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Standing and travelling waves in a spherical brain model

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The Nunez model[3]

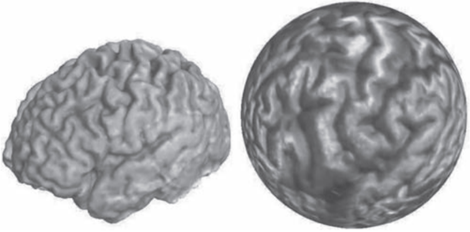
- Model for generation of EEG signals.
- Important observations:
  - Long range synaptic interactions excitatory while inhibitory interactions more short ranged.
  - Delays (local and global) important in generating robust human EEG frequencies.
  - Cortical white matter system topologically close to sphere - standing waves can occur via interference
- Model often studied in topologies quite different to the brain (e.g. line[1] or plane[2]).
- Two forms - damped wave equation and integro-differential equation (which we will use here with delays).

[1] V K Jirsa and H Haken. "Field theory of electromagnetic brain activity". In: *Physical Review Letters* 77 (1996), pp. 960–963.

[2] S Coombes et al. "Modeling electrocortical activity through improved local approximations of integral neural field equations". In: *Physical Review E* 76, 051901 (2007), p. 051901. DOI: 10.1103/PhysRevE.76.051901

Spherical models

Spherical models



(a) Brain cortex surface (b) Conformal brain mapping

Overview

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    - Neural field model on a sphere.
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   - Equivariant bifurcation theory tells us symmetries of periodic solutions which can exist after dynamic instability...
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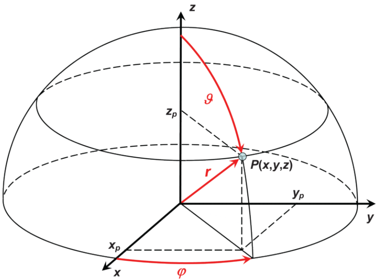
6. Further work.

A little bit of geometry



Polar angle:
$0 \leq \theta \leq \pi$
Azimuthal angle:
$0 \leq \phi \leq 2\pi$

Point on a sphere of radius R:

$$\mathbf{r} = \mathbf{r}(\theta, \phi) = R(\cos\phi \sin\theta, \sin\phi \sin\theta, \cos\theta)$$

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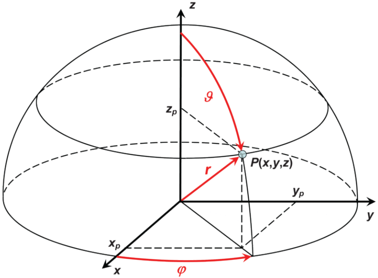

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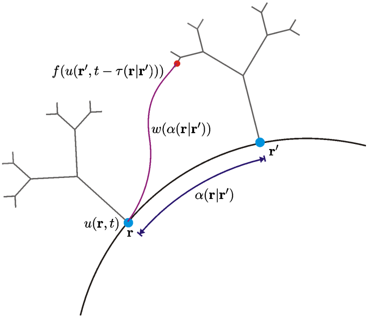
Distance between two points $\mathbf{r}$ and $\mathbf{r}'$:

$$\begin{aligned}\alpha(\mathbf{r}|\mathbf{r}') &= R\cos^{-1}\left(\mathbf{r}\cdot\mathbf{r}'/(|\mathbf{r}||\mathbf{r}'|)\right) \\ &= R\cos^{-1}\left(\cos\theta\cos\theta' + \sin\theta\sin\theta'\cos(\phi-\phi')\right).\end{aligned}$$

The model

$$\frac{\partial u}{\partial t} = -u + \int_{\Omega} w(\mathbf{r}|\mathbf{r}') f(u(\mathbf{r}', t - \tau(\mathbf{r}|\mathbf{r}')))\mathrm{d}\mathbf{r}'$$



