That is, under weak input limit, if we are going to fit the variance in this network, the angle decoded from population vector will be twice as large as the real angle. This ratio is always greater than 2 when input strength is in normal range.

### 5.1. Assumption

Here we define the length of population vector  $\hat{A} = \text{mod}(\frac{1}{N} \sum_{-\pi}^{\pi} R_i e^{j\theta})$   
 $= \frac{\rho}{ND} u_1 \sqrt{(2u_0 + u_2)^2 + u_3^2}$ ,  $\hat{A}$  is used to rescale the noise variance. We set  $J_{int} = 1$  and rewrite the noise term  $\sqrt{FI_b \hat{A}} \epsilon_1$ .

The noise temperature

$$\begin{aligned} T &= \frac{\sqrt{(2u_0 + u_2)^2 + u_3^2}}{2\pi N D u_1} F I_b \\ \bar{T} &= \frac{\sqrt{(2\bar{u}_0 + \bar{u}_2)^2 + \bar{u}_3^2}}{2\pi N \bar{D} \bar{u}_1} F I_b \end{aligned}$$

Consider weak input limit,  $u_0 \approx \bar{u}_0$

$$\kappa \approx \frac{\pi \tau N D}{F I_b u_0} u_1$$

$$\bar{\kappa} \approx \frac{\pi \tau N \bar{D}}{F I_b \bar{u}_0} \bar{u}_1$$

$c_0$  denotes the coefficient of  $u_1$  and  $\bar{u}_1$ , the concentration is proportional to the coefficient of the height mode.

$$\kappa = c_0 u_1$$

$$\bar{\kappa} = c_0 \bar{u}_1$$

From (4) and (5) we have

$$\left(\frac{F}{u_1}\right)^2 = (1 - HJ_{rc})^2 + (HJ_{rp})^2 - 2(1 - HJ_{rc})HJ_{rp}\cos\Delta s$$

$$u_1^2 = \frac{F^2}{(1 - HJ_{rc})^2 + (HJ_{rp})^2 - 2(1 - HJ_{rc})HJ_{rp}\cos\Delta s}$$

Actually  $HJ_{rp}$  is small, and  $\cos\Delta s = \cos[\Delta x - 2(s_1 - x_1)] \approx \cos\Delta x$ . We expand  $u_1^2$  and  $\tan(s_1 - x_1)$  then get

$$\tan(s_1 - x_1) = \frac{HJ_{rp}\sin\Delta s}{1 - HJ_{rc} - HJ_{rp}\cos\Delta s}$$

$$\approx \frac{HJ_{rp}\sin\Delta s}{1 - HJ_{rc}}$$

$$\approx \frac{HJ_{rp}\sin\Delta x}{1 - HJ_{rc} + HJ_{rp}\cos\Delta s}$$

$$u_1^2 \approx \frac{F^2}{(1 - HJ_{rc})^2} + \frac{2F^2 HJ_{rp}}{(1 - HJ_{rc})^3} \cos\Delta s$$

$$= \frac{F^2}{(1 - HJ_{rc})^4} [(1 - HJ_{rc})^2 - 2HJ_{rp}(1 - HJ_{rc})\cos(\pi - \Delta s)]$$

$$\approx \frac{F^2}{(1 - HJ_{rc})^4} [(1 - HJ_{rc})^2 - 2HJ_{rp}(1 - HJ_{rc})\cos(\pi - \Delta x) + (HJ_{rp})^2]$$

Finally we obtain

$$\tan(s_1 - x_1) \approx \frac{HJ_{rp}\sin\Delta x}{1 - HJ_{rc} + HJ_{rp}\cos\Delta s}$$

$$\kappa^2 \approx \frac{F^2}{c_0^2(1 - HJ_{rc})^4} [(1 - HJ_{rc})^2 - 2HJ_{rp}(1 - HJ_{rc})\cos(\pi - \Delta x) + (HJ_{rp})^2]$$

### 5.1.1. Only Cue 1

When  $I_1 = I$  and  $I_2 = 0$ , this network is asymmetric. The bump in module 2 is much weaker. We ignore the reciprocal coupling term then (4) and (5) in module 1 become

