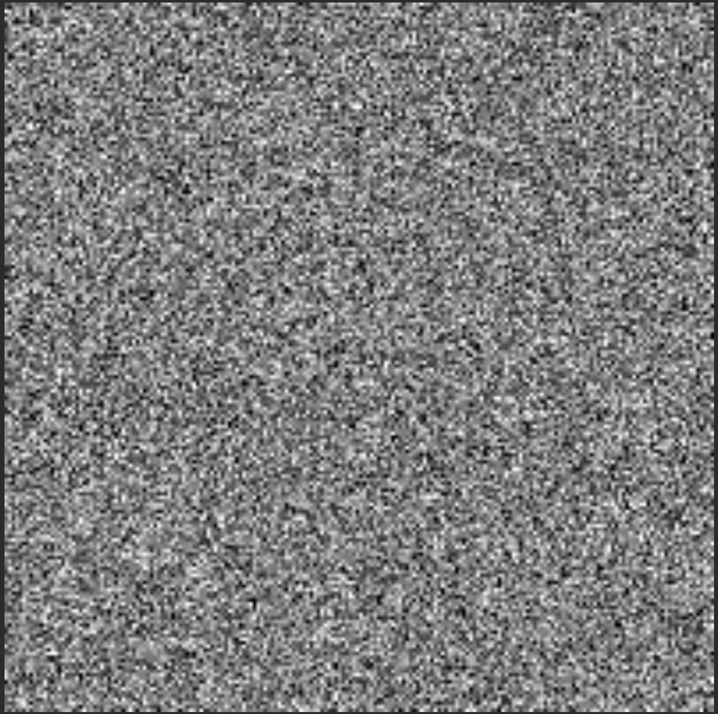
Which of these is more...

- interesting
- beautiful
- similar to the brain?



Lecture outline

- What is a dynamical system?
- Why consider dynamics in neuro?
- Machinery of dynamical systems
- Examples - feedback, dynamics are present across scales in the brain

Goals for this lecture

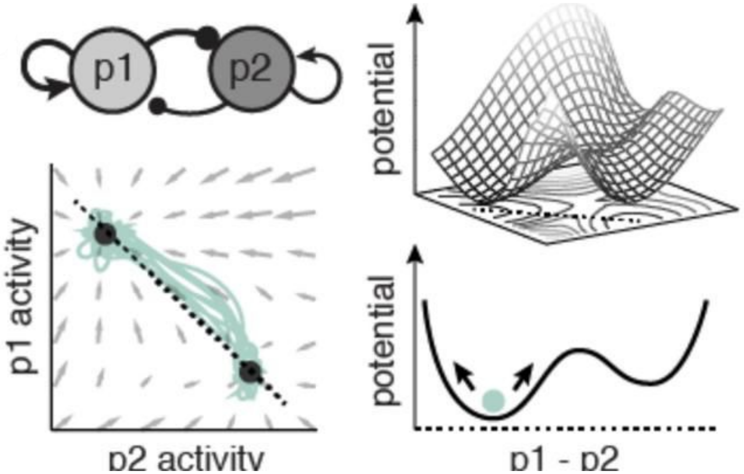
- Dynamics are general and useful
- Build intuition for what and how
- Eigenvalues are key
- Develop foundation for dynamics as computation

A dynamical system is ... $$\dot{x} = f(x, u)$$

A dynamical system is …

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

- A force field
- A network evolving in time
- A collection of flow subject to physics
- A landscape of solutions

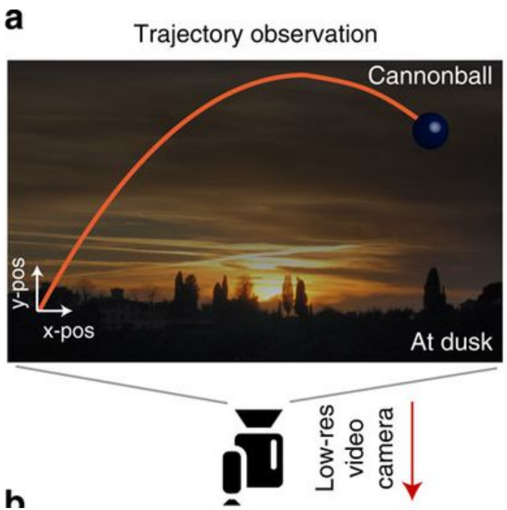


"The population doctrine revolution in cognitive neurophysiology" (2021) Ebitz et al.

Why study dynamics?

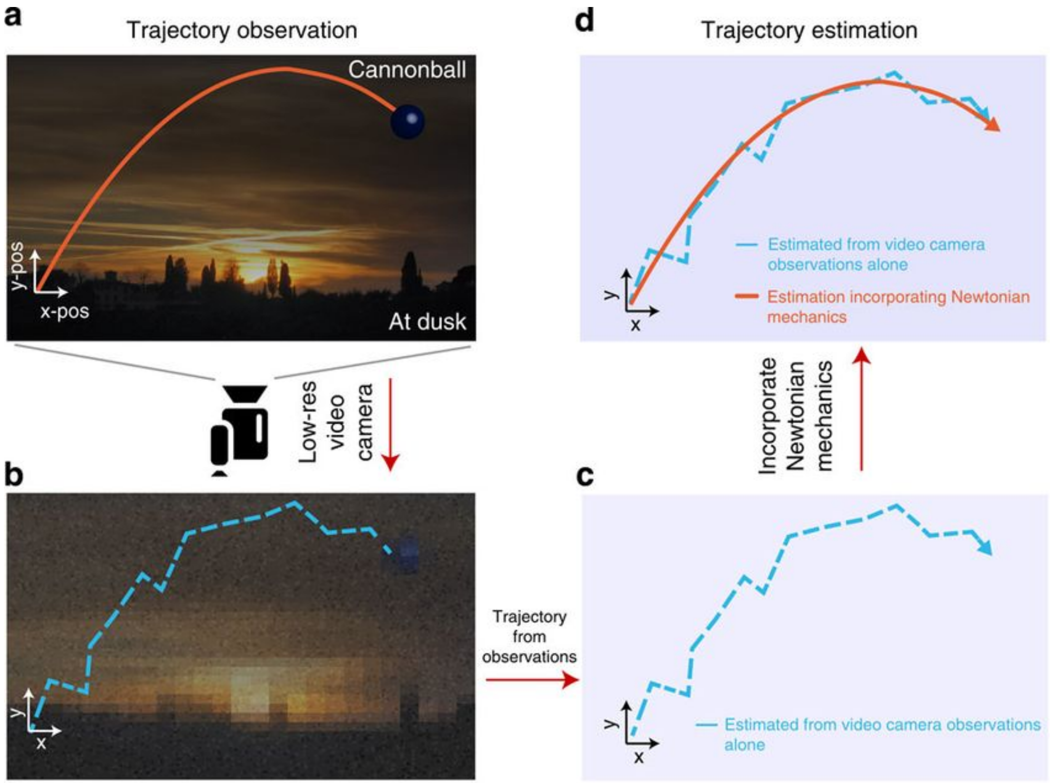
- Time matters for physical things in the world
- Dynamical models enable forecasting & remembering
- Huge history of successful application
- Bridges high-dimensional, noisy measurements to low-dimensional interpretable causes

Why study dynamics?



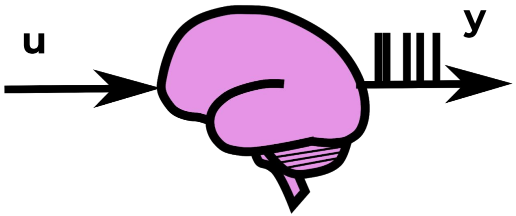
“Single-trial dynamics of motor cortex and their applications to brain-machine interfaces” (2015) Kao et al.

Why study dynamics?



"Single-trial dynamics of motor cortex and their applications to brain-machine interfaces" (2015) Kao et al.

