How do spatially distinct frequency specific MEG networks emerge from one underlying structural connectome? The role of the structural eigenmodes: Supplementary material on linearised networks

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1 Scalar networks - no delay

Consider $x_i(t) \in \mathbb{R}$, $t \geq 0$, $i = 1, \ldots, N$, with Hopfield style dynamics:

$$\frac{\mathrm{d}}{\mathrm{d}t} x_i(t) = -x_i(t) + f\left(\sum_{j=1}^{N} w_{ij} x_j(t)\right). \tag{1}$$

Here we shall assume that f is at least once differentiable and monotonically increasing (sigmoidal). The network steady state is given by $x_i(t) = \overline{x}_i$ and is determined by the simultaneous solution of the system of algebraic equations:

$$\overline{x}_i = f\left(\sum_{j=1}^{N} w_{ij} \overline{x}_j\right). \tag{2}$$

Now consider linearising around the steady state by writing $x_i(t) = \overline{x}_i + u_i(t)$ for some small set of perturbations $u_i(t)$. Substitution into (1) and expanding to first order gives

$$\frac{\mathrm{d}}{\mathrm{d}t} u_i(t) = -u_i(t) + \sum_{j=1}^{N} \widetilde{w}_{ij} u_j(t), \qquad \gamma_i = f'\left(\sum_{j=1}^{N} w_{ij} \overline{x}_j\right), \qquad \widetilde{w}_{ij} = \gamma_i w_{ij}. \tag{3}$$

Solutions of the form $u_i(t) = A_i \mathrm{e}^{\lambda t}$, $\lambda \in \mathbb{C}$, for some non-zero amplitudes A_i, satisfy

$$\lambda A_i = -A_i + \sum_{j=1}^{N} \widetilde{w}_{ij} A_j. \tag{4}$$

Now consider the vector of amplitudes to be an eigenvector of $\widetilde{w}$ such that

$$\sum_{j=1}^{N} \widetilde{w}_{ij} A_j^p = \mu_p A_i^p, \qquad p = 1, \ldots, N, \tag{5}$$

where p is used to index the eigenvector. Equation (4) then takes the simpler form

$$[\lambda + 1 - \mu_p] A_i = 0. \quad (6)$$

This system of linear equations for the amplitudes has non-trivial solutions if $\mathcal{E}(\lambda; p) \equiv [\lambda + 1 - \mu_p] = 0$. There is a bifurcation when Re $\lambda = 0$, namely when

$$\text{Re}\, \mu_p = 1, \quad (7)$$

for some value of p. If the eigenvalues of $\widetilde{w}$ are real (which would be the case if $\widetilde{w}$ were symmetric) then we can order them such that $\mu_1 > \mu_2 > \cdots > \mu_N$. In this case λ would be real too and the first instance where λ increases through zero from below would be for the eigenvector with eigenvalue μ_1.

2 Scalar networks - delay

Consider (1) with the inclusion of a set of discrete delays:

$$\frac{\mathrm{d}}{\mathrm{d}t} x_i(t) = -x_i(t) + f\left(\sum_{j=1}^{N} w_{ij} x_j(t - \tau_{ij})\right). \quad (8)$$

The steady state equation is given by (2). Linearisation around the steady state yields

$$\frac{\mathrm{d}}{\mathrm{d}t} u_i(t) = -u_i(t) + \sum_{j=1}^{N} \widetilde{w}_{ij} u_j(t - \tau_{ij}). \quad (9)$$

Solutions of the form $u_i(t) = A_i \mathrm{e}^{\lambda t}$, $\lambda \in \mathbb{C}$, for some non-zero amplitudes A_i, satisfy

$$\lambda A_i = -A_i + \sum_{j=1}^{N} \widetilde{w}_{ij} \mathrm{e}^{-\lambda \tau_{ij}} A_j. \quad (10)$$

Now introduce the complex matrix $W(\lambda)$ with components $W_{ij}(\lambda) = \widetilde{w}_{ij} \mathrm{e}^{-\lambda \tau_{ij}}$. Now assume a decomposition of the form

$$W_{ij}(\lambda) = \sum_{p=1}^{N} \mu_p(\lambda) v_i^p u_j^p, \quad (11)$$

where v and u are normalised right and left eigenvectors of $\widetilde{w}$ respectively. In this case the coefficients $\mu_p(\lambda)$ can be obtained by projection as

$$\mu_p(\lambda) = \sum_{i=1}^{N} \sum_{j=1}^{N} W_{ij}(\lambda) v_j^p u_i^p. \quad (12)$$

If we now consider the vector of amplitudes to be in the direction of v then (10) reduces to

$$[\lambda + 1 - \mu_p(\lambda)] v_i^p = 0. \quad (13)$$

This system of linear equations for the amplitudes has non-trivial solutions if $\mathcal{E}(\lambda; p) \equiv [\lambda + 1 - \mu_p(\lambda)] = 0$.