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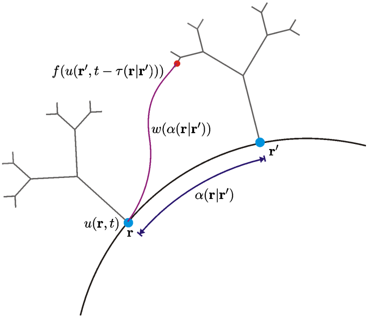
$O(3)$ invariant connectivity (synaptic kernel):

$$w(\mathbf{r}|\mathbf{r}') = w(\alpha) = A_1 \mathrm{e}^{-\frac{\alpha}{\sigma_1}} + A_2 \mathrm{e}^{-\frac{\alpha}{\sigma_2}}, \qquad \sigma_1 > \sigma_2, \quad A_1 A_2 < 0.$$



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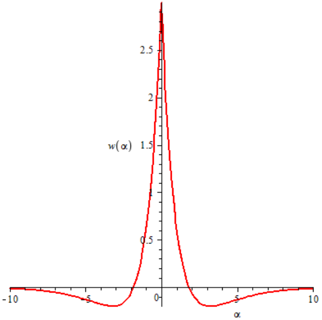
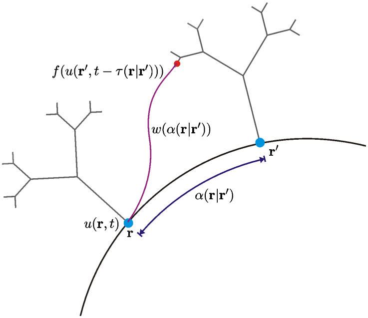
$A_1 + A_2 > 0$





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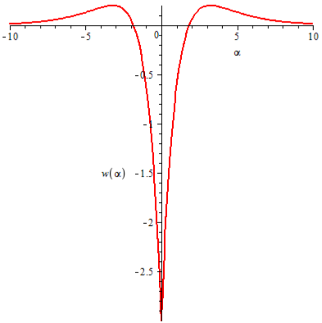

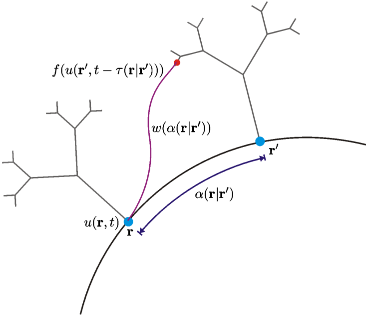

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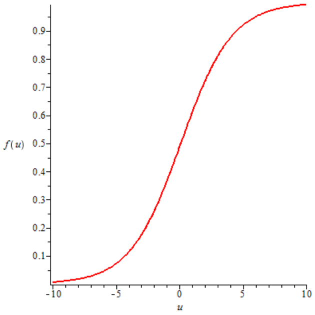
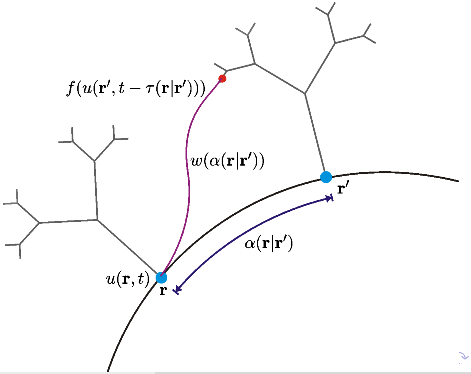
Firing rate : $$f(u) = \frac{1}{1 + \mathrm{e}^{-\beta(u-h)}}, \qquad \beta > 0,$$

h a threshold parameter, β controls the slope of the firing rate at threshold.





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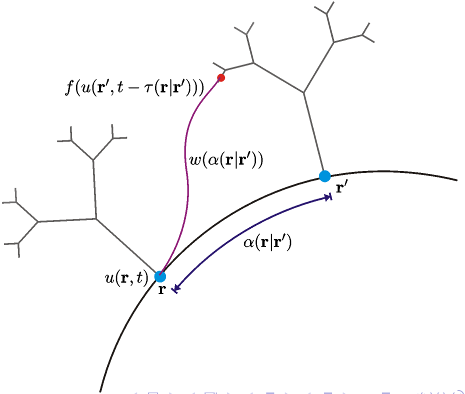
Delays : $$\tau(\mathbf{r}|\mathbf{r}') = \frac{\alpha(\mathbf{r}|\mathbf{r}')}{v} + \tau_0,$$

where

- v finite speed of action potentials.
- τ_0 constant delay representing delays caused by synaptic processes.

