Introduction to Computational Modelling (Part 2): Network Dynamics

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25 Aug 2025



Ordinary/Partial Differential Equations (ODEs/PDEs) for modelling neuronal network models:

- biophysical (HH/conductance-based) models
- spiking (IF) neuronal network models etc.

with synaptic models

ODEs, or more generally, dynamical systems

<u>Dynamical systems can be represented in the general forms:</u>

Differential equations:
$$\frac{dx}{dt} = F(x, p, t)$$
 for continuous dynamics

Discrete maps: $x_{k+1} = G(x_k, p) x_{p+1}$ for discrete dynamics

with state vector $\mathbf{x} = (x_1, x_2, ..., x_n)$, and a set of parameters $\mathbf{p} = (p_1, p_2, ..., p_n)$.

Useful tool for modelling and analysis in many fields: physics, engineering, chemistry, biology, computer science, psychology, finance, economics, sociology, etc.

→ Focus: Continuous dynamics

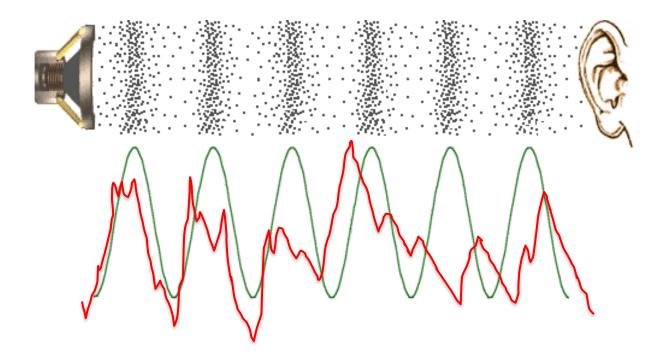
Are there ways to theoretically analyse and conceptually understand neural networks? Not just to fit and predict data? (explainable / interpretable)

How can network model behaviour be used to account for observable behaviour and understand their underlying cognitive processing?

Wait a minute... But we have previously discussed that the activity of neurons come in the form of discrete action potentials or spikes in neurons.

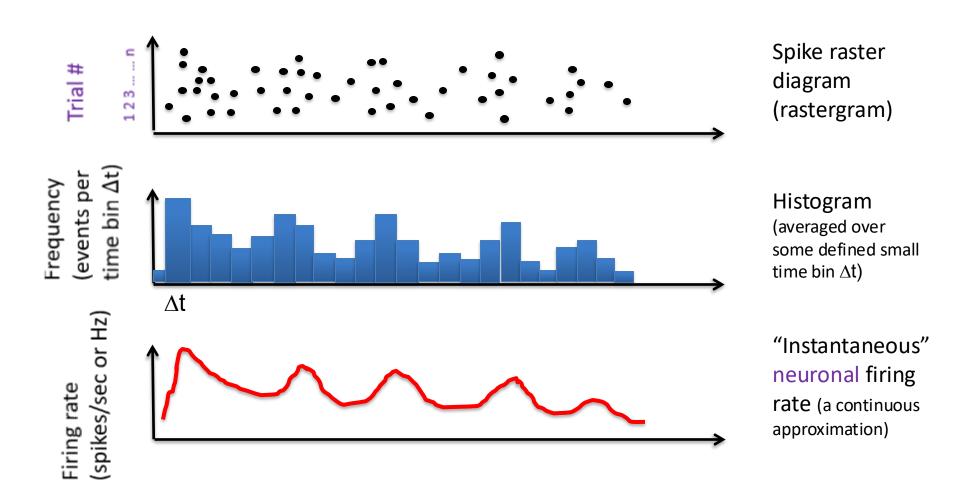
How can we relate that to continuous stream of neural activities (i.e. time series) to be modelled with differential equations?

Transforming from discretised to continuous activity

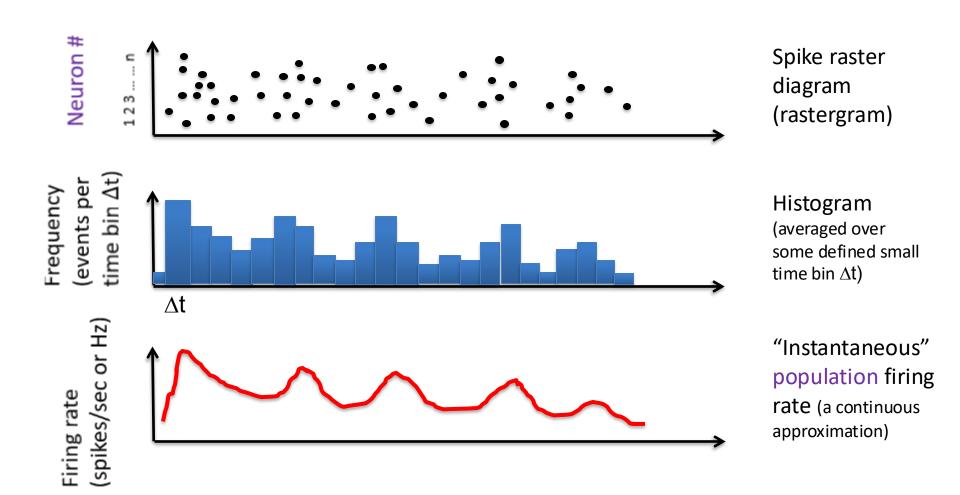


Analogy: from air particle movement to (approximate) continuous sound wave

Transforming from discretised noisy activity (neuronal spike times) to continuous activity (neuronal firing rate)



We can also do it for multiple (noisy) neurons by <u>averaging</u> over the neuronal activities (neuronal population activities)



Evidence of (firing) rate coding

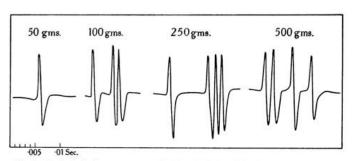


Fig. 5. Analysis of electrometer records, Exp. 2, showing that the size of individual impulses does not vary with the stimulus.

Adrian (1926)

- "Tuning" curves of primary visual cortex (Hubel and Wiesel)
- Motor preparation, movement, reaching (Georgopoulus, 1982)
- Oculomotor movement
- Head direction
- Decision-making
- Various forms of memory encoding and retrieval etc.

Neural response (spikes/sec) Stimulus orientation (deg) Hubel & Wiesel, 1968 PCA110.S01 Georgopoulus (1982) 135 225 315° НАПРЯМОК РУХУ

Firing rate models and their variants can relate to dynamics in neural recording

 Local field potential (LFP; electrical field in extracellular space)

http://www.scholarpedia.org/article/Local field potential

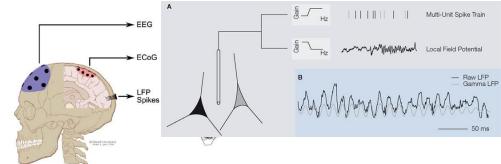
Electrical signals from electroencephalogram (EEG)

http://www.scholarpedia.org/article/Electroencephalogram

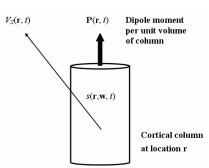
(or magnetic signals with MEG)

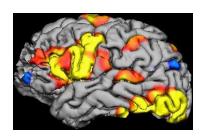
Functional MRI (fMRI) BOLD signals
 Heeger and Ress, Nat. Rev. Neurosci., 2002

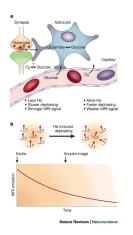
BOLD: Blood oxygen level dependent











Advantages of firing rate models:

- computationally efficient do not have to simulate every single neuronal spiking. Just treat activity as continuous function and averaged over population of neurons. Current computational neuroscience and NeuroAl even treat a neural unit in rate models as a single neuron to account for experimental data!
- used in most artificial neural networks (easier to train)
- more analytically tractable than spiking neural network models, and hence more conducive for deeper conceptual understanding of cognitive processes

(Firing) Rate Models

The instantaneous firing rate for a homogeneous population of neurons can be described by :

$$\tau_i \frac{df_i}{dt} = -f_i + F_i(I_i) \qquad I_i = \sum_i w_{ij} f_j + I_{i,ext}$$

where f_i is the mean firing rate for the i^{th} population, I_i is the total input current into a neuron averaged within the i^{th} population, w_{ij} is the synaptic weight from population j to i, and F_i is its (generally nonlinear) input-output (transfer) function. These 2 equations "close the loop".