$$1 \approx HJ_{rc} + \frac{F}{u_1} \cos(x_1 - s_1)$$

$$0 \approx \frac{F}{u_1} \sin(x_1 - s_1)$$

The solution to this problem is

$$s_1 = x_1$$

$$u_1 = \frac{F}{c_0(1 - HJ_{rc})}$$

The concentration decoded from module 1 is

$$\kappa_1 = \frac{F}{c_0(1 - HJ_{rc})}$$

### 5.1.2. Only Cue 2

When  $I_2 = I$  and  $I_1 = 0$ , (4) and (5) in module 1 become

$$1 = HJ_{rc} + HJ_{rp} \frac{u_{12}}{u_{11}} \cos \Delta s$$

$$0 = HJ_{rp} \frac{u_{12}}{u_{11}} \sin \Delta s$$

We obtain

$$s_1 = s_2 \approx x_2$$

$$u_{11} = \frac{HJ_{rp}}{1 - HJ_{rc}} u_{12}$$

From previous discussion we know the solution is

$$u_{12} = \frac{F}{1 - HJ_{rc}}$$

The concentration decoded from module 1 is

$$\kappa_{12} = \frac{u_{11}}{c_0} = \frac{FHJ_{rp}}{c_0(1 - HJ_{rc})^2}$$

### 5.1.3. Combined Cues

Compare the results, we have

$$\kappa e^{j(s_1 - x_1)} = \kappa_1 e^{jx_1} + \kappa_{12} e^{jx_2}$$

Where  $j$  is the imaginary unit.

The second and the third equations of opposite group are

$$1 = HJ_{rc} + HJ_{rp} \cos \Delta \bar{s} + \frac{F}{\bar{u}_1} \cos(x_1 - \bar{s}_1) \quad (6)$$

$$0 = -HJ_{rp} \sin \Delta \bar{s} + \frac{F}{\bar{u}_1} \sin(x_1 - \bar{s}_1) \quad (7)$$

Similarly, we have

$$\bar{\kappa} e^{j(\bar{s}_1 - x_1)} = \bar{\kappa}_1 e^{jx_1} + \bar{\kappa}_{12} e^{j(x_2 + \pi)}$$

This network can apply Bayesian inference for a wide range of values of the inputs.

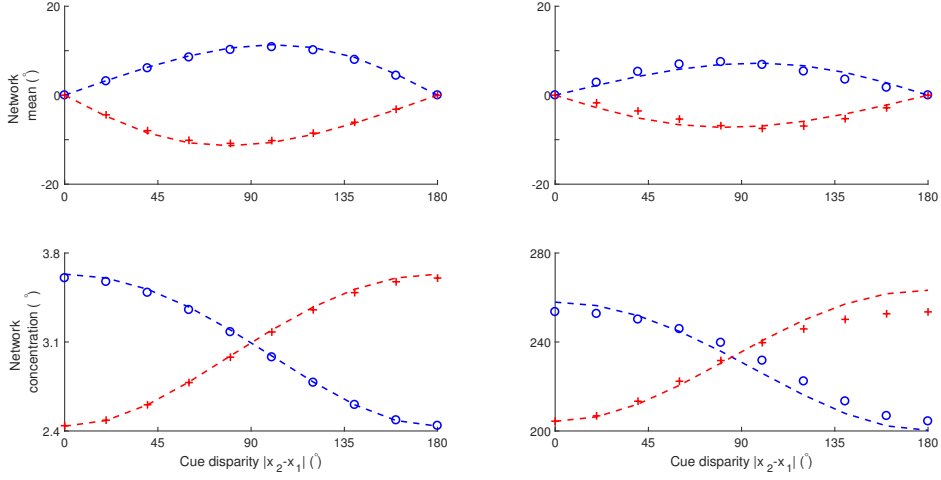


Figure 1: Weak input (left column) and strong input (right column). Symbols: network results; dash lines: Bayesian prediction. The blue and red colors represent congruent and opposite groups in module 1 respectively.

## 5.2. Results

The parameters are listed. Each network consist of  $N = 180$  congruent and opposite neurons respectively. The connection width  $a_0 = 3$  and the time step is  $0.01\tau$  using Euler method where  $\tau$  is rescaled to 1. The strength of background input is  $I_b = 1$ . The strength of divisive normalization  $\omega = 3 \times 10^{-4}$ .  $F$  in the noise term is the Fano factor which is set to 0.5.

In simulation we fix  $x_1 = 0$ , that is,  $\Delta x = x_2 - x_1 = x_2$ .  $J_c$  is the minimal recurrent strength and we choose  $J_{rc} = 0.3J_c$  and  $J_{rp} = 0.5J_{rc}$ .  $J_c$  can be found by solving the dynamic equations, which is given by

$$J_c = \sqrt{\frac{8\pi I_0(a_0/2)^2 \omega (1 + J_{int})}{I_0(a_0) \rho}}$$

$U_0$  is the rescaled input strength  $U_0 = \frac{J_c e^{a_0/2}}{2\pi \omega (1 + J_{int}) I_0(a_0/2)}$ . We compare the case of weak input  $I = 0.01U_0$  (left column) and strong input  $I = 0.7U_0$  (right coulumn) in module 1. The results are derived by solving dynamic equations. Figure 1 shows this network could implement Bayesian inference under weak input limit. When external inputs are strong, the prediction from this network is close to the Bayesian way.