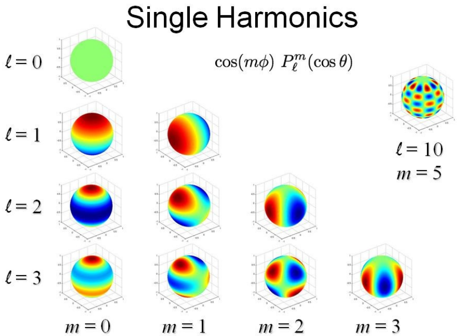


Spherical symmetry

Since we choose $w(\alpha(\mathbf{r}|\mathbf{r}'))$ to be $O(3)$ invariant we can write

$$w(\alpha(\mathbf{r}|\mathbf{r}')) = \sum_{n=0}^{\infty} w_n \sum_{m=-n}^{n} \overline{Y_n^m(\theta,\phi)} Y_n^m(\theta',\phi')$$

where $Y_n^m(\theta,\phi)$ are Spherical Harmonics. There are $2n+1$ spherical harmonics of degree n.



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Here

$$w_n = 2\pi \int_0^{\pi} \sin\theta d\theta \, w(R\theta) P_n(\cos\theta).$$

Synaptic kernel $w(\alpha)$ is balanced if

$$W := w_0 = \int_{\Omega} w(\mathbf{r}_0|\mathbf{r}') d\mathbf{r}' = 0$$

where $\mathbf{r}_0 \in \Omega$.

Linear stability of homogeneous steady state

$$\frac{\partial u}{\partial t} = -u + \int_\Omega w(\mathbf{r}|\mathbf{r}')f(u(\mathbf{r}', t - \tau(\mathbf{r}|\mathbf{r}')))\mathrm{d}\mathbf{r}'$$

Homogeneous steady states $\overline{u}$ satisfy

$$\overline{u} = Wf(\overline{u})$$

(so only one steady state $\overline{u} = 0$ when $W = 0$).

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Linearising about $\overline{u}$:

$$\frac{\partial u}{\partial t} = -u + \gamma \int_\Omega w(\mathbf{r}|\mathbf{r}')u(\mathbf{r}', t - \tau(\mathbf{r}|\mathbf{r}'))\mathrm{d}\mathbf{r}'$$

where $\gamma = f'(\overline{u})$.

Linear stability analysis

Consider separable solutions: $u(\mathbf{r},t) = \psi(\mathbf{r})\mathrm{e}^{zt}$ where $\psi(\mathbf{r})$ satisfies

$$0 = \mathcal{L}_z\psi(\mathbf{r}) := (1+z)\psi(\mathbf{r}) - \gamma \int_\Omega G(\alpha(\mathbf{r}|\mathbf{r}'); z)\psi(\mathbf{r}')\mathrm{d}\mathbf{r}' \qquad (1)$$

where

$$\begin{aligned} G(\alpha; z) &= w(\alpha)\exp(-z\tau_0 - z\alpha/v) \\ &= \sum_{n=0}^{\infty} G_n(z) \sum_{m=-n}^{n} \overline{Y_n^m(\theta,\phi)}\, Y_n^m(\theta',\phi') \end{aligned}$$

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Then (1) has solutions of the form $\psi(\mathbf{r}) = Y_n^m(\theta,\phi)$ if there exists eigenvalue λ such that

$$\mathcal{E}_n(\lambda) := 1 + \lambda - \gamma G_n(\lambda) = 0.$$

Linear stability analysis

- Homogeneous steady state is stable if $\mathrm{Re}\,\lambda < 0$ for all n.
- Dynamic instability occurs if (under parameter variation) eigenvalues cross imaginary axis away from origin
  - Expect emergence of travelling or standing waves
- Static instability occurs if eigenvalues cross along real axis
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Remark Without delays ($\tau_0 = 0$ and $v \to \infty$) the eigenvalues are real and given explicitly by

$$\lambda_n = -1 + \gamma w_n.$$

i.e. Dynamic instabilities are not possible.

Dynamic instabilities

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  for different values of n. (Remember $G_n(z)$ depends on parameters A_1, A_2, σ_1, σ_2, v, τ_0.)