The Machinery of Dynamical Systems

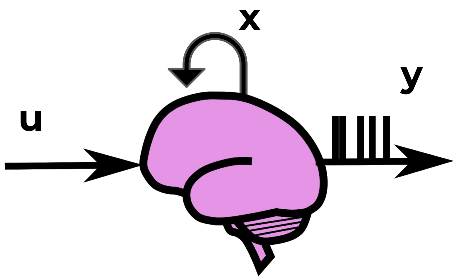


representational model

$$y = f(u)$$

dynamical system model

$$\dot{x} = f(x, u)$$
$$y = g(x)$$



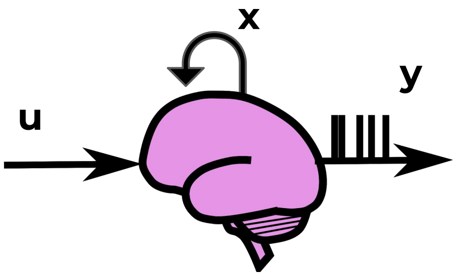
Contrast from representational view

Activity is often dominated by feedback connections rather than sensory drive

This is a very general language

Lots of early through modern models of the world and the brain can be described under this umbrella

The Machinery of Dynamical Systems

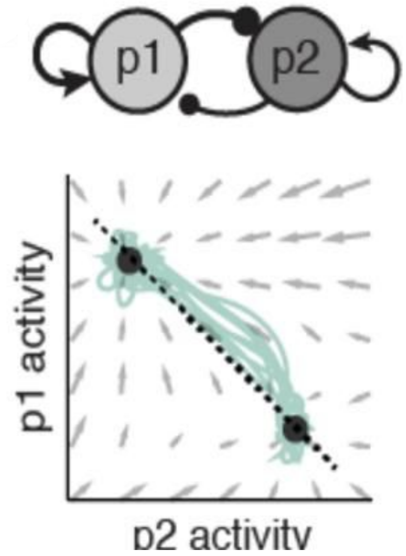


$$\frac{dx_1}{dt} = a_{11}x_1 + a_{21}x_2$$

$$\frac{dx_2}{dt} = a_{12}x_1 + a_{22}x_2$$

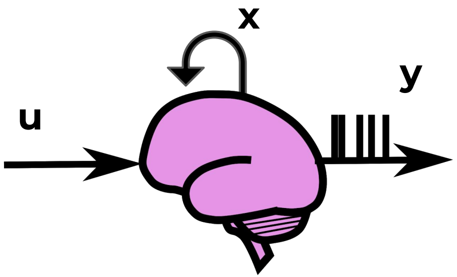
System dynamics depend on a linear transformation of its current state plus a term which describes the influence of external inputs

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \begin{bmatrix} u \end{bmatrix}$$



"The population doctrine revolution in cognitive neurophysiology" (2021) Ebitz et al.

The Machinery of Dynamical Systems



linear dynamics:

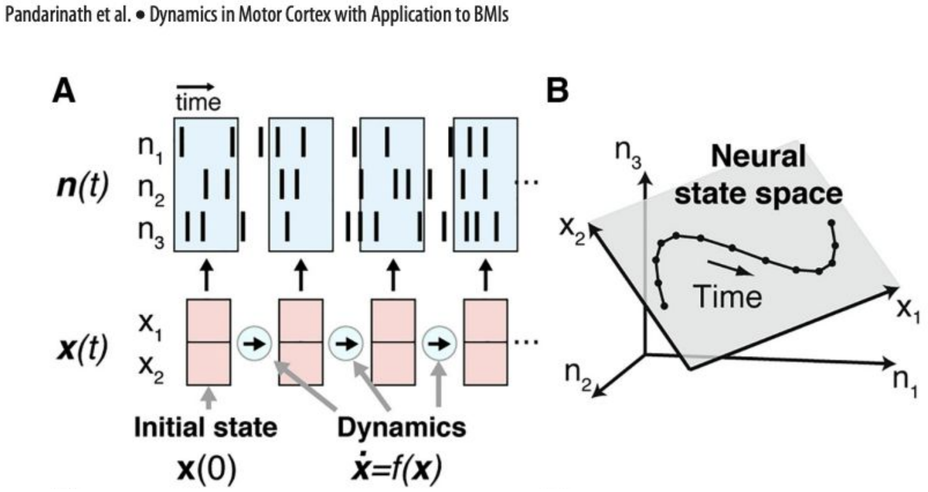
$$\dot{x} = Ax + Bu$$

with noise and measurement:

$$\dot{x} = Ax + Bu + w$$
$$y = Cx + v$$

Poisson LDS (common in neuro):

$$\dot{x} = Ax + Bu + w$$
$$y = Poisson(f(Cx))$$

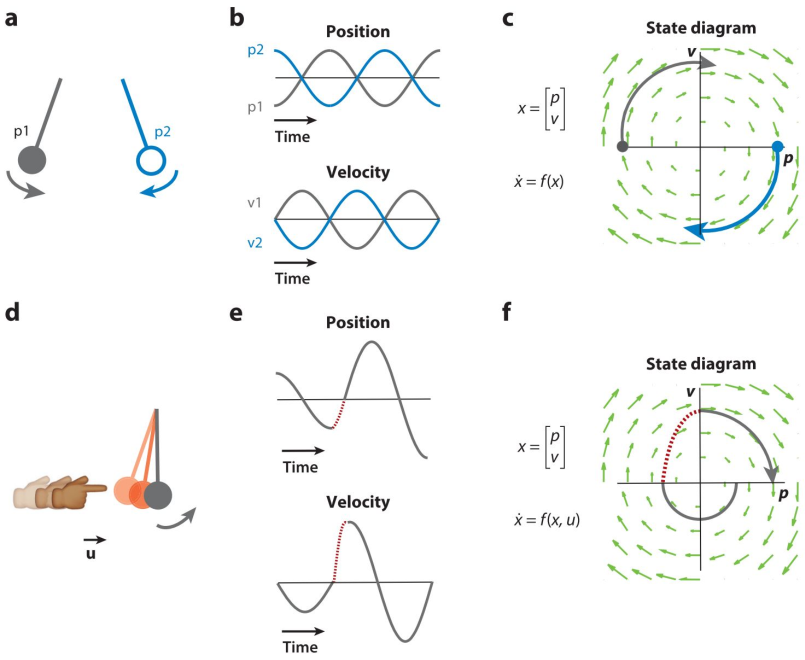


What is "state" ?

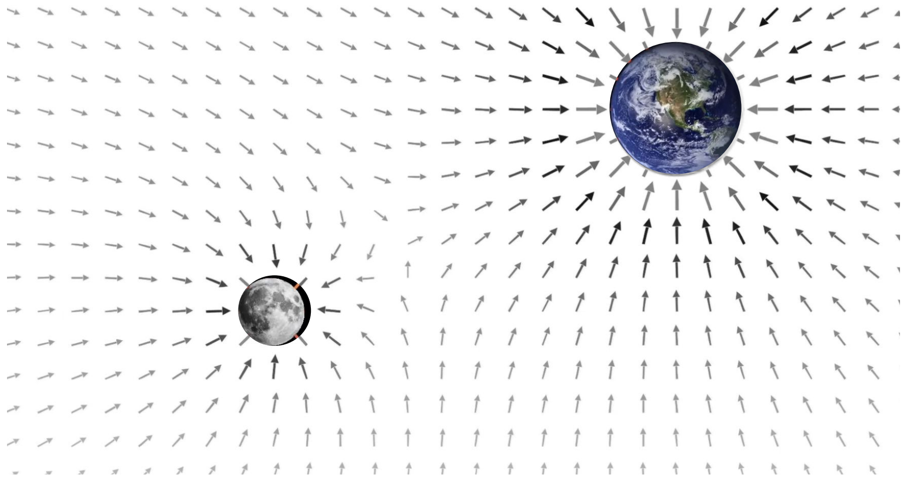
"Latent factors and dynamics in motor cortex and their application to brain-machine interfaces" (2018) Pandarinath et al.

The Machinery of Dynamical Systems

What is a phase plane? *Dynamics as flow in a force field*



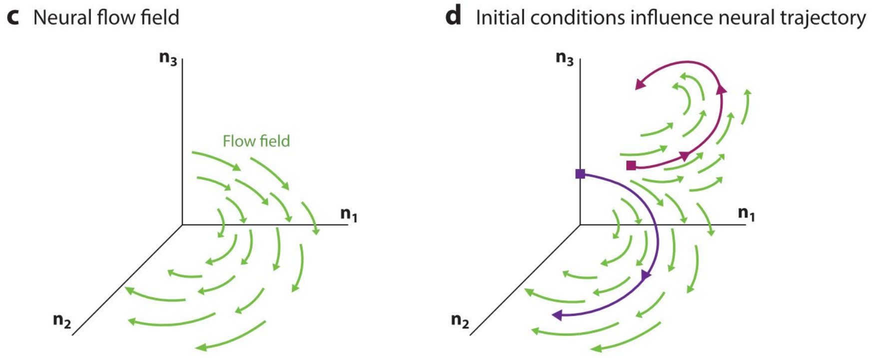
"Computation through Neural Population Dynamics" (2020) Vyas et al.