The eigenvalues of the spectral problem can be practically constructed by considering the decomposition $\lambda = \nu + i\omega$ and simultaneously solving the pair of equations $\mathcal{G}(\nu, \omega; p) = 0$ and $\mathcal{H}(\nu, \omega; p) = 0$, where $\mathcal{G}(\nu, \omega; p) = \text{Re}\, \mathcal{E}(\nu + i\omega; p)$ and $\mathcal{H}(\nu, \omega; p) = \text{Im}\, \mathcal{E}(\nu + i\omega; p)$. A steady state solution is stable if $\text{Re}\, \lambda < 0$. We distinguish two types of instability: i) when a real eigenvalue crosses from the left hand complex plane to the right, with a bifurcation defined by $\mathcal{E}(0; p) = 0$, and ii) when a complex conjugate pair of eigenvalues cross from the left hand complex plane to the right, with a bifurcation defined by $\mathcal{E}(i\omega; p) = 0$. In either case the p value that ensures a bifurcation, say when $p = p_c$, determines which pattern of network activity ($u \sim v^{p_c}$) is excited. If the bifurcation arises from the crossing of a complex conjugate pair then the emergent spatial pattern will also oscillate in time with a frequency determined by ω_c with $\mathcal{E}(i\omega_c; p_c) = 0$.

If $\tau_{ij} = 0$ for all i, j then $W = \widetilde{w}$ and the spectral problem reduces to that in §1. If $\tau_{ij} = \tau > 0$ for all i, j then $\mu_p(\lambda) = \text{e}^{-\lambda\tau} \mu_p$, where μ_p is an eigenvalue of $\widetilde{w}$.

3 Arbitrary nonlinear networks - no delay

Now consider $x(t) = (x^1(t), \ldots, x^m(t)) \in \mathbb{R}^m$, $t \geq 0$, with *local* dynamics

$$\frac{\text{d}}{\text{d}t} x = F(x) + G(w^{\text{loc}} x), \tag{14}$$

where $F, G : \mathbb{R}^m \mapsto \mathbb{R}^m$, and $w^{\text{loc}} \in \mathbb{R}^{m \times m}$. Now use this to construct a network of N interconnected nodes according to

$$\frac{\text{d}}{\text{d}t} x_i = F(x_i) + G(w^{\text{loc}} x_i + s_i), \qquad s_i = \sum_{j=1}^{N} w_{ij} H(x_j) \tag{15}$$

where $i = 1, \ldots, N$, and $H : \mathbb{R}^m \mapsto \mathbb{R}^m$ selects which local component mediates interactions. For example if interactions are only mediated by the first component of the local dynamics then we would choose $H(x) = (x^1, 0, \ldots, 0)$.

The network steady state is given by $0 = F(\overline{x}_i) + G(w^{\text{loc}} \overline{x}_i + \overline{s}_i)$, with $\overline{s}_i = \sum_{j=1}^{N} w_{ij} H(\overline{x}_j)$. Linearise around the steady state by writing $x_i(t) = \overline{x}_i + u_i(t)$ for some small set of perturbations $u_i(t) \in \mathbb{R}^m$ for $i = 1, \ldots, N$. Substitution into (15) and expanding to first order gives

$$\frac{\text{d}}{\text{d}t} u_i = \left[DF(\overline{x}_i) + DG(w^{\text{loc}} \overline{x}_i + \overline{s}_i) w^{\text{loc}} \right] u_i + \sum_{j=1}^{N} DG(w^{\text{loc}} \overline{x}_i + \overline{s}_i) DH(\overline{x}_j) w_{ij} u_j. \tag{16}$$