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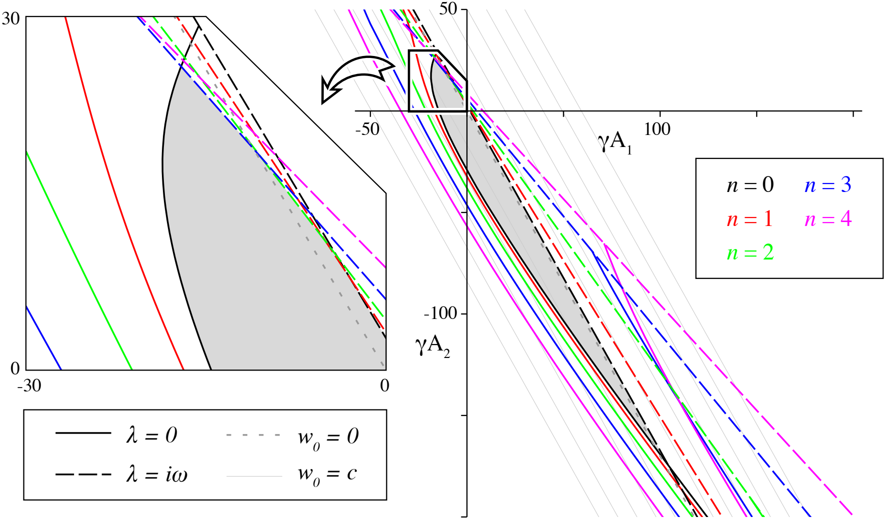
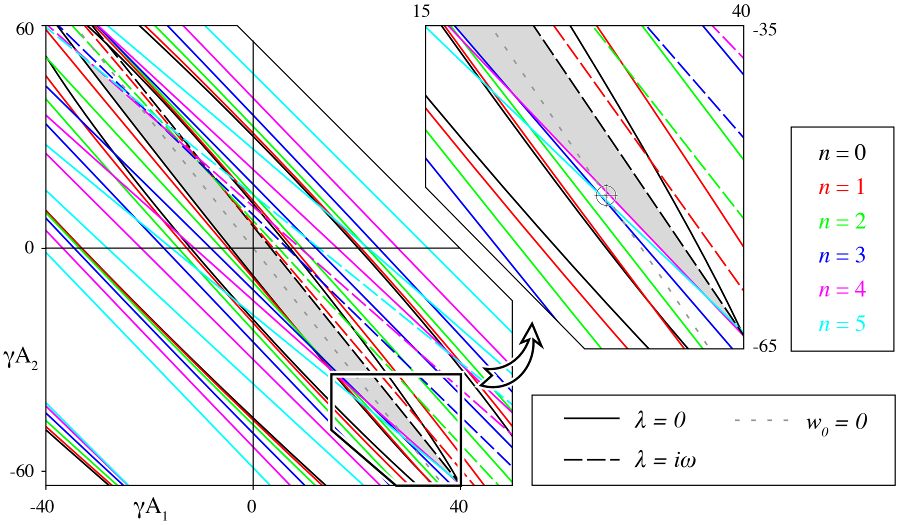
  for different values of n. (Remember $G_n(z)$ depends on parameters A_1, A_2, σ_1, σ_2, v, τ_0.)
- For fixed values of σ_1, σ_2, v, τ we can plot curves in A_1, A_2 plane where Hopf bifurcations of each mode can occur
- Can similarly find solutions of $1 = \gamma G_n(0)$ to locate static instabilities.

$\tau_0 = 0$



$\tau_0 \neq 0$



What kind of spatiotemporal patterns can exist?

From linear stability analysis we expect to excite a dynamic pattern of the form

$$u_{n_c}(\theta, \phi, t) = \sum_{m=-n_c}^{n_c} z_m \mathrm{e}^{i\omega_c t} Y_{n_c}^m(\theta, \phi) + \mathrm{cc},$$

where n_c and ω_c determined using spectral equation. Here the z_m are slowly varying amplitudes and $\mathbf{z} = (z_{-n_c}, \ldots, z_{n_c}) \in \mathbb{C}^{2n_c+1}$.