Wilson & Cowan, 1972; 1973

Sometimes, in neural mass modelling, the population i's mean (postsynaptic) membrane potential V_i is used instead of current I_i .

Freeman, 1975; Jansen & Rit, 1995

Among the most influential theoretical neuroscience papers:

Wilson & Cowan (1972) Excitatory and inhibitory interactions in localized populations of model neurons. Biophysical Journal 12:1-24. Wilson & Cowan (1973) A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue. Kybernetik 13:33-80.

For a simple "threshold-linear" input-output (transfer/activation) function, or rectifier (ReLU) activation function,

$$f = \begin{bmatrix} I - \theta \end{bmatrix}_{+}$$

$$\theta$$

$$\tau_i \frac{df_i}{dt} = -f_i + F_i(I_i) = -f_i + [I_i - \theta_i]_+$$

For
$$I_i > \theta_i$$
, and $I_i = \sum_i w_{ij} f_j + I_{i,ext} + \theta_i$

$$\tau_i \frac{df_i}{dt} = -f_i + I_i$$

$$= -f_i + \sum_i w_{ij} f_j + I_{i,ext}$$

Fully linear regime

or in matrix/linear algebraic form

$$\frac{d\mathbf{f}}{dt} = \mathbf{W} \cdot \mathbf{f} + \mathbf{I}_{ext}$$

where f and I_{ext} are vectors, and W is $(-\mathbb{I} + w_{ij})$ a matrix with \mathbb{I} being a identity/unit matrix.

What value of τ_i to use? Based on neuronal or synaptic dynamics?

Off-track: Multiple timescale system

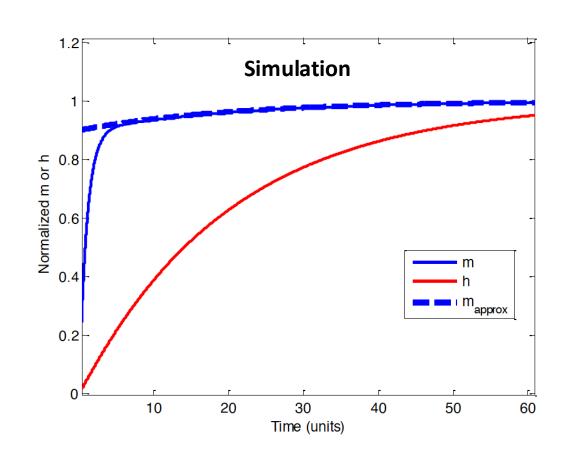
Suppose we have a system consisting of 2 coupled variables m and h with very different timescales described by:

$$\tau_m \frac{dm}{dt} = -m + 0.1 \, \frac{h}{h} + 0.9$$

$$\tau_h \frac{dh}{dt} = -h + 0.1 m + 0.9$$

where $\tau_m = 1$ and $\tau_h = 20$, i.e. an order of magnitude different. This means variable m is intrinsically much faster than variable h.

m quickly reaches its steadystate value (dashed line) while h continues to vary



Method: Separation of timescales, stiff ODEs

Multiple timescale neural networks

In (firing) rate models,

Case I: For
$$\tau_m >> \tau_{syn}$$

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$$\tau_{\rm m} >> \tau_{\rm syn}$$

$$I_{syn,ij} = g_{syn,ij} \sum_{j} \delta \left(t - t_{j}\right)$$

$$\left\langle I_{syn,ij} \right\rangle \sim g_{syn,ij} f_{j}$$

$$\tau_{m,i} \frac{df_{i}}{dt} = -f_{i} + F_{i}(\left\langle I_{syn,ij} \right\rangle)$$

Instantaneous synapses

Averaged over neurons

Governed by membrane potential dynamics (Wilson-Cowan)

Case II: For $\tau_{m} << \tau_{syn}$

(or with large noise)

we cannot ignore synaptic dynamics

$$\frac{dI_{syn,ij}}{dt} = -\frac{I_{ij}}{\tau_{syn,ij}} + g_{syn,ij} \sum_{i} \delta(t - t_{j})$$

$$\frac{d\langle I_{syn,ij}\rangle}{dt} = -\frac{\langle I_{syn,ij}\rangle}{\tau_{syn,ij}} + g_{syn,ij} f_j$$

Governed by synaptic dynamics

while
$$\frac{df_i}{dt} \approx 0$$
, i.e. $f_i = F_i((I_{syn,ij}))$

Instantaneous neurons

Hold on! But where is the driving force (V-E) in the synaptic currents/weights? We have so far assumed them to be approximately constant. It turns out that Case II in previous slide still holds (see Ermentrout and Terman, Mathematical Foundations of Neuroscience, book chapter 11.1.2), but with the form:

$$\frac{ds}{dt} = -\frac{s}{\tau_{syn}} + \alpha F(I) (1 - s)$$

where s is the population averaged synaptic gating variable describing the dynamics of synapses. The qualitative coarser network effects can still be captured.

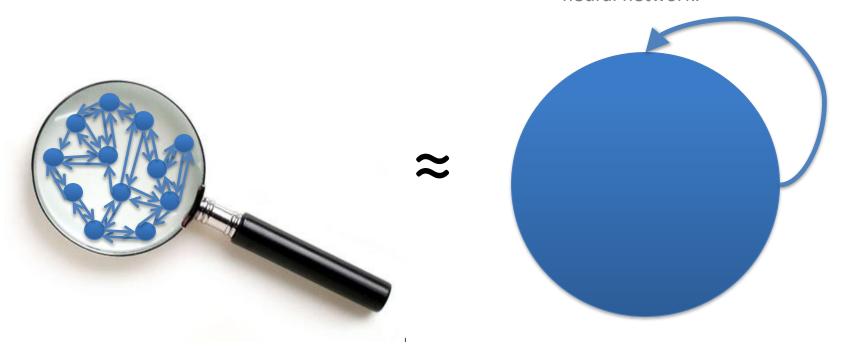
More realistic techniques can be used for more realistic spiking neural network models — (extended) "mean-field" approach. (Requires multiple nonlinearly coupled equations to be solved simultaneously i.e. self-consistency calculations!)

E.g. Renart, Brunel and Wang, Computational Neuroscience: A Comprehensive Approach, book chapter 15, 2003; Brunel and Wang, J. Comput. Neurosci., 2001; Nicola and Cambell, J. Comput. Neurosci., 2013; Amit and Tsodyks, Network, 1991a; 1991b.