Here $DF, DG, DH \in \mathbb{R}^{m \times m}$ are Jacobians. It is now convenient to introduce the abbreviations $D\widetilde{F}_i = DF(\overline{x}_i) + DG(w^{\text{loc}} \overline{x}_i + \overline{s}_i) w^{\text{loc}}$ and $D\widetilde{G}_i = DG(w^{\text{loc}} \overline{x}_i + \overline{s}_i) DH(\overline{x}_j)$ (realising that $DH(\overline{x}_j)$ is independent of the label j) to write (16) in the succinct form

$$\frac{\text{d}}{\text{d}t} U = \begin{bmatrix} D\widetilde{F}_1 & & 0 \\ & \ddots & \\ 0 & & D\widetilde{F}_N \end{bmatrix} U + \begin{bmatrix} D\widetilde{G}_1 & & 0 \\ & \ddots & \\ 0 & & D\widetilde{G}_N \end{bmatrix} (w \otimes I_m) U, \tag{17}$$

where $U = (u_1^1, \dots, u_1^m, u_2^1, \dots, u_2^m, \dots, u_N^1, \dots, u_N^m)$ and I_m is the $m \times m$ identity matrix. The tensor product $A \otimes B$ of two matrices $A \in \mathbb{R}^{n_1 \times n_2}$ and $B \in \mathbb{R}^{n_3 \times n_4}$ is defined by

$$A \otimes B = \begin{bmatrix} A_{11}B & \dots & A_{1n_2}B \\ \vdots & \ddots & \vdots \\ A_{n_1 1}B & \dots & A_{n_1 n_2}B \end{bmatrix}. \tag{18}$$

The following properties are readily established. If AB and CD exist then

$$(A \otimes B)(C \otimes D) = (AC) \otimes (BD), \tag{19}$$

and if A and B are non-singular then

$$(A \otimes B)^{-1} = A^{-1} \otimes B^{-1}. \tag{20}$$

Now introduce the matrix of normalised eigenvectors of w as P with a corresponding diagonal matrix of eigenvalues Λ such that $wP = P\Lambda$ and consider the change of variables $V = (P \otimes I_m)^{-1}U$. In this case (17) transforms to

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}V = (P \otimes I_m)^{-1} &\begin{bmatrix} D\widetilde{F}_1 & & 0 \\ & \ddots & \\ 0 & & D\widetilde{F}_N \end{bmatrix} (P \otimes I_m)V \\ + (P \otimes I_m)^{-1} &\begin{bmatrix} D\widetilde{G}_1 & & 0 \\ & \ddots & \\ 0 & & D\widetilde{G}_N \end{bmatrix} (w \otimes I_m)(P \otimes I_m)V. \end{aligned} \tag{21}$$

Assuming a homogeneous system such that $\overline{x}_i$ is independent of i, which is natural for identical units with a network connectivity with a row-sum constraint $\sum_{j=1}^N w_{ij} = \text{const}$ for all i, then we have the useful simplification $D\widetilde{F}_i = D\widetilde{F}$ and $D\widetilde{G}_i = D\widetilde{G}$ for all i. It is simple to establish that for any block diagonal matrix A, formed from N equal matrices of size $m \times m$, that $(P \otimes I_m)^{-1}A(P \otimes I_m) = A$. Moreover, from (19) and (20) we have that $(w \otimes I_m)(P \otimes I_m) = (wP) \otimes I_m = (P\Lambda) \otimes I_m = (P \otimes I_m)(\Lambda \otimes I_m)$. Hence, if we denote $\text{diag}(\Lambda) = (\mu_1, \dots \mu_N)$ then (21) becomes

$$\frac{\mathrm{d}}{\mathrm{d}t}V = \begin{bmatrix} D\widetilde{F} & & 0 \\ & \ddots & \\ 0 & & D\widetilde{F} \end{bmatrix} V + \begin{bmatrix} \mu_1 D\widetilde{G} & & 0 \\ & \ddots & \\ 0 & & \mu_N D\widetilde{G} \end{bmatrix} V. \tag{22}$$

The system (22) is in a block diagonal form and so it is equivalent to the set of decoupled equations given by

$$\frac{\mathrm{d}}{\mathrm{d}t}\xi_p = \left[D\widetilde{F} + \mu_p D\widetilde{G}\right]\xi_p, \qquad \xi_p \in \mathbb{C}^m, \qquad p = 1, \dots, N. \tag{23}$$