- Near the bifurcation point we expect to see classes of solutions with symmetry that breaks the $O(3) \times S^1$ symmetry of the homogeneous steady state $\overline{u}$.
- Equivariant bifurcation theory can tell us about these solutions using symmetry arguments alone.

Symmetry arguments

- V_{n_c} = space of spherical harmonics of degree n_c and $u_{n_c} \in V_{n_c} \oplus V_{n_c}$.
  - The action of $O(3) \times S^1$ on u_{n_c} is determined by its action on $\mathbf{z} \in \mathbb{C}^{2n_c+1}$
- The amplitudes $\mathbf{z}$ evolve according to $\dot{\mathbf{z}} = g(\mathbf{z})$ where

$$\gamma \cdot g(\mathbf{z}) = g(\gamma \cdot \mathbf{z}) \qquad \text{for all } \gamma \in O(3). \tag{2}$$

  - Taylor expansion of g to any given order also commutes with action of S^1.
  - We can use symmetry to compute form of g to cubic order. These amplitude equations contain a number of coefficients which are model dependent

Spatiotemporal symmetries of periodic solutions

- Equivariant Hopf theorem guarantees the existence of periodic solutions of $\dot{\mathbf{z}} = g(\mathbf{z})$ with certain spatiotemporal symmetries (certain classes of subgroups of $O(3) \times S^1$)
  - $(\gamma, \psi) \in O(3) \times S^1$ is a spatiotemporal symmetry of a periodic solution $\mathbf{z}(\tau)$ if
$$(\gamma, \psi) \cdot \mathbf{z}(\tau) \equiv \gamma \cdot \mathbf{z}(\tau + \psi) = \mathbf{z}(\tau) \qquad \text{for all } \tau. \tag{3}$$
  - The subgroups $\Sigma \subset O(3) \times S^1$ which satisfy the Equivariant Hopf theorem fix a two-dimensional subspace of $V_{n_c} \oplus V_{n_c}$, i.e. $\{\mathbf{z} \in \mathbb{C}^{2n_c+1} \ : \ \sigma \cdot \mathbf{z} = \mathbf{z} \ \text{ for all } \sigma \in \Sigma\}$ is two dimensional.
  - Which subgroups of spatiotemporal symmetries satisfy the Equivariant Hopf theorem depends on the value of n_c and have been determined for all values of n_c using group theoretic methods[4],[5].

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[4] M Golubitsky, I Stewart, and D G Schaeffer. *Singularities and Groups in Bifurcation Theory, Volume II*. . Springer Verlag, 1988.

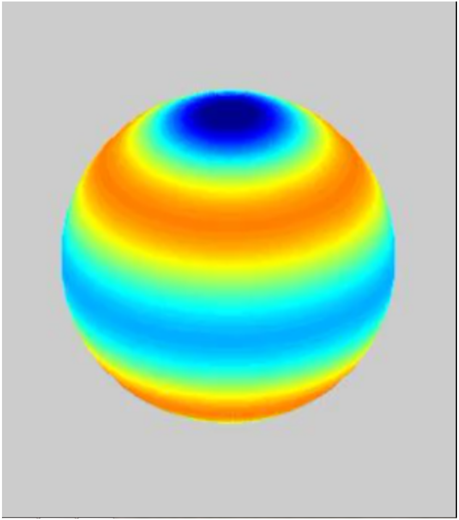
[5] R Sigrist. "Hopf bifurcation on a sphere". In: *Nonlinearity* 23 (2010), pp. 3199–3225.

Example $n_c = 4$

Table: The **C**-axial subgroups of $O(3) \times S^1$ for the natural representations on $V_4 \oplus V_4$. Here $H = J \times \mathbb{Z}_2^c$.