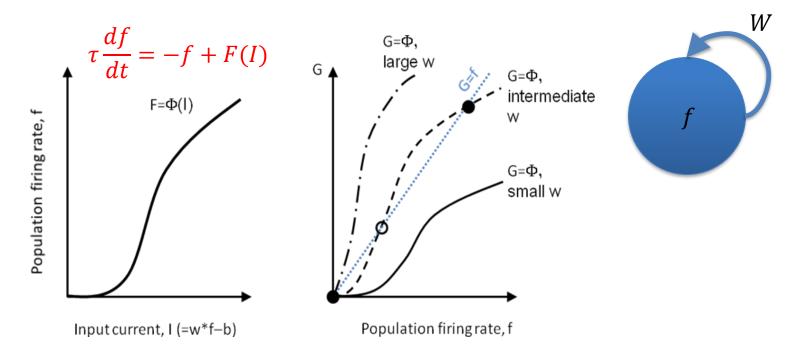
A (homogeneous) population of neurons recurrently connected – an autapse

The simplest recurrent neural network (RNN) model

"Autapse (auto-synapse)": effectively a "self-connected" system. The simplest recurrent neural network.



Multi-stability model for memory encoding Categorical (discretised) memory



Suppose F is some nonlinear input-output function Φ (e.g. a sigmoidal function) [left panel]. At steady state, $\frac{df}{dt} = 0$, which means the firing rate $f = F(I) = \Phi(Wf - b)$.

When (function) F is plotted as a function against (variable) f, the intersection points between the functions G = f (i.e. diagonal line) and $G = \Phi$ will produce the steady states [line intersections in circles] of the system, by the definition of steady state.

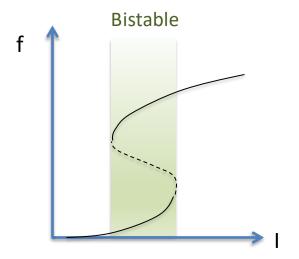
"Working" memory: remembering a brief stimulus

Effective input-output function:

Weak recurrent self-excitation

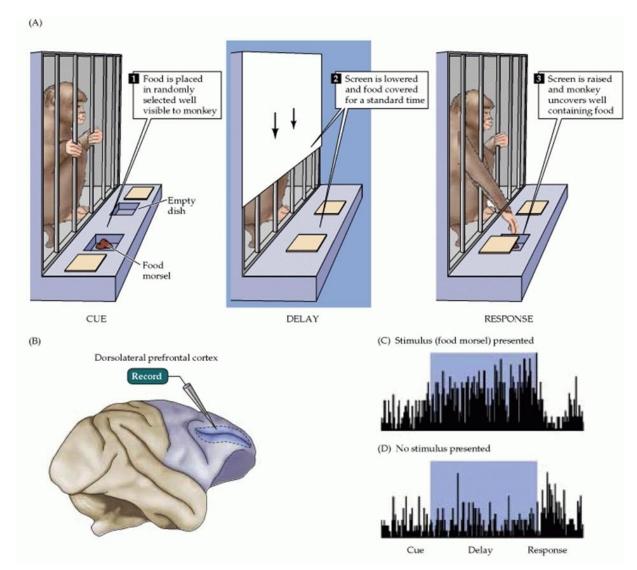
f

Sufficiently strong recurrent self-excitation → "kinks"



Hysteresis as in a magnetic system being magnetised!

Evidence of persistent activity to support working memory during delay period

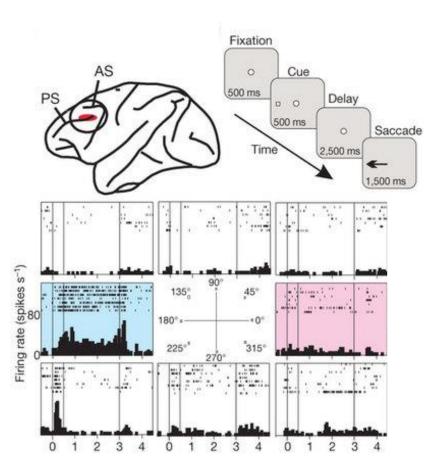


Joaquin Fuster

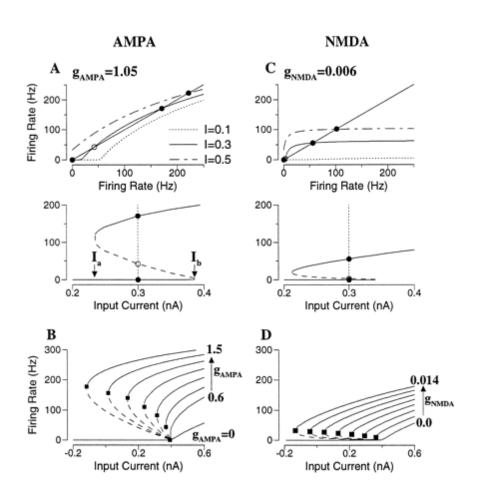


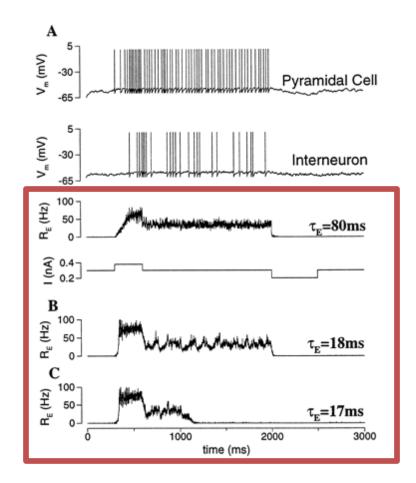
Patricia Goldman-Rakic





Importance of slow (e.g. NMDA-mediated) synapses for robust, low-firing persistent activity





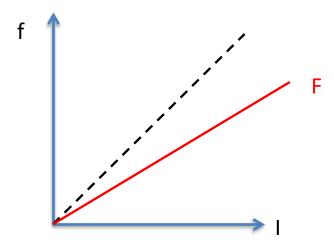


X-J Wang, J. Neurosci., 1999

What if the input-output function *F* is linear?

Parametric (continuous) memory

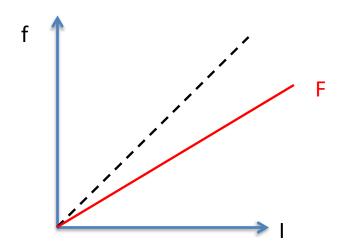
Weak recurrent excitation



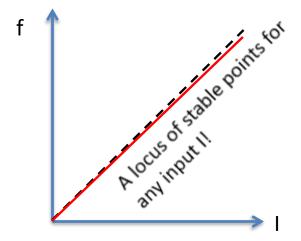
What if the input-output function *F* is linear?