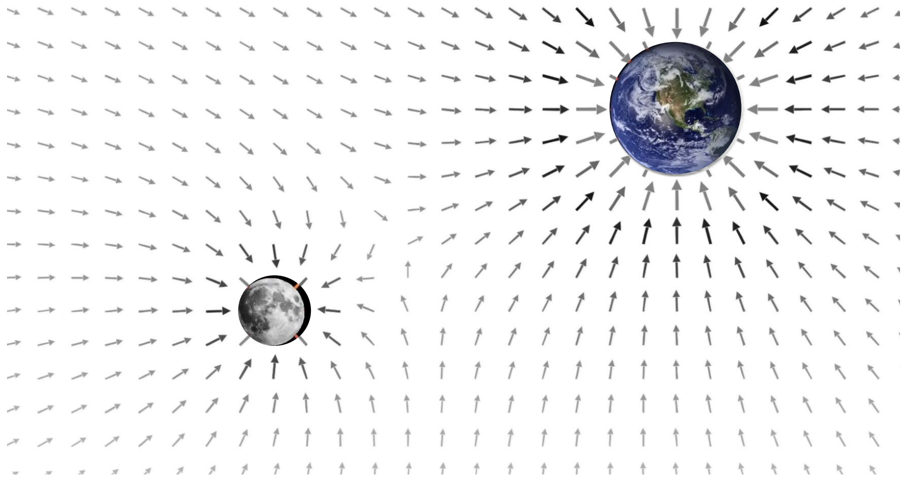
Divergence and curl: The language of Maxwell's equations, fluid flow, and more - 3Blue1Brown

The Machinery of Dynamical Systems

Flow fields reveal key aspects of computation
"The Dynamical Skeleton" - David Sussilo



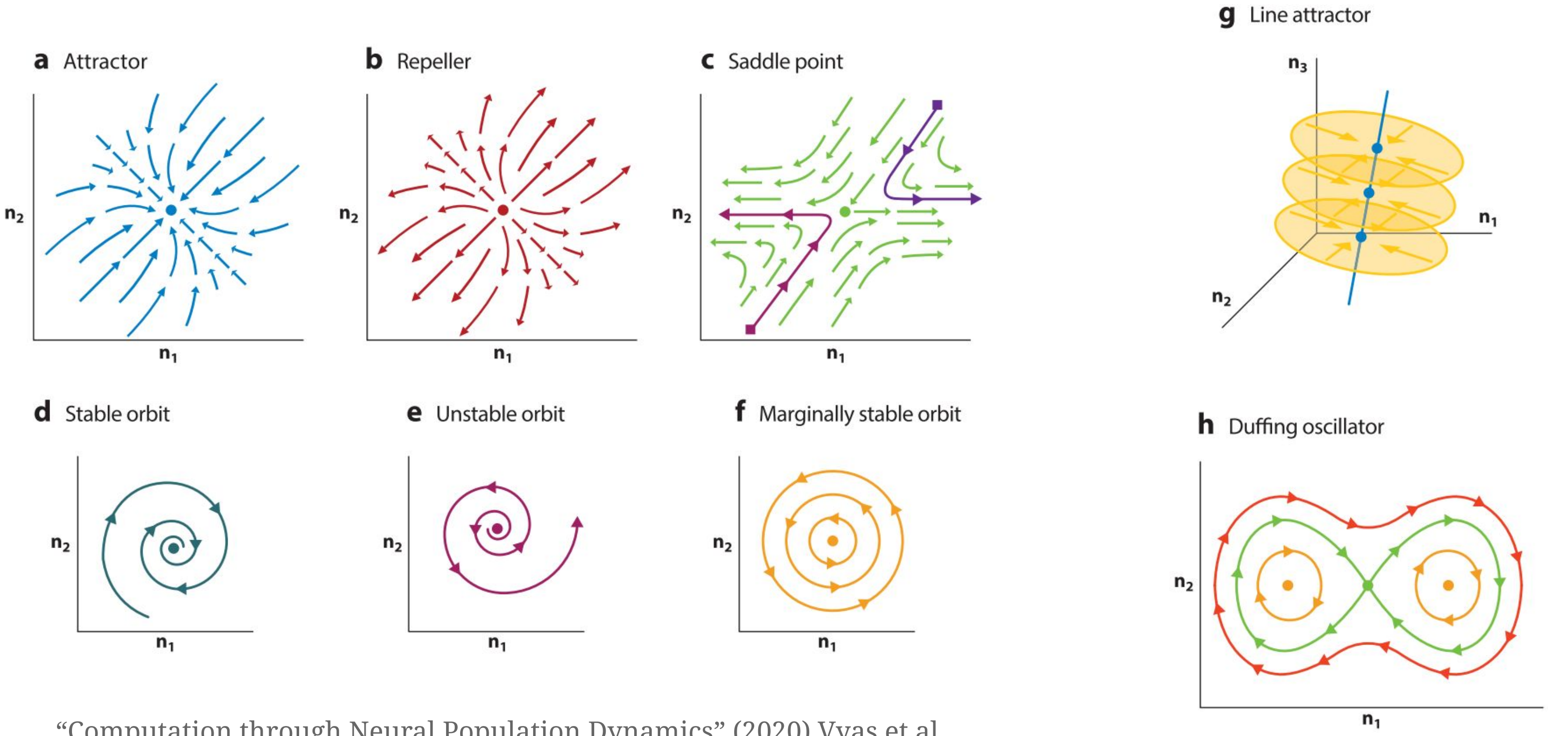
"Computation through Neural Population Dynamics" (2020) Vyas et al.



"*Divergence and curl: The language of Maxwell's equations, fluid flow, and more*" - *3Blue1Brown*

(gain intuition from other physical systems - "virtual physics")

Patterns of flow within dynamical systems



"Computation through Neural Population Dynamics" (2020) Vyas et al.

Emergent Features of Dynamical Systems (DEMO)

Eigenvalues & Dynamics Demo:
https://awillats.github.io/dynamics-visualizer-p5/

$$\frac{dx_1}{dt} = a_{1\leftarrow 1}x_1 + a_{1\leftarrow 2}x_2$$

$$\frac{dx_2}{dt} = a_{2\leftarrow 1}x_1 + a_{2\leftarrow 2}x_2$$

System dynamics depend on a linear transformation of its current state plus a term which describes the influence of external inputs

$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} a_{1\leftarrow 1} & a_{1\leftarrow 2} \\ a_{2\leftarrow 1} & a_{2\leftarrow 2} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \begin{bmatrix} u \end{bmatrix}$$

Emergent Features of Dynamical Systems (DEMO)

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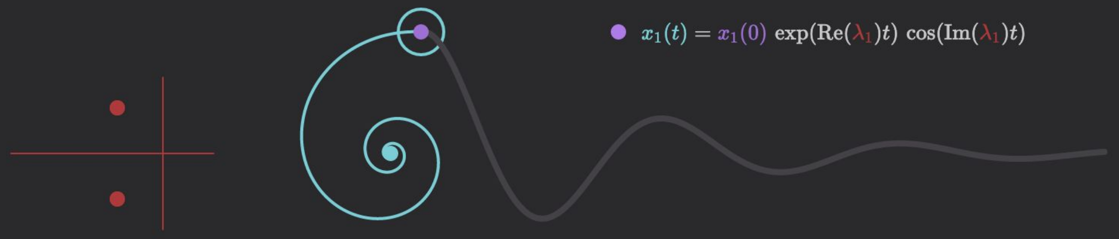


$$\begin{bmatrix}\dot{x}_1\\ \dot{x}_2\end{bmatrix} = \begin{bmatrix}a_{11} & a_{12}\\ a_{21} & a_{22}\end{bmatrix}\begin{bmatrix}x_1\\ x_2\end{bmatrix} + \begin{bmatrix}b_1\\ b_2\end{bmatrix}[u]$$

System dynamics depend on a linear transformation of its current state plus a term which describes the influence of external inputs

the solution to this differential equation looks like

$x_1(t) = x_1(0)\, e^{\lambda_1 t}$

the **real part** of the eigenvalues scale the rate of decay for trajectories of $x(t)$ in the direction of the associated eignevector

the **imaginary part** of the eigenvalues scale the rate of oscillation for trajectories of $x(t)$

Emergent Features of Dynamical Systems (DEMO)