Σ	J	K	$\alpha(H)$	$\mathrm{Fix}(\Sigma)$
$\widetilde{\mathbf{O(2)}}$	$\mathbf{O(2)}$	$\mathbf{O(2)} \times \mathbb{Z}_2^c$	$\mathbb{1}$	$\{(0,0,0,0,z,0,0,0,0)\}$
$\widetilde{\mathbb{O}}$	$\mathbb{O}$	$\mathbb{O} \times \mathbb{Z}_2^c$	$\mathbb{1}$	$\{(\sqrt{5}z,0,0,0,\sqrt{14}z,0,0,0,\sqrt{5}z)\}$
$\widetilde{\mathbb{T}}$	$\mathbb{T}$	$\mathbf{D}_2 \times \mathbb{Z}_2^c$	$\mathbb{Z}_3$	$\{(\sqrt{7}z,0,\sqrt{12}iz,0,-\sqrt{10}z,0,\sqrt{12}iz,0,\sqrt{7}z)\}$
$\widetilde{\mathbf{D}_8}$	$\mathbf{D}_8$	$\mathbf{D}_4 \times \mathbb{Z}_2^c$	$\mathbb{Z}_2$	$\{(z,0,0,0,0,0,0,0,z)\}$
$\widetilde{\mathbf{D}_6}$	$\mathbf{D}_6$	$\mathbf{D}_3 \times \mathbb{Z}_2^c$	$\mathbb{Z}_2$	$\{(0,z,0,0,0,0,0,z,0)\}$
$\widetilde{\mathbf{D}_4}$	$\mathbf{D}_4$	$\mathbf{D}_2 \times \mathbb{Z}_2^c$	$\mathbb{Z}_2$	$\{(0,0,z,0,0,0,z,0,0)\}$
$\widetilde{\mathbf{SO(2)}_4}$	$\mathbf{SO(2)}$	$\mathbb{Z}_4 \times \mathbb{Z}_2^c$	S^1	$\{(z,0,0,0,0,0,0,0,0)\}$
$\widetilde{\mathbf{SO(2)}_3}$	$\mathbf{SO(2)}$	$\mathbb{Z}_3 \times \mathbb{Z}_2^c$	S^1	$\{(0,z,0,0,0,0,0,0,0)\}$
$\widetilde{\mathbf{SO(2)}_2}$	$\mathbf{SO(2)}$	$\mathbb{Z}_2 \times \mathbb{Z}_2^c$	S^1	$\{(0,0,z,0,0,0,0,0,0)\}$
$\widetilde{\mathbf{SO(2)}_1}$	$\mathbf{SO(2)}$	$\mathbb{Z}_2^c$	S^1	$\{(0,0,0,z,0,0,0,0,0)\}$

$n_c = 4$ standing and travelling wave solutions

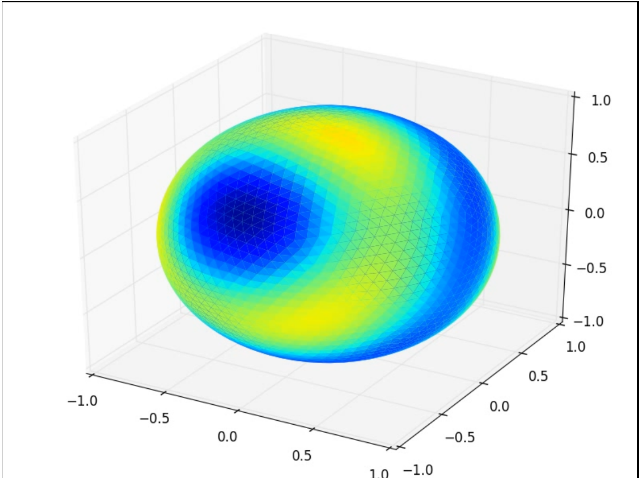


Play/Pause

An $n_c = 4$ periodic solution

- Other solutions to amplitude equations may exist (in addition to those guaranteed by Equivariant Hopf theorem)
- Using a bespoke numerical scheme we can simulate the (discretised) integro-differential equation near the $n_c = 4$ dynamic instability
  - New approach required to solve integro-differential equations with delays on large meshes

An $n_c = 4$ periodic solution



Play/Pause

Stability

- Symmetry can tell you form of the amplitude equations to any given order and maximal solutions
  - For example if $n_c = 1$ modes become unstable at Hopf bifurcation then using equivariance, to cubic order amplitudes $\mathbf{z} = (z_{-1}, z_0, z_1)$ satisfy

$$\dot{z}_m = \mu z_m + A z_m |\mathbf{z}|^2 + B \hat{\mathbf{z}}_m (z_0^2 - 2 z_{-1} z_1)$$

$$|\mathbf{z}|^2 = \sum_{p=-1}^{1} |z_p|^2, \quad \hat{\mathbf{z}} = (-\overline{z_1}, \overline{z_0}, -\overline{z_{-1}}).$$

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- But which solutions are stable depends on values of coefficients - model dependent.
- Weakly nonlinear analysis can be used to determine values of coefficients for particular model.