Parametric (continuous) memory

Weak recurrent excitation

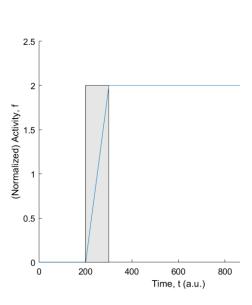


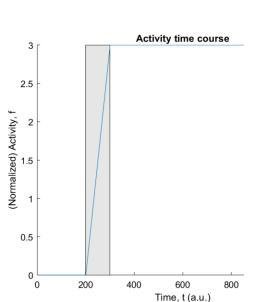
Sufficiently strong recurrent excitation, i.e. memorise continuous values perfectly

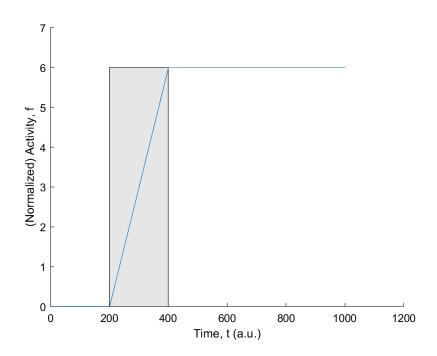


What if the input-output function *F* is linear?

Parametric (continuous) memory







Input: 0.2
Duration: 100

Input: 0.3
Duration: 100

Input: 0.3
Duration: 200

Parametric memory's stability and effective temporal dynamics controlled by synaptic weight W Seung (2003)

Suppose F is linear, then $\tau \frac{df}{dt} = -f + (Wf + b) = (W - 1)f + b$, absorbing the leak term.

- If W > 1, then the solution f amplifies exponentially without any upper bound, i.e. f keeps growing.
- If W < 1, then the solution f can reach a certain stable steady state (ss), obtained by setting $\frac{df}{dt} = 0$, i.e. (1 W)f = b or

$$f_{ss} = b/(1-W)$$

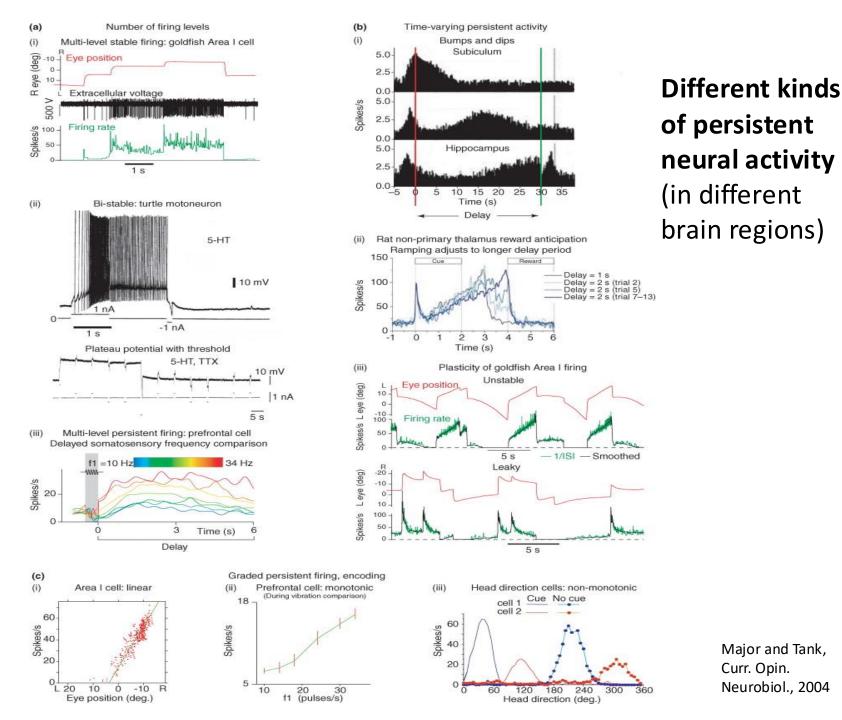
Thus, if 0 < W < 1, the network can reach a steady state level which is dependent on not only the input but can be amplified if $W \approx 1^-$. Furthermore, the time constant to reach this steady state also depends on W; rewriting the equation,

$$\frac{\tau}{1-W}\frac{\mathrm{df}}{\mathrm{dt}} = -f + \frac{b}{1-W}$$

one can see that the effective time constant is

$$\tau_{eff} = \frac{\tau}{1 - W}$$

and if $W \approx 1^-$, the dynamics will be very slow. If W = 1, $f = \frac{b}{\tau} t + constant$, i.e. a perfect integrator with no information leakage.



Major and Tank, Curr. Opin. Neurobiol., 2004

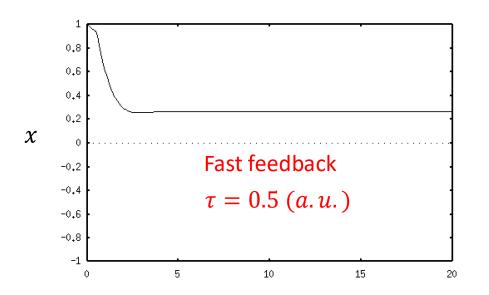
Example: A simple self-inhibitory feedback population of neurons with time delay

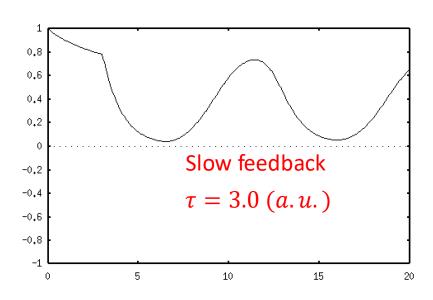
$$\frac{dx}{dt} = -x + F(x - \tau)$$

$$F(x) = \frac{1}{1 + \exp(-x)}$$

Time delay, τ

For some inhibitory feedback delay of time au





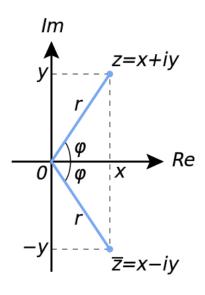
Time t (a.u.)

What if we have 2 neural populations/units interacting?

Off-track refresher: Complex numbers

 $i^2=-1$ or $i=\sqrt{-1}$, i.e. if $i^2=-y$, $i=\sqrt{-1}\times y=\sqrt{-1}\sqrt{y}=i$ y=1 In general: x+iy, where x is real (Re) while iy is imaginary (Im)

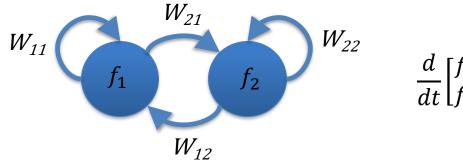




Geometric representation: Complex plane

Imaginary numbers, useful for the construction of non-real complex numbers, have essential concrete applications in a variety of scientific and related areas such as dynamical systems theory, signal processing, control theory, electromagnetism, fluid dynamics, quantum mechanics, cartography, and vibration analysis.

Example: State space and stability in 2-dimensional systems



$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix}$$
 2 general coupled nonlinear equations

in vector form

Suppose we absorb the leak term and the time constant into the weights W and bias input b

$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

For linear coupled equations in matrix form

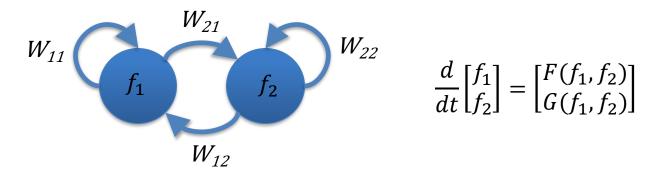
We can rewrite it in a more compact manner as $\frac{d\mathbf{f}}{dt} = \mathbf{W}\mathbf{f} + \mathbf{b}$

where
$$\mathbf{f}=\begin{bmatrix}f_1\\f_2\end{bmatrix}$$
 , $\mathbf{W}=\begin{bmatrix}W_{11}&W_{12}\\W_{21}&W_{22}\end{bmatrix}$, and $\mathbf{b}=\begin{bmatrix}b_1\\b_2\end{bmatrix}$.

