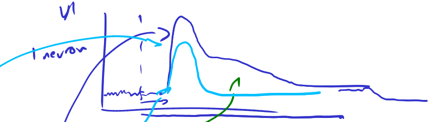
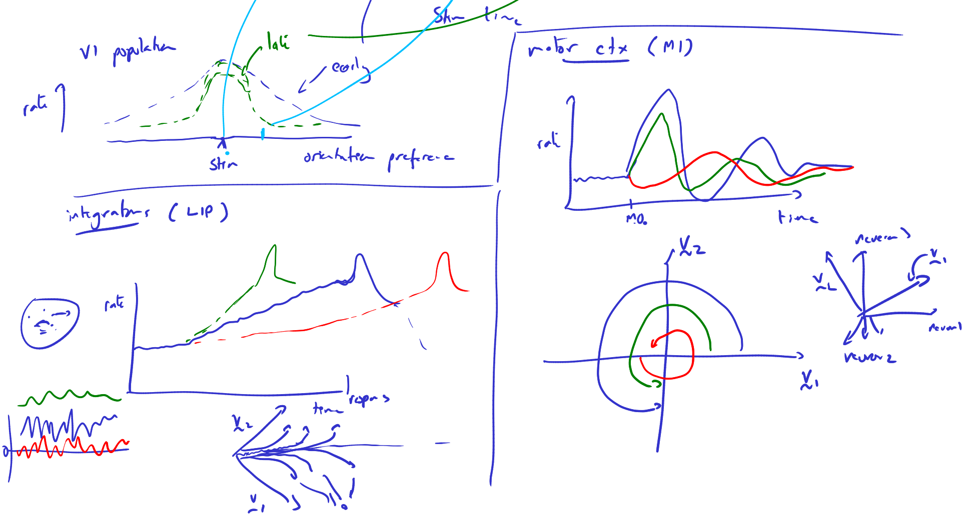
Population Dynamics

March 2024

Traces of dynamics

- visual transients
- motor cortex
- integrators





Recurrent networks

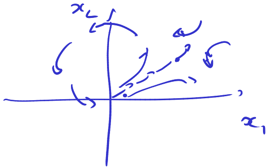
- First order dynamics (for input $\mathbf{u}$:

  $$\tau \dot{\mathbf{x}} = F(\mathbf{x}, \mathbf{u})$$

  characterised by properties of F.
- Neural population models (Wilson-Cowan)

  $$\tau \dot{\mathbf{x}} = -\mathbf{x} + f(A\mathbf{x} + \mathbf{u}) \qquad \text{or} \qquad \tau \dot{\mathbf{x}} = -\mathbf{x} + Af(\mathbf{x}) + \mathbf{u}$$

  where f acts element-wise. (The difference is roughly whether $\mathbf{x}$ models firing rate or membrane potential).
- Dynamics of pyramidal/projection neurons alone may be second- or higher-order through interations with other cell types and other areas
- Can be expressed as first order in more variables: *state space* and *flows*.



↳ (position, momentum)

Linear dynamics

- May be a good phenomenlogical fit for dynamics in some areas/epochs.
- Helps to understand non-linear systems through linearisation.

continuous-time

$$\tau \dot{\mathbf{x}} = A\mathbf{x}$$

propagators $$\mathbf{x}(t) = e^{At/\tau}\mathbf{x}(0)$$

discrete-time

$$\mathbf{x}_{t+1} = A\mathbf{x}_t$$

$$\mathbf{x}_t = A^t\mathbf{x}_0$$

Eigenmodes

$A\underset{\sim}{u} = \lambda \underset{\sim}{u} \Rightarrow AV = V\Lambda$

$$A = V\Lambda V^{-1}$$

$V = \begin{bmatrix} | & | & & | \\ \underset{\sim}{u}_1 & \underset{\sim}{u}_2 & \cdots & \underset{\sim}{u}_D \\ | & | & & | \end{bmatrix}$ $\Lambda = \begin{bmatrix} \lambda_1 & & 0 \\ & \ddots & \\ 0 & & \lambda_D \end{bmatrix}$

$(V\Lambda V^{-1})^t = V\Lambda \cancel{V^{-1}V}\Lambda \cancel{V^{-1}} \cdots$

$$\mathbf{x}(t) = e^{\overset{\to V\Lambda V^{-1}}{At/\tau}}\mathbf{x}(0) = Ve^{\Lambda t/\tau}V^{-1}\mathbf{x}(0)$$

$$\Rightarrow V^{-1}\mathbf{x}(t) = e^{\Lambda t/\tau}V^{-1}\mathbf{x}(0)$$

$$\mathbf{x}_t = A^t\mathbf{x}_0 = V\Lambda^t V^{-1}\mathbf{x}_0$$

$$\underbrace{V^{-1}\mathbf{x}_t} = \cancel{V}\Lambda^t \underbrace{V^{-1}\mathbf{x}_0}$$

$\begin{bmatrix} \\ v \\ \\ \end{bmatrix}(t) = \begin{bmatrix} e^{\lambda_1 t/\tau} & & \\ & e^{\lambda_2 t/\tau} & 0 \\ 0 & & \ddots \end{bmatrix} \begin{bmatrix} \\ v \\ \\ \end{bmatrix}(0)$

$\Lambda^t = \begin{bmatrix} \lambda_1^t & & 0 \\ & \ddots & \\ 0 & & \lambda_D^t \end{bmatrix}$

Dynamics in $\mathbf{v} = V^{-1}\mathbf{x}$ are decoupled.

$$v_i(t) = e^{\lambda_i t/\tau}v_i(0)$$

$$v_{it} = \lambda_i^t v_{i0}$$

Stability dictated by (real part) of eigenvalues.