Eigenvalues & Dynamics Demo:
https://awillats.github.io/dynamics-visualizer-p5/

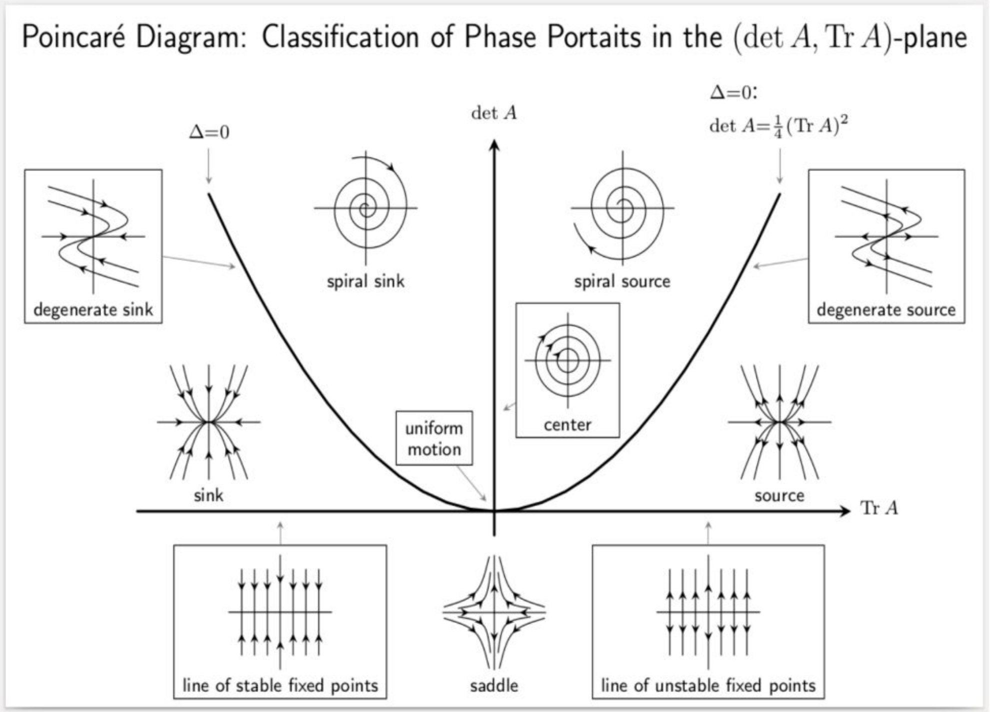
$$\begin{bmatrix} \dot{x}_1 \\ \dot{x}_2 \end{bmatrix} = \begin{bmatrix} a_{1\leftarrow 1} & a_{1\leftarrow 2} \\ a_{2\leftarrow 1} & a_{2\leftarrow 2} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

A matrix = connectivity + behavior

Fixed points / attractors

Eigenvalues

- Stability
- Oscillations

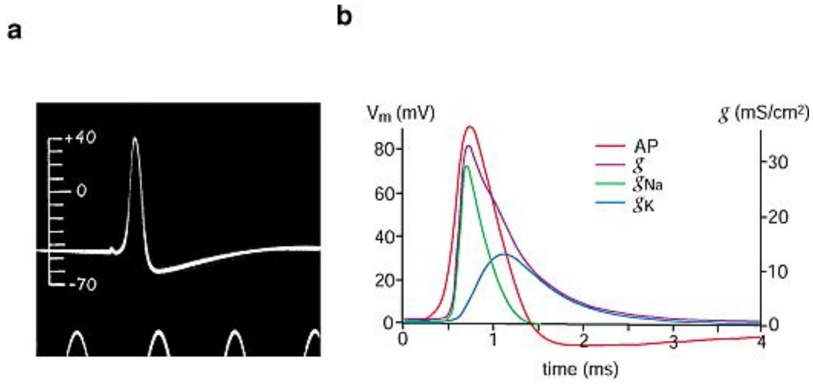


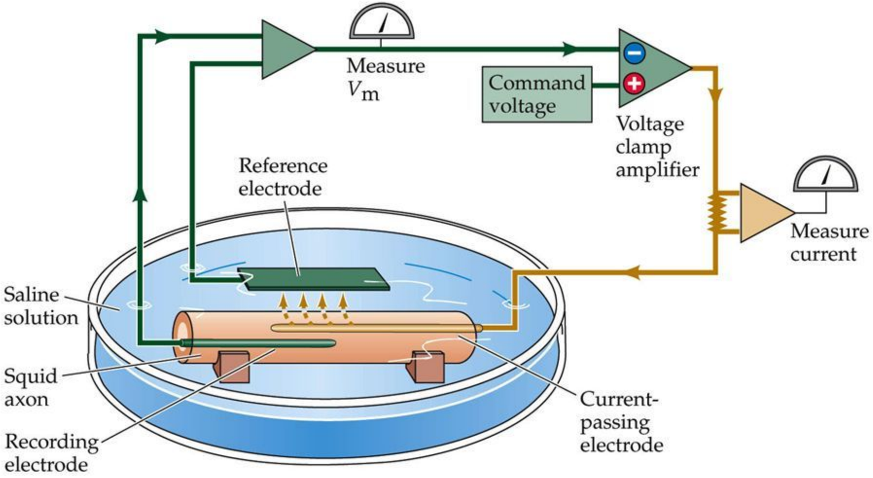
[Theoretical Neuro. Course notes](#) (2018) Menendez

Feedback + dynamics are ubiquitous features across scales

- **cell:** feedback voltage dynamics
- **circuit motifs:** reciprocal inhibition
- **circuits:** sensory feedback circuits
- **systems & behavior:** motor-environment feedback loops

Neuro Application 1: Hodgkin & Huxley





"Neuroscience" (2004) Purves et al

"Measurement of current-voltage relations in the membrane of the giant axon of Loligo" (1952) Hodgkin, Huxley, Katz

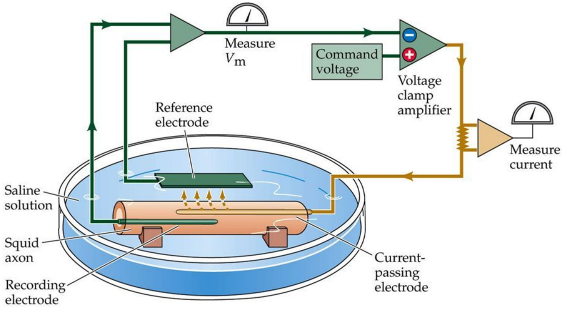
Nonlinear
Data-driven
system identification

- *Was able to predict the micro-scale structure of ion channels from macro-scale dynamics!*

Neuro Application 1: Hodgkin & Huxley

$$\frac{dV}{dt} = -I - kV$$

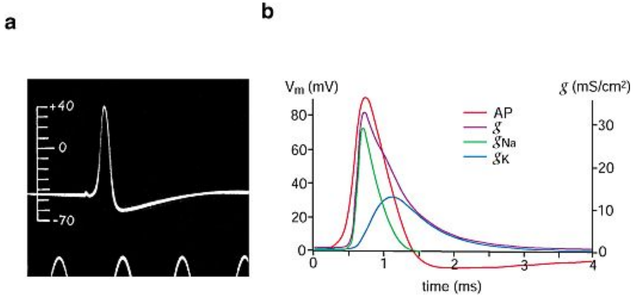
$$\frac{dV}{dt} = -I + g_{Na} m^3 h (V_{Na} - V) + \dots$$



"[Neuroscience](#)" (2004) Purves et al

"[Measurement of current-voltage relations in the membrane of the giant axon of Loligo](#)" (1952) Hodgkin, Huxley, Katz

"[A brief historical perspective: Hodgkin and Huxley](#)" (2012) Schwiening



Nonlinear
Data-driven
system identification

- *Was able to predict the micro-scale structure of ion channels from macro-scale dynamics!*