Note that we can always define a new set of coordinates such that the "origin" lies at coordinate $\begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$. This simplifies the equation to

$$\frac{d\mathbf{f}}{dt} = \mathbf{W}\mathbf{f}$$

Example: State space and stability in 2-dimensional systems



In in principle, we can determine the steady states (ss) of the system by setting

$$\frac{d\mathbf{f}}{dt} = \mathbf{0}$$
 and solving for $\mathbf{f}_{ss} = \begin{bmatrix} f_{1,ss} \\ f_{2,ss} \end{bmatrix}$.

Next, we find the Jacobian matrix J of matrix W evaluated at the steady state f_{ss} .

Jacobian matrix,
$$J = \begin{bmatrix} \frac{\partial F}{\partial f_1} & \frac{\partial F}{\partial f_2} \\ \frac{\partial G}{\partial f_1} & \frac{\partial G}{\partial f_2} \end{bmatrix}$$

$$=\begin{bmatrix} \frac{\partial (W_{11}f_1+W_{12}f_2)}{\partial f_1} & \frac{\partial (W_{11}f_1+W_{12}f_2)}{\partial f_2} \\ \frac{\partial (W_{21}f_1+W_{22}f_2)}{\partial f_1} & \frac{\partial (W_{21}f_1+W_{22}f_2)}{\partial f_2} \end{bmatrix}$$
 For linear case

The (local) stability of the system will depend on the characteristics of the **eigenvalues** λ_1 and λ_2 of this Jacobian matrix at that steady state.

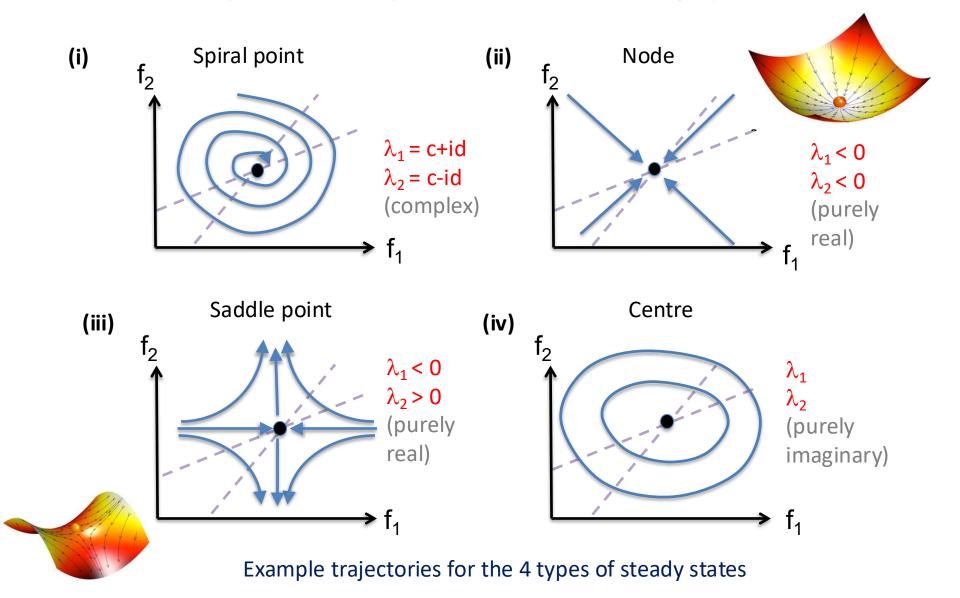
Example: State space and stability in 2-dimensional systems

In 2-D activity (phase or state) space, there are **4 cases**:

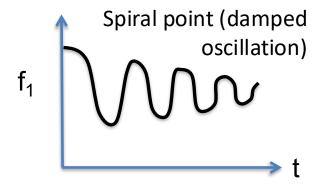
- (i) **Spiral point**, which can result in damped (or amplifying) oscillation of the system. Requires eigenvalues to be both real (both negative for damped, and positive for amplifying) and non-zero imaginary parts;
- (ii) **Node**, which can result in strictly attracting towards (or repelling away) from certain activity level. Requires both eigenvalue to be strictly negative (or positive) with no imaginary parts;
- (iii) Saddle point, which can result in a mixture of attracting and repelling dynamics. Requires one eigenvalue to be strictly positive and the other negative, none with imaginary parts;
- (iv) Center, which can result in oscillatory behaviour. Requires both eigenvalues to be strictly imaginary with no real parts.

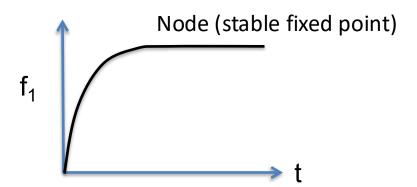
4 cases of stability in 2-dimensional state/phase space

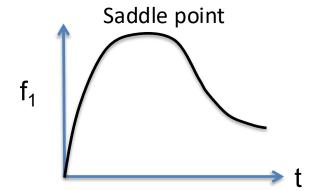
2-D systems have 2 eigenvalues and 2 corresponding eigenvectors

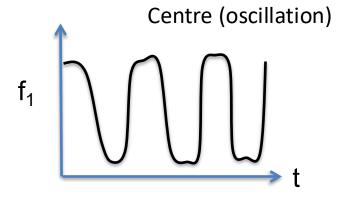


Examples of activity time courses for one of the neural units f₁









Mimicking cognitive functions?

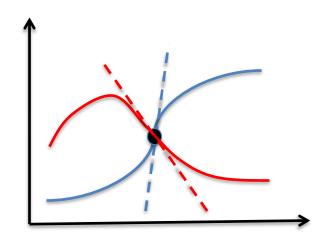
- Stable node: Storing information for cognitive tasks. Short-term or long-term memory; decisions.
- Oscillation (centre): Spontaneous neural oscillations; timing or clock (e.g. circadian); integration through binding of information; motor activity or locomotion (central pattern generators); perceptual rivalry; computational neuroimaging (e.g. EEG, MEG).
- Metastable (saddle): Creates barrier between cognitive (e.g. memory) states; decisions.

Technique discussed can be extended to N>2 dimensional coupled systems

Of course, the dynamics can get more complex

What if the system is nonlinear?

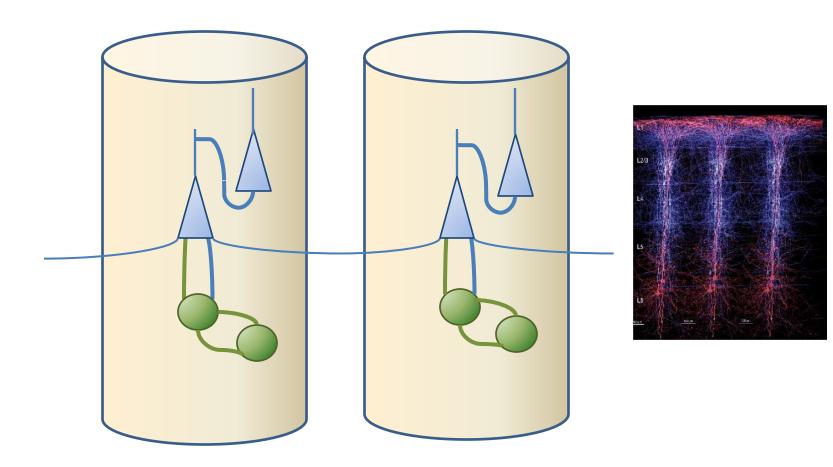
We can still use the same technique (linear stability analysis) as for linear system – It turns out that according to a mathematical theorem, the stability of a nonlinear system's dynamics *sufficiently near a steady state* is the **same** as the linear system near the *same* steady state!