This has solutions of the form $\xi_p = A_p \mathrm{e}^{\lambda t}$ for some amplitude vector $A_p \in \mathbb{C}^m$. For a non-trivial set of solutions we require $\mathcal{E}(\lambda; p) = 0$ where

$$\mathcal{E}(\lambda; p) = \det\left[\lambda I_m - D\widetilde{F} - \mu_p D\widetilde{G}\right], \qquad p = 1, \dots, N. \tag{24}$$

3.1 Wilson-Cowan network example

Consider a Wilson-Cowan network consisting of an excitatory population E_i and an inhibitory population I_i, for $i = 1, \ldots, N$, with dynamics given by

$$\begin{bmatrix} 1 & 0 \\ 0 & \tau \end{bmatrix} \frac{\mathrm{d}}{\mathrm{d}t} \begin{bmatrix} E_i \\ I_i \end{bmatrix} = - \begin{bmatrix} E_i \\ I_i \end{bmatrix} + f \left(\begin{bmatrix} w^{EE} E_i + w^{EI} I_i + \sum_{j=1}^N w_{ij} E_j \\ w^{IE} E_i + w^{II} I_i \end{bmatrix} \right). \tag{25}$$

This may be written in the form (15) with the identification $x_i = (E_i, I_i)$, $H(x) = (E, 0)$, $F(x) = -\Gamma^{-1} x$, and $G(x) = \Gamma^{-1} f(x)$, where

$$\Gamma = \begin{bmatrix} 1 & 0 \\ 0 & \tau \end{bmatrix}, \qquad w^{\mathrm{loc}} = \begin{bmatrix} w^{EE} & w^{EI} \\ w^{IE} & w^{II} \end{bmatrix}. \tag{26}$$

The network steady state is given by $0 = -\overline{x}_i + f(w^{\mathrm{loc}} \overline{x}_i + \overline{s}_i)$, with $\overline{s}_i = \sum_{j=1}^N w_{ij} H(\overline{x}_j)$. We also have that

$$D\widetilde{F}_i = -\Gamma^{-1} \left[I_2 - Df(w^{\mathrm{loc}} \overline{x}_i + \overline{s}_i) \right] w^{\mathrm{loc}}, \qquad D\widetilde{G}_i = \Gamma^{-1} Df(w^{\mathrm{loc}} \overline{x}_i + \overline{s}_i) \begin{bmatrix} 1 & 0 \\ 0 & 0 \end{bmatrix}. \tag{27}$$

Here $[Df(x)]_{ij} = f'(x^i)\delta_{ij}$. The spectral equation (24) can be written in the form $\mathcal{E}(\lambda; p) = \det [\lambda I_2 - \mathcal{A}(p)] = 0$, where

$$\mathcal{A}(p) = - \begin{bmatrix} 1 & 0 \\ 0 & \tau^{-1} \end{bmatrix} \left\{ I_2 - Df(w^{\mathrm{loc}} \overline{x}_p + \overline{s}_p) \left[w^{\mathrm{loc}} + \begin{bmatrix} \mu_p & 0 \\ 0 & 0 \end{bmatrix} \right] \right\}. \tag{28}$$

Hence the complete set of eigenvalues that determine the stability of the network steady state is given by

$$\lambda_{\pm}(p) = \frac{1}{2} \left[\mathrm{Tr}\, \mathcal{A}(p) \pm \sqrt{\mathrm{Tr}\, \mathcal{A}(p)^2 - 4 \det \mathcal{A}(p)} \right], \qquad p = 1, \ldots, N. \tag{29}$$

4 Arbitrary nonlinear networks - delay

In the presence of delays we let

$$s_i(t) \to \sum_{j=1}^N w_{ij} H(x_j(t - \tau_{ij})). \tag{30}$$

The steady state equation is precisely that of §3, with the spectral equation given by (24) under the replacement $\mu_p \to \mu_p(\lambda)$ with

$$\mu_p(\lambda) = \sum_{i=1}^N \sum_{j=1}^N w_{ij} \mathrm{e}^{-\lambda \tau_{ij}} u_i^p v_j^p. \tag{31}$$

Here v^p (u^p) is a right (left) normalised eigenvector of w.