Neuro Application 1: Hodgkin & Huxley

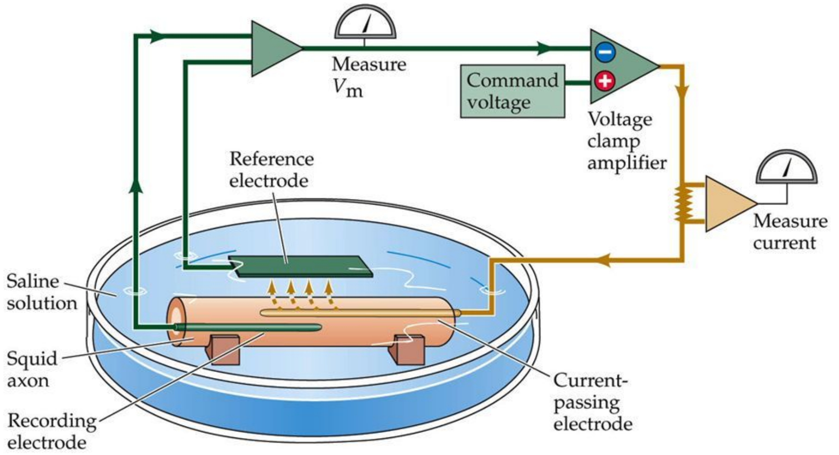
$$\frac{dV}{dt} = -I - kV$$

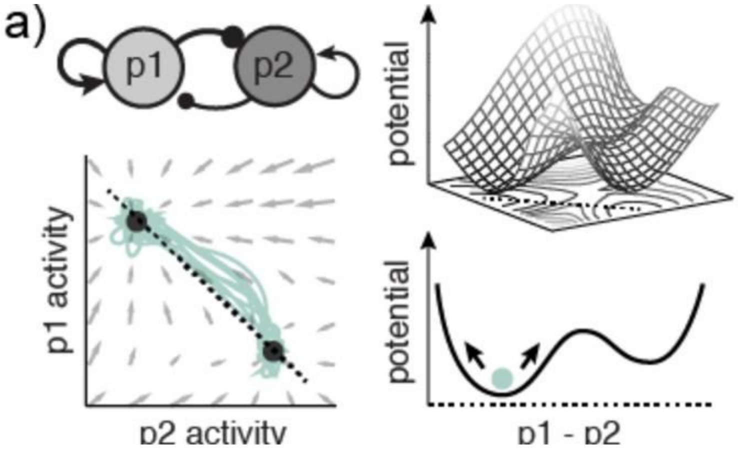
$$I = C_m \frac{\mathrm{d}V_m}{\mathrm{d}t} + \bar{g}_{\mathrm{K}} n^4 (V_m - V_K) + \bar{g}_{\mathrm{Na}} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l),$$

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$

$$\frac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h$$





Nonlinear
Data-driven
system identification

- *Was able to predict the micro-scale structure of ion channels from macro-scale dynamics!*

Neuro Application 1: Hodgkin & Huxley

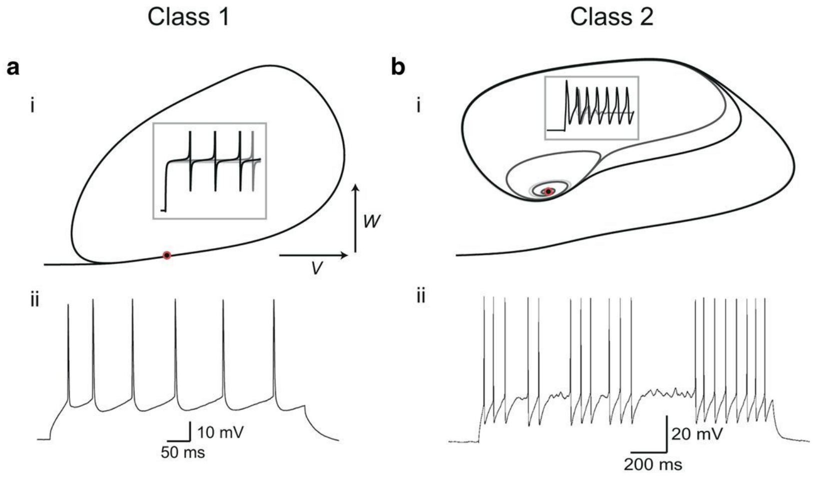
Phase planes summarize the connection between biophysics and dynamics

$$I = C_m \frac{\mathrm{d}V_m}{\mathrm{d}t} + \bar{g}_{\mathrm{K}} n^4 (V_m - V_K) + \bar{g}_{\mathrm{Na}} m^3 h (V_m - V_{Na}) + \bar{g}_l (V_m - V_l),$$

$$\frac{dn}{dt} = \alpha_n(V_m)(1-n) - \beta_n(V_m)n$$

$$\frac{dm}{dt} = \alpha_m(V_m)(1-m) - \beta_m(V_m)m$$

$$\frac{dh}{dt} = \alpha_h(V_m)(1-h) - \beta_h(V_m)h$$



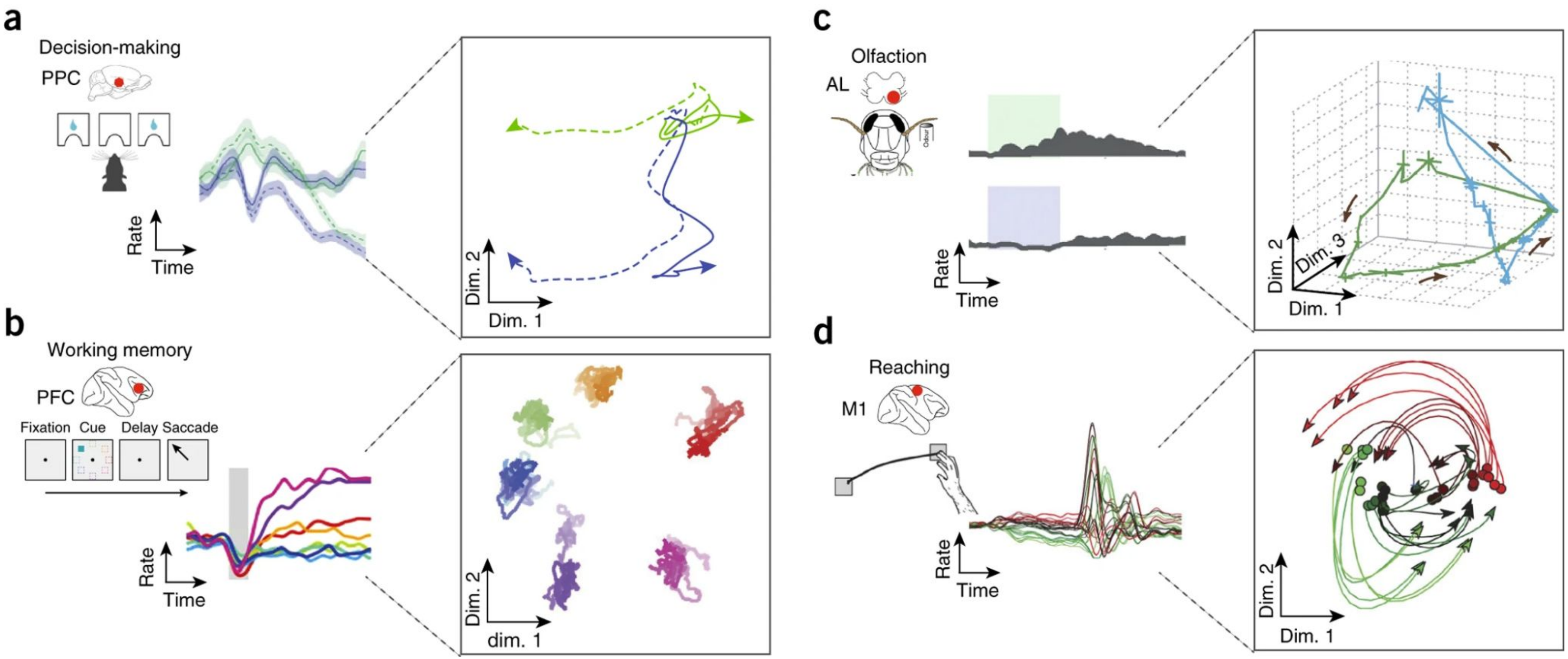
"The Hodgkin-Huxley Heritage: From Channels to Circuits" (2012) Catterall et al.

See also:
"Neuronal Dynamics - Ch 4.4 Type I and Type II Neurons" (2014) Gerstner et al.