Weakly nonlinear analysis

- $$u_1(\theta, \phi, t) = \sum_{m=-n_c}^{n_c} z_m(\tau) \mathrm{e}^{i\omega_c t} Y_{n_c}^m(\theta, \phi) + \mathrm{cc},$$

  where $\tau = \epsilon^2 t$.
- Consider perturbation expansion

$$u = \overline{u} + \epsilon u_1 + \epsilon^2 u_2 + \epsilon^3 u_3 + \dots$$
$$f(u) = f(\overline{u}) + \beta_1(u - \overline{u}) + \beta_2(u - \overline{u})^2 + \beta_3(u - \overline{u})^3 + \dots$$

  where $\beta_1 = \beta_c + \epsilon^2 \delta$ and dynamic instability occurs at β_c (δ is a measure of distance from bifurcation).
- Get hierarchy of equations by balancing terms at each order in epsilon.
- Solvability condition (here at order ϵ^3) gives values of coefficients.

- For the example where $n_c = 1$

$$\mu = \frac{\delta(1 + i\omega_c)}{\beta_c}$$

$$A = \frac{(1 + i\omega_c)}{10\pi\beta_c}\left[2\beta_2^2\left(5C_{0,0} + C_{2,0} + 3C_{2,2}\right) + 9\beta_3\right]$$

$$B = \frac{(1 + i\omega_c)}{20\pi\beta_c}\left[2\beta_2^2\left(5C_{0,2} + 6C_{2,0} - 2C_{2,2}\right) + 9\beta_3\right]$$

where

$$C_{m,n} = \frac{G_m(in\omega_c)}{1 + in\omega_c - \beta_c G_m(in\omega_c)}.$$

More interesting solutions?

Direct numerical simulations suggest quasi-periodic behaviour is supported through interaction of modes 0 and 1. (See spectral diagram when $\tau_0 = 0$)

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- Complex conjugate eigenvalues cross through imaginary axis simultaneously.
- Two distinct (not rationally related) emergent frequencies.
- Excited pattern:

$$u_1(\theta, \phi, t) = (w_0 Y_0^0(\theta, \phi)\mathrm{e}^{i\omega_0 t} + \mathrm{cc}) + \sum_{m=0\pm1} (z_m Y_1^m(\theta, \phi)\mathrm{e}^{i\omega_1 t} + \mathrm{cc}),$$

  for slowly evolving w_0 and z_m with $m = 0, \pm 1$, and frequencies ω_0 and ω_1.

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  for slowly evolving w_0 and z_m with $m = 0, \pm 1$, and frequencies ω_0 and ω_1.
- Amplitude equations to cubic order (from symmetry):

$$\frac{\mathrm{d}w_0}{\mathrm{d}\tau} = \mu_1 w_0 + a_1 w_0 |w_0|^2 + a_2 w_0 |\mathbf{z}|^2,$$
$$\frac{\mathrm{d}z_m}{\mathrm{d}\tau} = \mu_2 z_m + b_1 z_m |\mathbf{z}|^2 + b_2 \hat{\mathbf{z}}_m (z_0^2 - 2z_{-1}z_1) + b_3 z_m |w_0|^2, \qquad m = 0, \pm 1,$$

  where $\hat{\mathbf{z}} = (-\overline{z_1}, \overline{z_0}, -\overline{z_{-1}})$.
- Values of the coefficients μ_1, a_1, a_2, μ_2, b_1, b_2, b_3 can be computed using weakly nonlinear analysis.