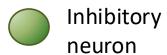
But we may also need to look at the *global* dynamics which may not be captured by local dynamics.

Example: Excitatory-inhibitory networks

Cartoon representation of cortical "columns"

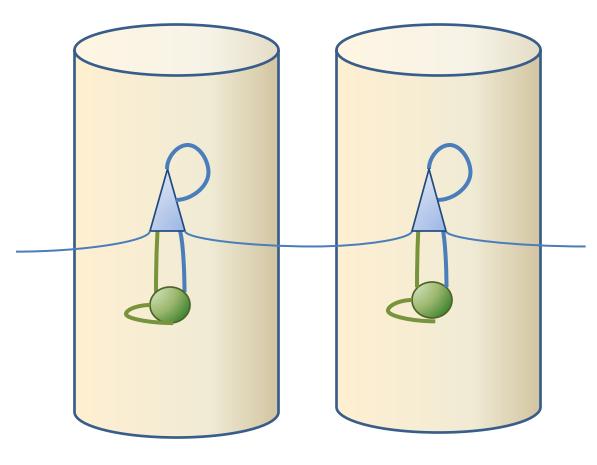




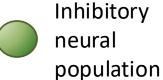


Example: Excitatory-inhibitory networks

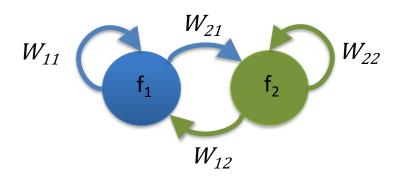
A simplified network architecture (assuming homogenous neurons)



Excitatory neural population



What kind of dynamics can an excitatoryinhibitory coupled network produce?



$$W_{22} \qquad \frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix}$$

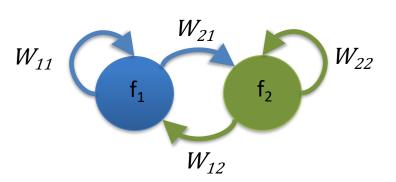
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

Suppose f_1 is an excitatory population of neurons, and f_2 an inhibitory population of neurons, then

$$W_{11} > 0$$
, $W_{12} < 0$, $W_{21} > 0$, $W_{22} < 0$

according to **Dale's principle**, which states that a neuron performs the same chemical action at all of its synaptic connections to other cells, regardless of the identity of the target cell.

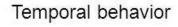
What kind of dynamics can an excitatoryinhibitory coupled network produce?



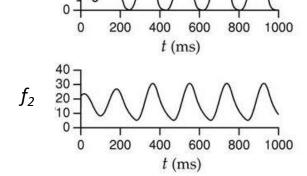
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix}$$

$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} W_{11} & W_{12} \\ W_{21} & W_{22} \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

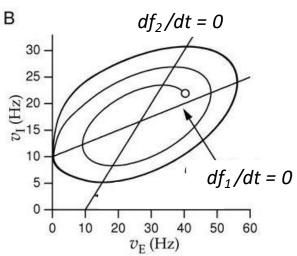
Oscillations



Α

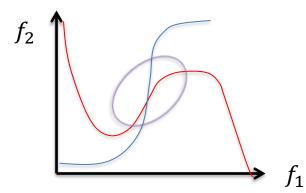


Unstable fixed point – limit cycle



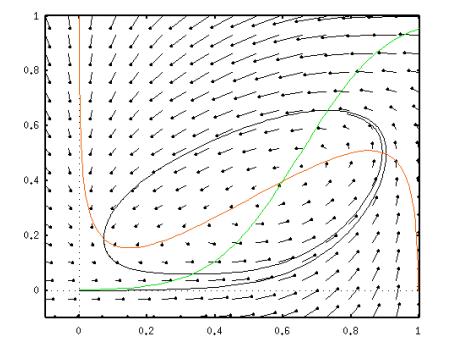
Linear
Nullclines
Nullclines are
obtained by
algebraically
solving each
differential
equation with a
variable not
changing over time

 $W_{21} > 0$, $W_{12} < 0$ Weak $W_{11} > 0$, $W_{22} < 0$



Nonlinear nullclines in nonlinear systems (blue and red lines):

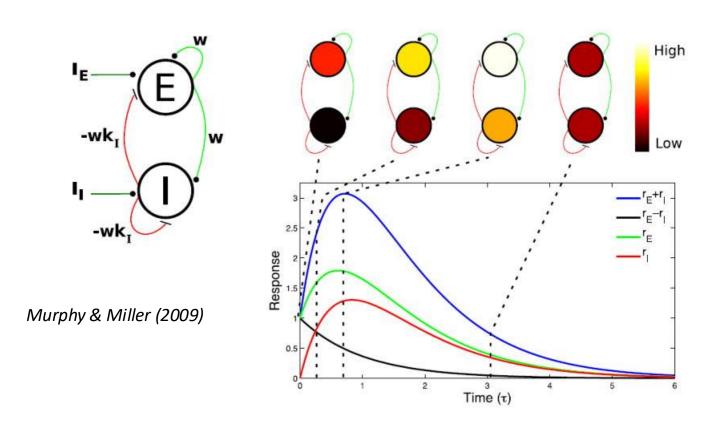
Excitatory-inhibitory network (Wilson-Cowan type)



With vector field (arrows) and nullclines (orange and green) (using XPPAUT software)

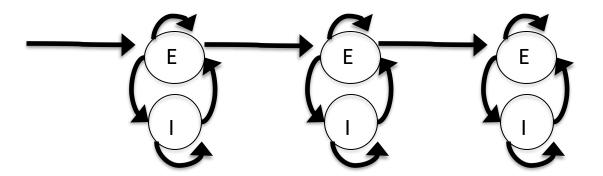
http://www.math.pitt.edu/~bard/xpp/xpp.html

Example: Phasic (transient) activation



Possible functions: Sensory encoding; brief activity burst for information "gate" encoding

What if we connect a series of network with such phasic activation?

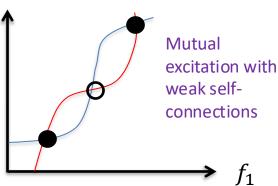


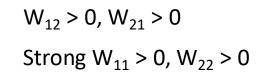
What functions?