$\lambda_i \in \mathbb{R}$

$\lambda_i < 0$	stable, $v_i(\infty) = 0$	$\lvert\lambda_i\rvert < 1$
$\lambda_i = 0$	linear equilibrium	$\lvert\lambda_i\rvert = 1$
$\lambda_i > 0$	unstable	$\lvert\lambda_i\rvert > 1$

Complex modes

$$A \in \mathbb{R}^{D\times D} \Rightarrow \lambda_i \in \mathbb{C}\setminus\mathbb{R} \Rightarrow \exists\ \lambda_k = \lambda_i^*$$

$$\underset{\sim}{u}_k = \underset{\sim}{u}_i^*$$

$$\underset{\sim}{x}(0) \in \text{span}(\underset{\sim}{u}_i, \underset{\sim}{u}_i^*)$$

real

$$v_k = \underset{\sim}{u}_k^T \underset{\sim}{x} = \underset{\sim}{u}_i^{*T} \underset{\sim}{x} = v_i^*$$

$$\underset{\sim}{x}(t) = v_i^{(t)} \underset{\sim}{u}_i + v_k^{(t)} \underset{\sim}{u}_k$$

$\tau = 1$

$$v_i(t) = e^{\lambda_i t} v_i(0)$$

$$= e^{(\text{Re}\,\lambda_i + j\,\text{Im}\,\lambda_i)t} v_i(0)$$

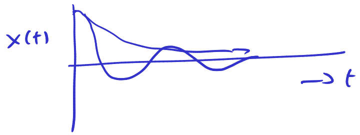
$$= e^{\lambda_i^{Re} t} e^{j\lambda_i^{Im} t} \left(v_i^{Re}(0) + j v_i^{Im}(0)\right)$$

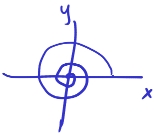
$$v_k(t) = v_i^*(t) = e^{\lambda_i^{Re} t} e^{-j\lambda_i^{Im}(t)} \left(v_i^{Re}(0) - j v_i^{Im}(0)\right)$$

$$\underset{\sim}{x}(t) = e^{\lambda_i^{Re} t}\left(2\cos(\lambda_i^{Im} t)\, v_i^{Re}(0) \cancelto{0}{+2j\sin(\lambda^{Im}(t))\, v_i^{Im}(0)}\right)$$

damped $\lambda_i^{Re} < 0$

cosine

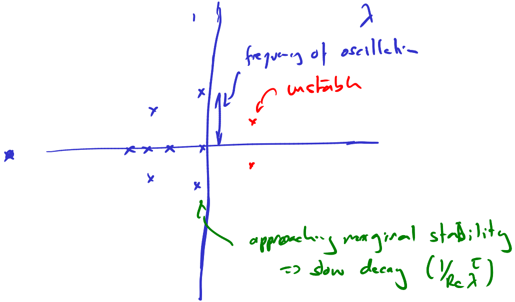




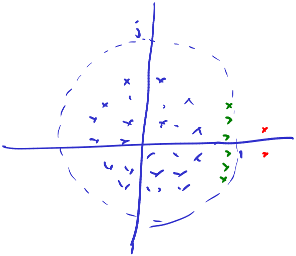
~~Complex modes~~

Eigendescription of Dynamical System

Continuous



discrete



$$V(t) = e^{\lambda_i^{Re} t/\tau}\, V(0)$$

$1/\lambda_i^{Re}$ → effective τ scaling

Input/output coupling

- "Left" and "right" eigenvectors dictate coupling.
- Measured transients are sums of (decaying, complex) exponentials.

Eigenvalues give dynamics of eigenprojection $\underset{\sim}{v} = V^{-1}\underset{\sim}{x}$. Real system $\underset{\sim}{x}(t) = V\underset{\sim}{v}(t)$.