Secondary bifurcations

Secondary bifurcations to quasi-periodic solutions are possible:

- Similarly to Ermentrout and Cowan[6] (two populations, no delays).
- Letting $z_1 = R\mathrm{e}^{i\phi}$, $w_0 = re^{i\theta}$, $z_0 = z_{-1} = 0$, equations for (r, R) and (θ, ϕ) decouple:

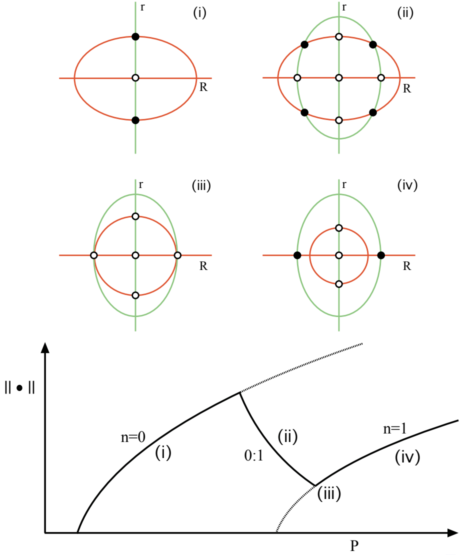
$$\frac{\mathrm{d}r}{\mathrm{d}t} = r\left[\mu_1^R + a_1^R r^2 + a_2^R R^2\right],$$
$$\frac{\mathrm{d}R}{\mathrm{d}t} = R\left[\mu_2^R + b_1^R R^2 + b_3^R r^2\right]$$

  where $\mu_i^R = \operatorname{Re}\mu_i$, $a_i^R = \operatorname{Re} a_i$, $b_i^R = \operatorname{Re} b_i$

- Nullclines are r-axis, the R-axis, and a pair of ellipses (which only exist for certain values of coefficients).
- Suppose coefficients depend on a bifurcation parameter P then we could have ...

[6] G B Ermentrout and J D Cowan. "Secondary bifurcation in neuronal networks". In: *SIAM Journal on Applied Mathematics* 39 (1980), pp. 323–340.

Quasi-periodic solutions



Quasi-periodic solutions

- Transition from a stable $n = 0$ mode to a stable $n = 1$ mode via an intermediate stable 0:1 mode.
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Quasi-periodic solutions

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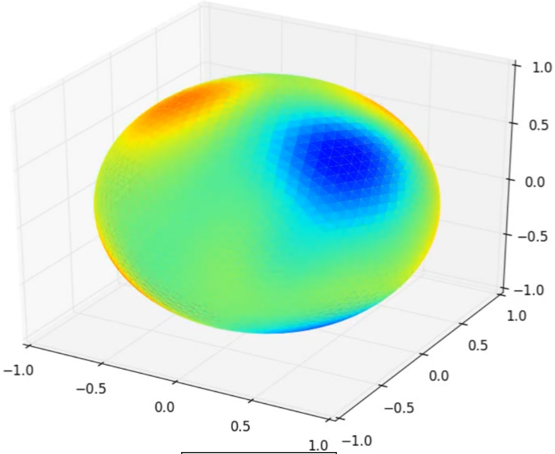
- As noted by Ermentrout and Cowan, this would allow smooth transition from one frequency ($\sim \omega_0$) to another ($\sim \omega_1$),
    - May provide a mechanistic explanation for the gradual transition from tonic to clonic phases during an epileptic seizure.
    - Stage (i) - Small amplitude bulk oscillation (tonic phase).
    - Stage (ii) - Stable 0:1 quasi-periodic solution (tonic-clonic transition).
    - Stage (iv) - Stable $n = 1$ mode (full clonic phase).

A chaotic solution?



Play/Pause

Summary and further work

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- Wide range of spatiotemporal states can be supported in neural models of Nunez type on a sphere with only simple representations for anatomical connectivity, axonal delays and population firing rates.
- Highlighted importance of delays in generating spatiotemporal patterned states.
- Looked at degenerate bifurcations allowing for quasi-periodic behaviour reminiscent of evolution of some epileptic seizures.
- More complex (chaotic?) solutions also found using bespoke numerical scheme.

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Further Work

- Numerical scheme not limited to spherical geometry - can also handle folded cortical structures.
- Localised states (working memory) for steep sigmoidal firing rate and Mexican-hat connectivity.

Thank you

Coming soon to arXiv

S Coombes, R Nicks, and S Visser. "Standing and travelling waves in a spherical brain model: the Nunez model revisited". In: ()