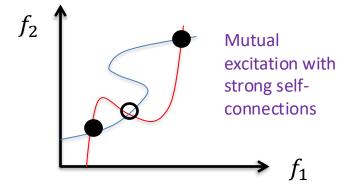
Mutually inhibitory neural units (various cases)

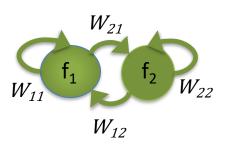
 f_2

 $W_{12} > 0, W_{21} > 0$ Weak $W_{11} > 0, W_{22} > 0$

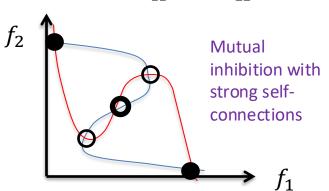




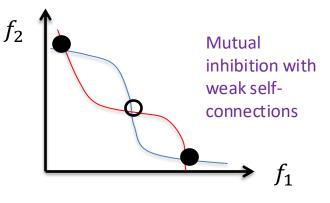




- $W_{12} < 0, W_{21} < 0$
- Strong $W_{11} > 0$, $W_{22} > 0$



 $W_{12} < 0, W_{21} < 0$ Weak $W_{11} > 0, W_{22} > 0$

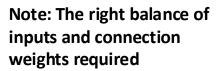




Stable

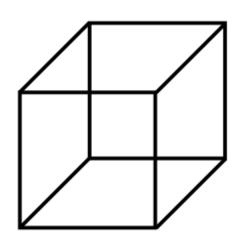
Metastable

(saddle)



Example: Perceptual oscillations – Binocular rivalry

Multiple states of the mind (for the same stimulus)

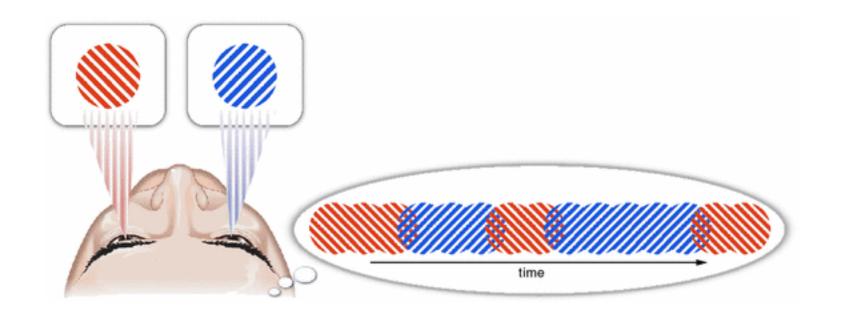






Necker cube

Binocular rivalry: A phenomenon of visual perception in which perception alternates between different images presented to each eye.



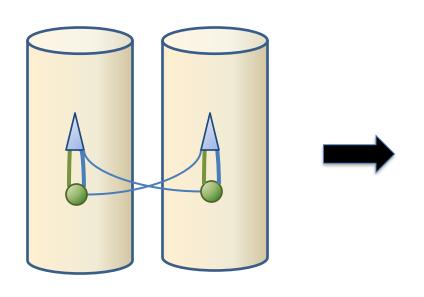






http://www.scholarpedia.org/article/Binocular_rivalry

A basic model for perceptual alternation



Mutual (effectively) inhibitory population - Implicitly incorporate inhibitory populations

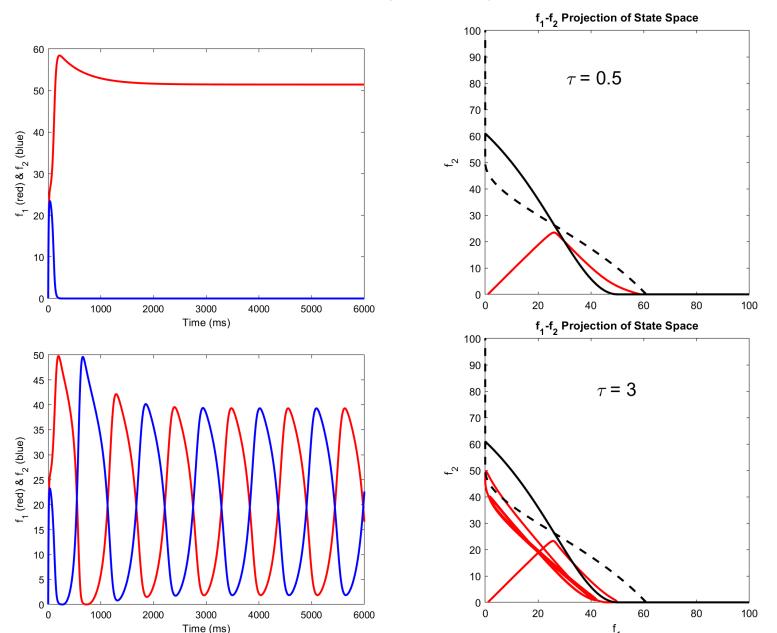


Assume some slow adaption neural mechanism, A, with each unit *i* having (i.e. 4 dynamical equations):

$$\frac{df_i}{dt} = F(W_{ij}, A_i, b_i)$$

$$\tau \frac{dA_i}{dt} = -A_i + \beta_i f_i \quad \text{for} \quad \beta_i > 0$$

A basic model for perceptual alternation

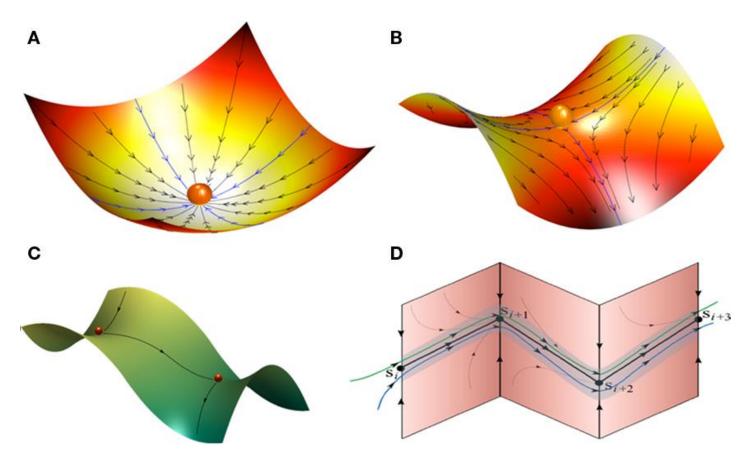


Wilson (1999)

Are there other types of neural network dynamics?

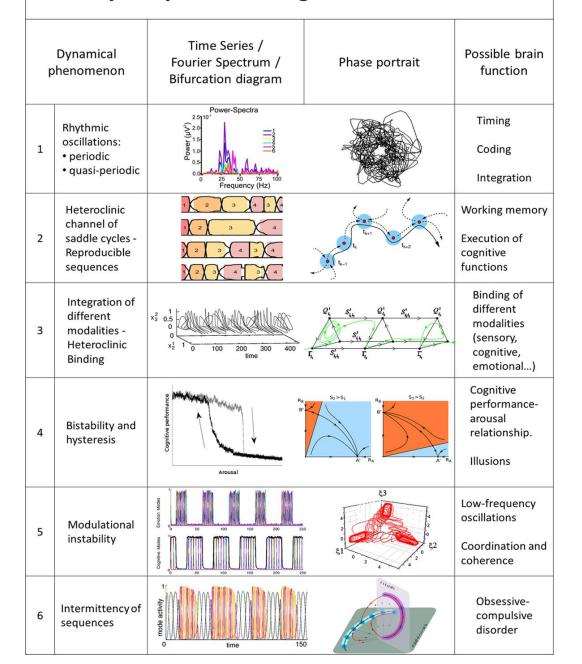
Landscape metaphors for brain dynamics (A–C)

- (A) simple attractor (stable fixed point) in phase space.
- (B) a metastable state (saddle fixed point) with two stable and two unstable separatrices/manifolds (a separatrix is a surface or curve that refers to the boundary separating two modes of behavior in the phase space of a dynamical system).
- (C) a simple heteroclinic chain with two connected metastable states.
- (D) a stable heteroclinic channel robust sequence of metastable states.