Applications of dynamics to perception, cognition, and behavior

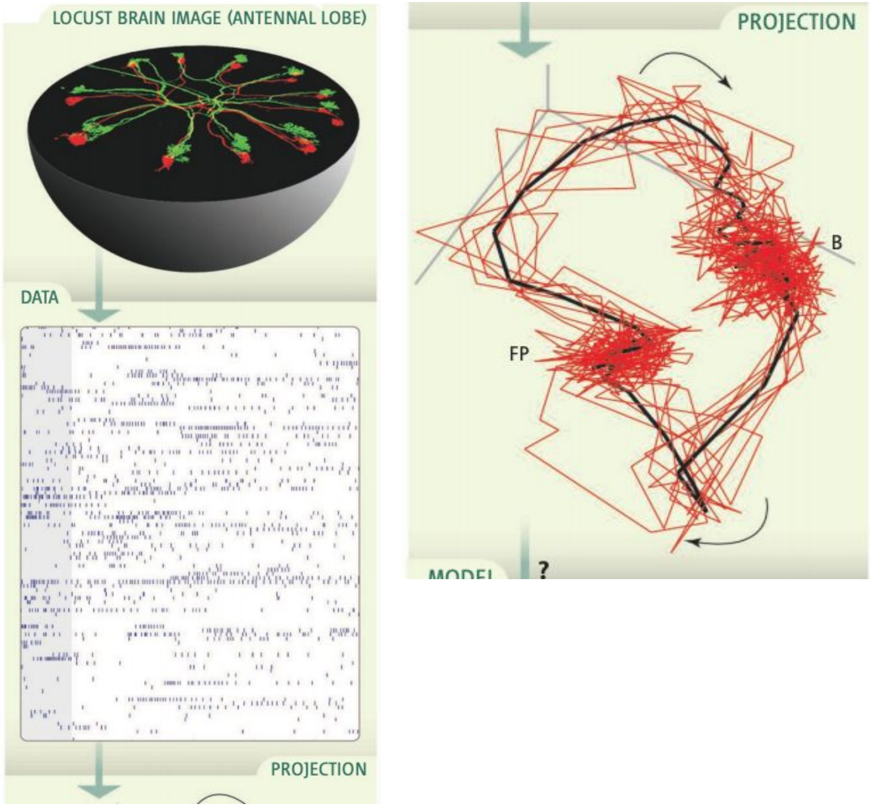
- Decision making
- Working memory
- Olfaction
- Reaching

Applications of dynamics to perception, cognition, and behavior



"Structure in neural population recordings: an expected byproduct of simpler phenomena?" (2017) Elsayed & Cunningham

Transient dynamics of odor perception



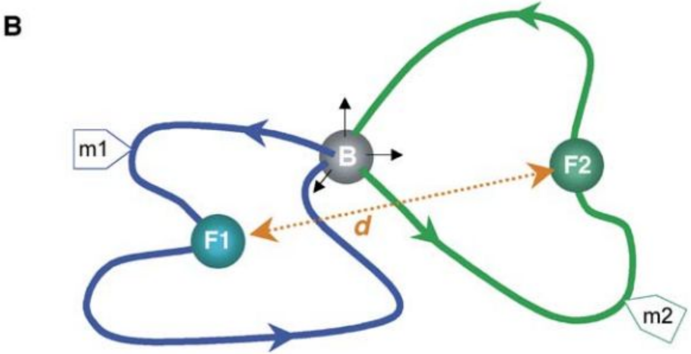


Figure 8. Schematic Diagram of Odor-Evoked PN Activity

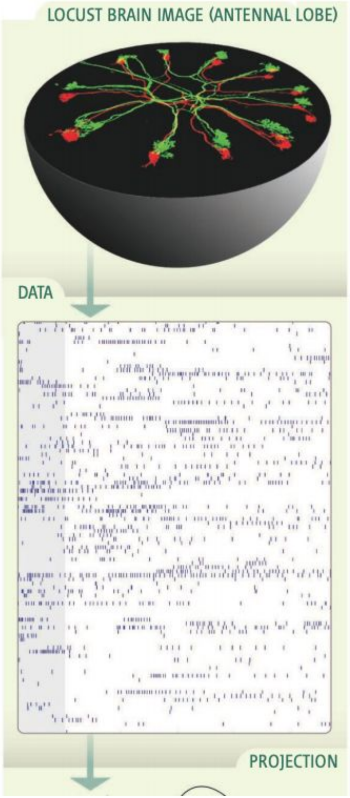
(Ai) Idealized odor trajectory in PN space. *B*, baseline; *F*, fixed point; t_i, times corresponding to one oscillation cycle. During the on transient, synchronization is the highest and most spikes occur within a single 10–20 ms period. Activity thus “hops” from one oscillation cycle to the next while the identities of the responding PNs evolve (see [Aii]).

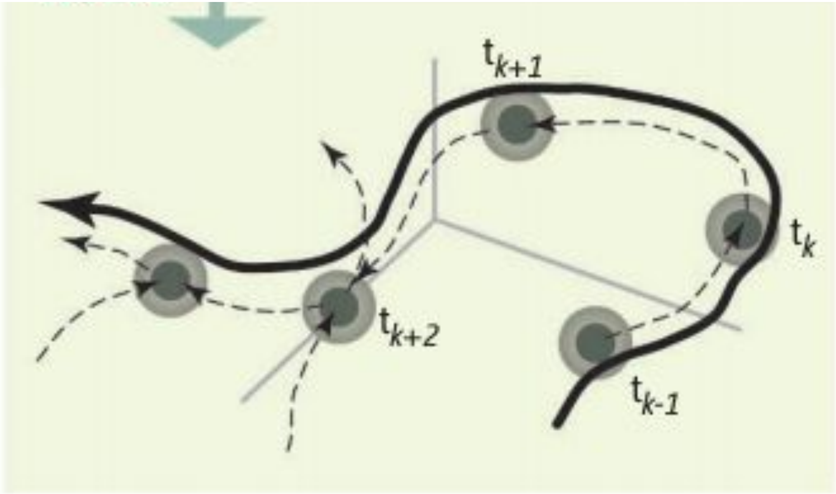
(Aii) Evolving PN activity that underlies the trajectory in (Ai), green squares represent responsive PNs.

(B) Idealized trajectories for two different odors. Odor trajectories differ at their fixed points (*F1* and *F2*) but are maximally distant during the transient response phases (e.g., *m1* and *m2*). (d, Euclidian distance.)

“Transient Dynamics for Neural Processing” (2011) Rabinovich, Huerta, Laurent
“Transient Dynamics versus Fixed Points in Odor Representations by Locust Antennal Lobe Projection Neurons” (2005) Mazor, Laurent

Transient dynamics of odor perception





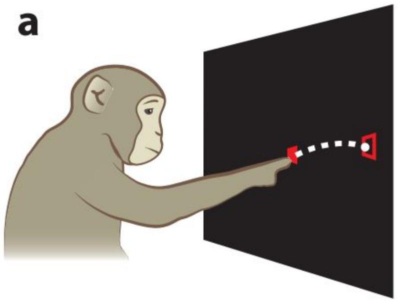
Differences in odor perception encoded in *transient* differences in low-D trajectories (but not steady states)

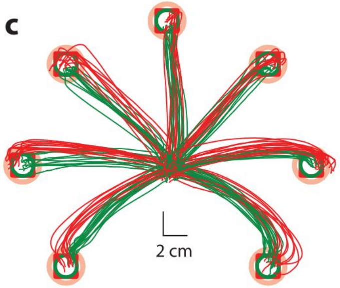
"Transient Dynamics for Neural Processing" (2011) Rabinovich, Huerta, Laurent
"Transient Dynamics versus Fixed Points in Odor Representations by Locust Antennal Lobe Projection Neurons" (2005) Mazor, Laurent

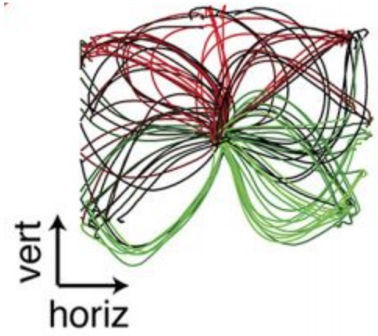
Population Dynamics

behavior

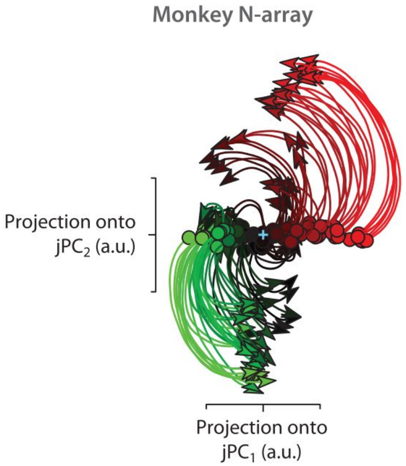
task







Neural dynamics



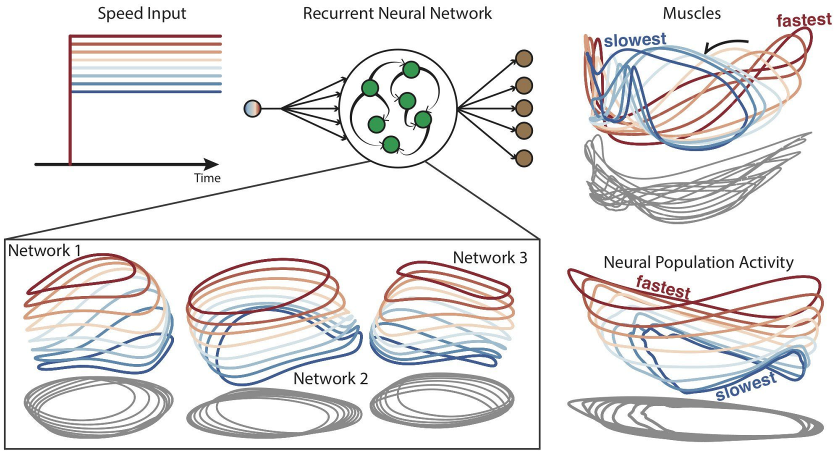
“Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach” (2006) Churchland et al.