$V^{-1} = V^{T} \Rightarrow \underline{AA^{T}} = V\Lambda V^{-1} V^{-T}\Lambda^{T} V^{T} = V\Lambda \cancel{V^{-1}V}\Lambda V^{-1} = A^2 = \underline{A^{T}A}$ $\quad$ <u>Normal</u>

$\rightarrow$ special case $\qquad \underset{\sim}{u}_i \cdot \underset{\sim}{u}_j = \delta_{ij}$ $\rightarrow$ just a "rotation"

General:

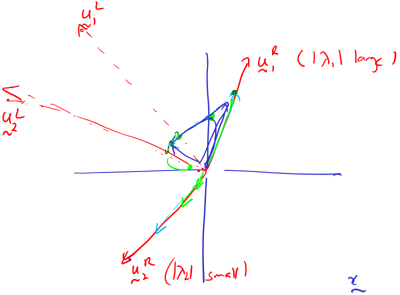
$$V^{-1} = \begin{bmatrix} \underset{\sim}{u}^{L} \text{ (rows)} \end{bmatrix} \cdot \begin{bmatrix} V: \underset{\sim}{u}^{R} \text{ (columns)} \end{bmatrix} = I \Rightarrow \underset{\sim}{u}_i^{L} \cdot \underset{\sim}{u}_j^{R} = \delta_{ij}$$

$AV = V\Lambda \Rightarrow A\underset{\sim}{u}_i^{R} = \lambda_i \underset{\sim}{u}_i^{R}$ $\Leftarrow$ "right" eigenvectors

$V^{-1}A = \Lambda V^{-1} \Rightarrow \underset{\sim}{u}_i^{L} A = \lambda_i \underset{\sim}{u}_i^{L}$ $\Leftarrow$ "left" eigenvectors rows of V^{-1}

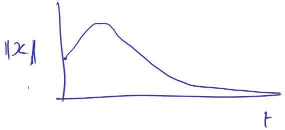
Non-normality

- Eigenvector geometry: normal or non-normal A.
- (Stable) normal system with real eigenvalues always decays.
- (Stable) non-normal system may show transient amplication even with real eigenvalues.



$$\underset{\sim}{x}(0) = \overbrace{\begin{bmatrix} | & | \\ u_1^R & u_2^R \\ | & | \end{bmatrix}}^{V} \underset{\sim}{v} \qquad \underset{\sim}{v} = \overbrace{\begin{bmatrix} - & u_1^L & - \\ - & u_2^L & - \end{bmatrix}}^{V^{-1}} \underset{\sim}{x}$$

$$\underset{\sim}{x}(t) = e^{\lambda_1 t} v_1(0)\, \underset{\sim}{u}_1^R + e^{\lambda_2 t} v_2(0)\, \underset{\sim}{u}_2^R$$



Non-normality: SVD and Schur decomposition

- Extended time constants.
- E-I systems are always non-normal.

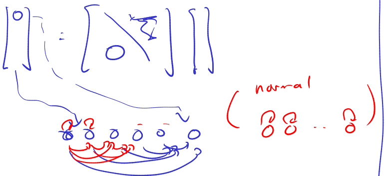
Schur decomposition

$A = U T U^T$ $\quad (V \Lambda V^{-1})$ unique

U orthogonal

T is upper triangular

$U^T x_{t+1} = T U^T x_t$



→ transient amplification

→ effective time constant $> 1/|\log \lambda_{max}|$

SVD

$A = U S V^T$ $\quad \left(\begin{array}{l} U: \text{eigenvectors of } AA^T \\ V: \quad " \quad " \quad A^TA \end{array} \right)$

$\underset{\sim}{x}_{t+1} = A \underset{\sim}{x}_t$

$= U S \underbrace{V^T \underset{\sim}{x}_t}$

orthogonal basis projection

scaling

orthogonal basis reconstruction

$\approx \left\{ \begin{array}{l} \underset{\sim}{u}_1 \parallel \underset{\sim}{v}_1, \; s_1 > 1 \Rightarrow \text{unstable} \\ \underset{\sim}{u}_1 \cdot \underset{\sim}{v}_1 < s_1 \end{array} \right.$

E-I system

$A = \left[\begin{array}{c|c} >0 & <0 \end{array} \right] \begin{bmatrix} E \\ I \end{bmatrix}$

$AA^T = \left[\begin{array}{c|c} >0 & <0 \end{array} \right] \begin{bmatrix} >0 \\ \hline <0 \end{bmatrix} > 0$

$A^T A = \left[\begin{array}{c|c} >0 & <0 \\ \hline <0 & >0 \end{array} \right]$

Linear systems with input

$$\left.\begin{array}{rcl} \dot{\mathbf{x}} & = & A\mathbf{x} + B\mathbf{u} \\ \mathbf{y} & = & C\mathbf{x} + D\mathbf{u} \end{array}\right] \text{LTI system (linear systems and control theory)}$$

- Transfer functions

Linear systems with input

- Transfer functions

Stochastic linear systems

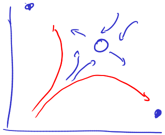
- Stationarity.
- Lyapunov equations.

Grammians: controllability and observability

Describing population activity with dynamics

Non-linear dynamics

$$\dot{x} = 0 \Rightarrow f(x, u) = 0$$



Fixed point and attractors.

- point attractors and decision boundaries
- line attractors
- limit cycles and pseudoperiodicity (chaos)

Input-shaped dynamics.