Rabinovich MI and Varona P (2011) Robust transient dynamics and brain functions. *Front. Comput. Neurosci.* **5**:24. doi: 10.3389/fncom.2011.00024. Nice not-too-technical review.

Gallery of dynamical images and brain functions

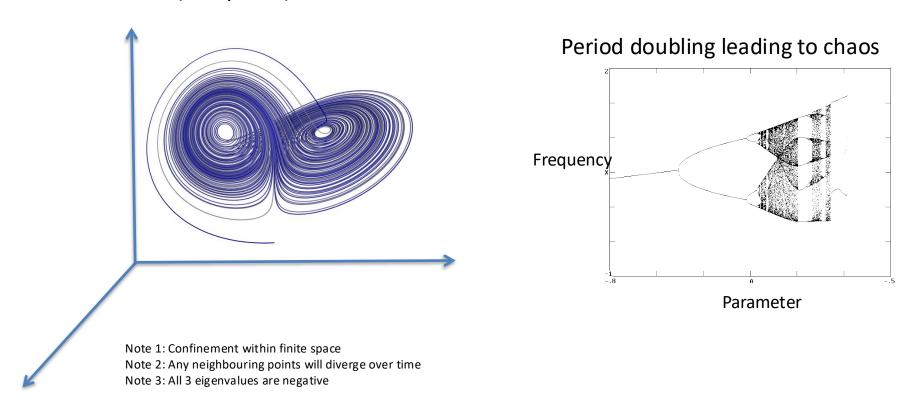


Rabinovich & Varona (2011) Robust transient dynamics and brain functions. *Front. Comput. Neurosci.* **5**:24. doi: 10.3389/fncom.2011. 00024

Another one ... chaotic (strange) attractor

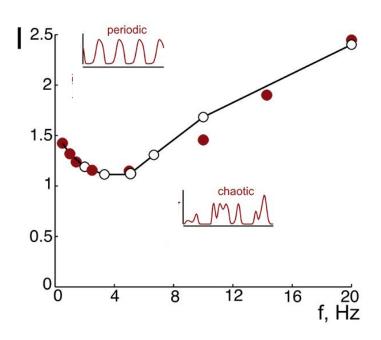
- Deterministic chaos

Lorenz attractor (3D system)



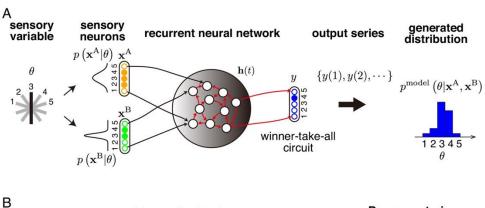
Model complex or chaotic system (e.g. weather – fluid dynamics, finance, cryptography, robotics, networks).

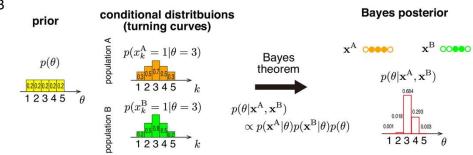
Input *I* controls between periodic oscillations and chaos in randomly connected RNNs



Rajan, Abbott & Sompolinsky (2010)

See also: Van Vreewijk & Somolinsky (1996) Engelken, Wolf & Abbott (2023) Randomly connected RNNs utilise irregular dynamics to represent probabilistic distributions for cue integration, and generalise to novel situations with partly missing inputs

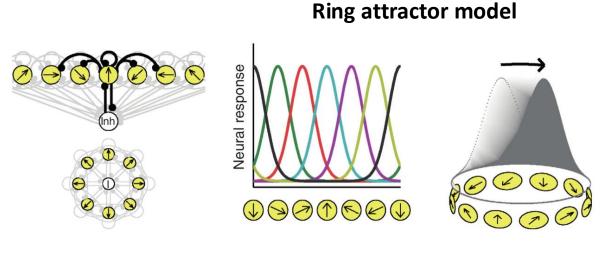




Terada & Toyoizumi (2024)

Beyond just temporal dimension ...

E.g. with additional spatial directional dimension



Protocerebral Bridge (PB)

R

odd Right 6L

R

odd Left 6R

3R

7L

R

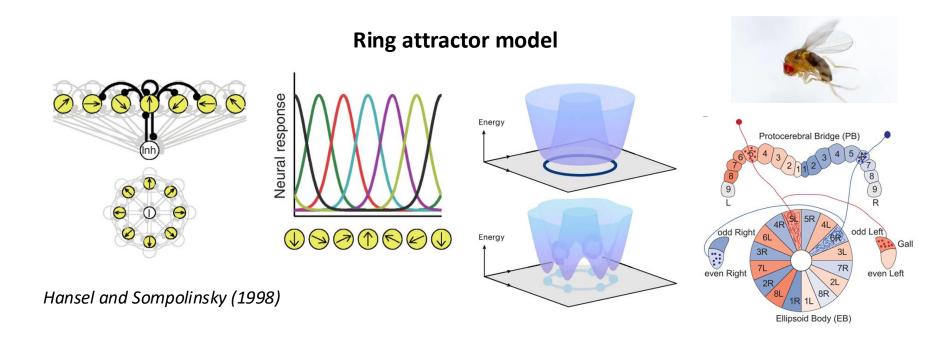
Ellipsoid Body (EB)

Hansel and Sompolinsky (1998)

Applications: (parametric) working memory, heading direction, spatial navigation, sensory integration and decision making

Beyond just temporal dimension ...

E.g. with additional spatial directional dimension



Applications: (parametric) working memory, heading direction, spatial navigation, sensory integration and decision making

Summary

- Neural network (connectionist) modelling approach as a useful neurobiologically grounded tool for mechanistic understanding of cognitive processing in biological brains and artificial intelligence (AI).
- Neural network models can be theoretically analysed not truly "black box" as AI researchers might have thought! Need to identify or develop theoretical tools for more complex network models. As neural network models are mathematically represented by ODEs and SDEs, dynamical systems theory naturally become useful.
- By studying simple or reduced "cognitive building blocks" of network models, we can seek towards understanding more complex models.

References

- X-J Wang, Theoretical Neuroscience: Understanding Cognition, CRC Press, 2025.
- HR Wilson, Spikes, Decisions and Actions: Dynamical Foundations of Neuroscience, Oxford University Press, 1999.
- From Neuron to Cognition via Computational Neuroscience, Chapters 2, 3 and 11, (MA Arbib & J Bonaiuto) *Cambridge, MA: MIT Press* (2016).
- P Dayan and LF Abbott, Theoretical Neuroscience, chapter 7 "Network models", MIT Press, 2001.
- G Bard Ermentrout & DH Terman, Mathematical Foundations of Neuroscience, book chapter 11 "Firing rate models", Springer, NY, 2010.
- HS Seung. Amplification, Attenuation, and Integration. In: The Handbook of Brain Theory and Neural Networks: Second Edition (MA Arbib, Ed.) Cambridge, MA: MIT Press, pp. 94-97 (2003).
- Some papers: Brinkman et al. (2022) Metastable dynamics of neural circuits and networks. Applied Physics Reviews, 9(1):011313; Hancock et al. (2025) Metastability demystified the foundational past, the pragmatic present and the promising future, Nature Reviews Neuroscience, 26:82-100.

Additional:

 Steven Strogatz, Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering, CRC Press, 2015.