“Latent factors and dynamics in motor cortex and their application to brain-machine interfaces” (2018) Pandarinath et al.

Next lecture

Lecture B: (population) dynamics for computation

- Motor control
- Optimal feedback
- Memory
- Decision making



"Motor cortex activity across movement speeds is predicted by network-level strategies for generating muscle activity" (2021) Saxena et al.

Challenge question

The dynamical systems hypothesis is now seemingly both ubiquitous and (arguably) obvious: how would you possible disprove such a hypothesis?

More discussion about limitations & potential pitfalls:

https://www.simonsfoundation.org/2020/07/14/discoveries-of-rotational-dynamics-add-to-puzzle-of-neural-computation/

Analysis of neuronal ensemble activity reveals the pitfalls and shortcomings of rotation dynamics

- https://www.nature.com/articles/s41598-019-54760-4
- "While these observations suggest that temporal sequences of neuronal responses could be visualized as rotations with various methods, we express doubt about Churchland et al.'s bold assessment that such rotations are related to “an unexpected yet surprisingly simple structure in the population response”, which “explains many of the confusing features of individual neural responses”. Instead, we argue that their approach provides little, if any, insight on the underlying neuronal mechanisms employed by neuronal ensembles to encode motor behaviors in any specie"

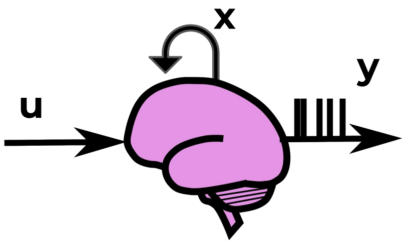
- https://twitter.com/MarkChurchland/status/1283421054820667400
- when a computation depends on network dynamics, noise-robustness demands low tangling. For many tasks, rotational dynamics are the most natural way of maintaining low tangling.

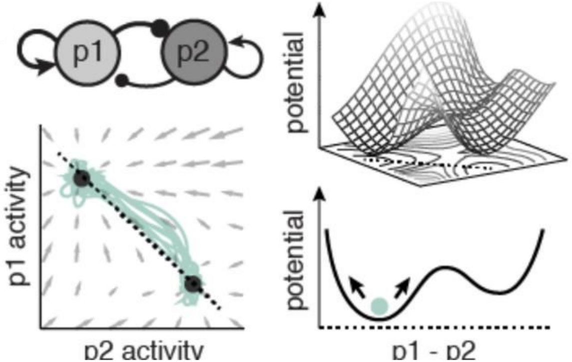
https://twitter.com/andpru/status/1226195050989867014

$$\dot{x} = f(x, u)$$
$$y = g(x)$$

Takeaway Points

- Dynamics help us interpret high-dimensional data on single-trials
- Feedback, connectivity, dynamics are all closely interrelated
    - Seeing dynamical systems from multiple perspectives is insightful
- Eigenvalues are key to describing patterns of dynamics
- Dynamical models enable forecasting & remembering





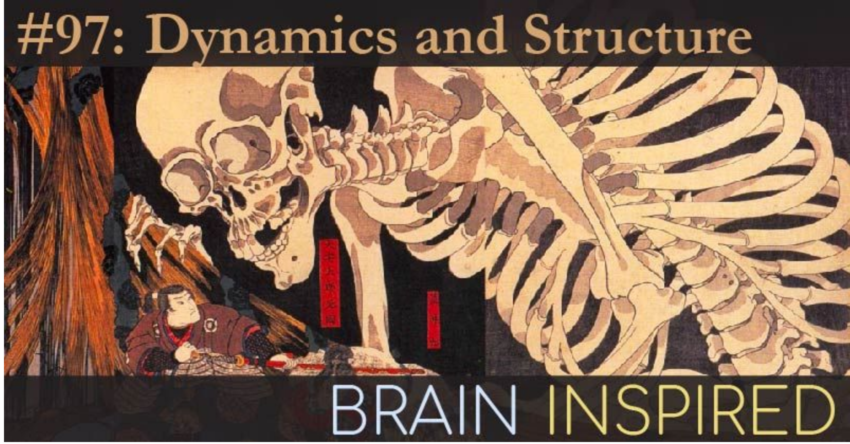
"The population doctrine revolution in cognitive neurophysiology" (2021) Ebitz et al.

Additional resources

Interactive eigenvalues & dynamics demo:
https://awillats.github.io/dynamics-visualizer-p5/

High-level references for understanding dynamics in neuro

- "Neural circuits as computational dynamical systems" (2014) Sussillo
- "Latent Factors and Dynamics in Motor Cortex and Their Application to Brain–Machine Interfaces" (2018) Pandarinath et al.
- "Neural field models for latent state inference: Application to large-scale neuronal recordings" (2019) Rule et al.
- "Computation through Neural Population Dynamics" (2020) Vyas et al.



w/Omri Barak and David Sussillo
https://braininspired.co/podcast/97/

Great lectures on dynamics

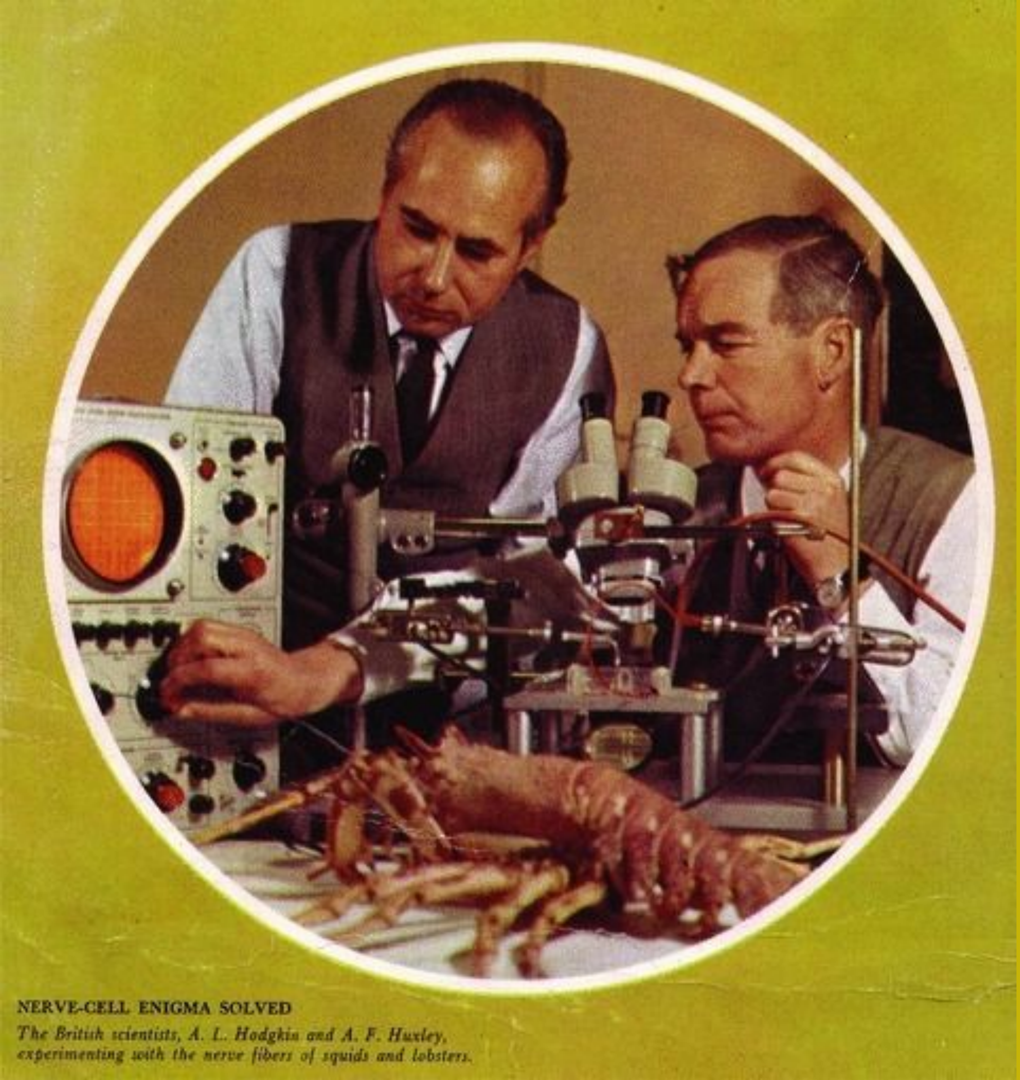
- "Data-Driven Dynamical Systems Overview" Steve Brunton
- "Differential equations, a tourist's guide" 3blue1brown
  - e^(iπ) in 3.14 minutes, using dynamics
  - Divergence and curl: The language of Maxwell's equations, fluid flow, and more

Textbooks

- **Neuronal Dynamics - Gerstner et al.**
  - Has video lectures and python exercises
  - Covers a lot of math very clearly
- Nonlinear Dynamics and Chaos - Strogatz
- "Neuroscience" (2004) Purves et al

Additional Slides

My favorite picture of Hodgkin, Huxley, and their lobster lab assistant



From “A brief historical perspective: Hodgkin and Huxley” (2012) Schwiening

Hallucination is clear evidence of latent representations

These are perceptions in the absence of external stimuli. So something must be happening internally to drive perception

“What geometric visual hallucinations tell us about the visual cortex” (2002) Bressloff, Cowan et al.

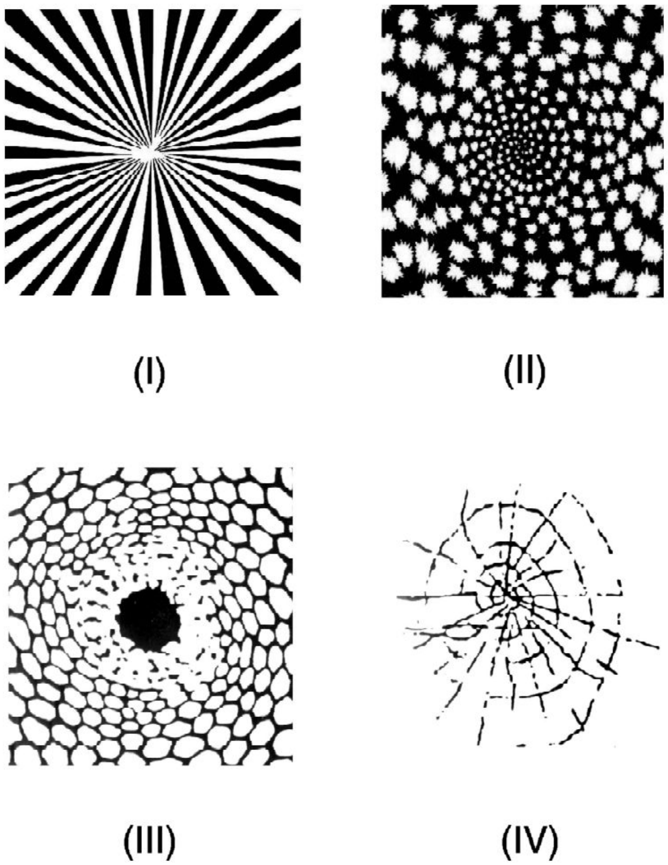
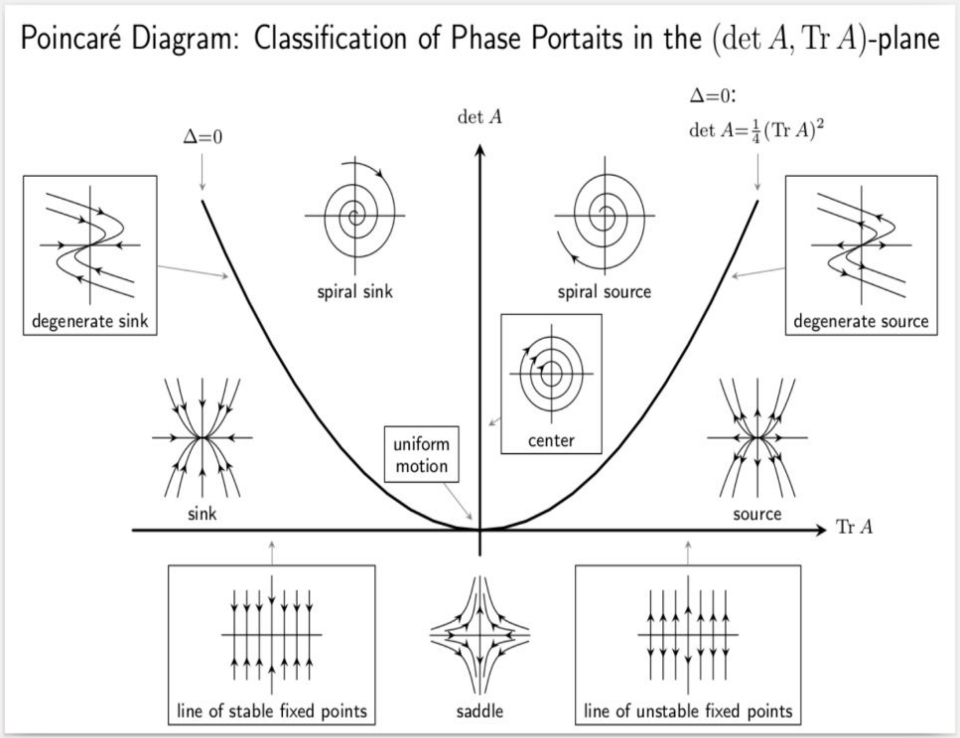
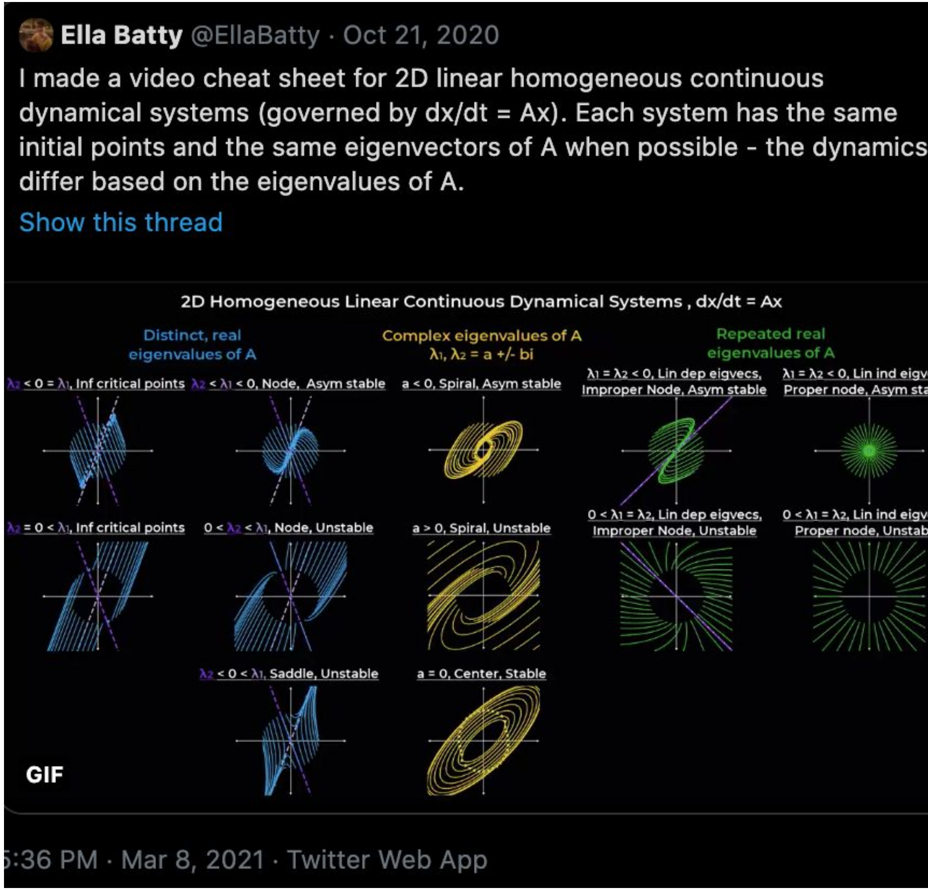


Figure 1: Hallucinatory form constants. (I) Funnel and (II) spiral images seen following ingestion of LSD (redrawn from Siegel & Jarvik, 1975), (III) honeycomb generated by marijuana (redrawn from Siegel & Jarvik, 1975), and (IV) cobweb petroglyph (redrawn from Patterson, 1992).

Zoo of dynamic behaviors

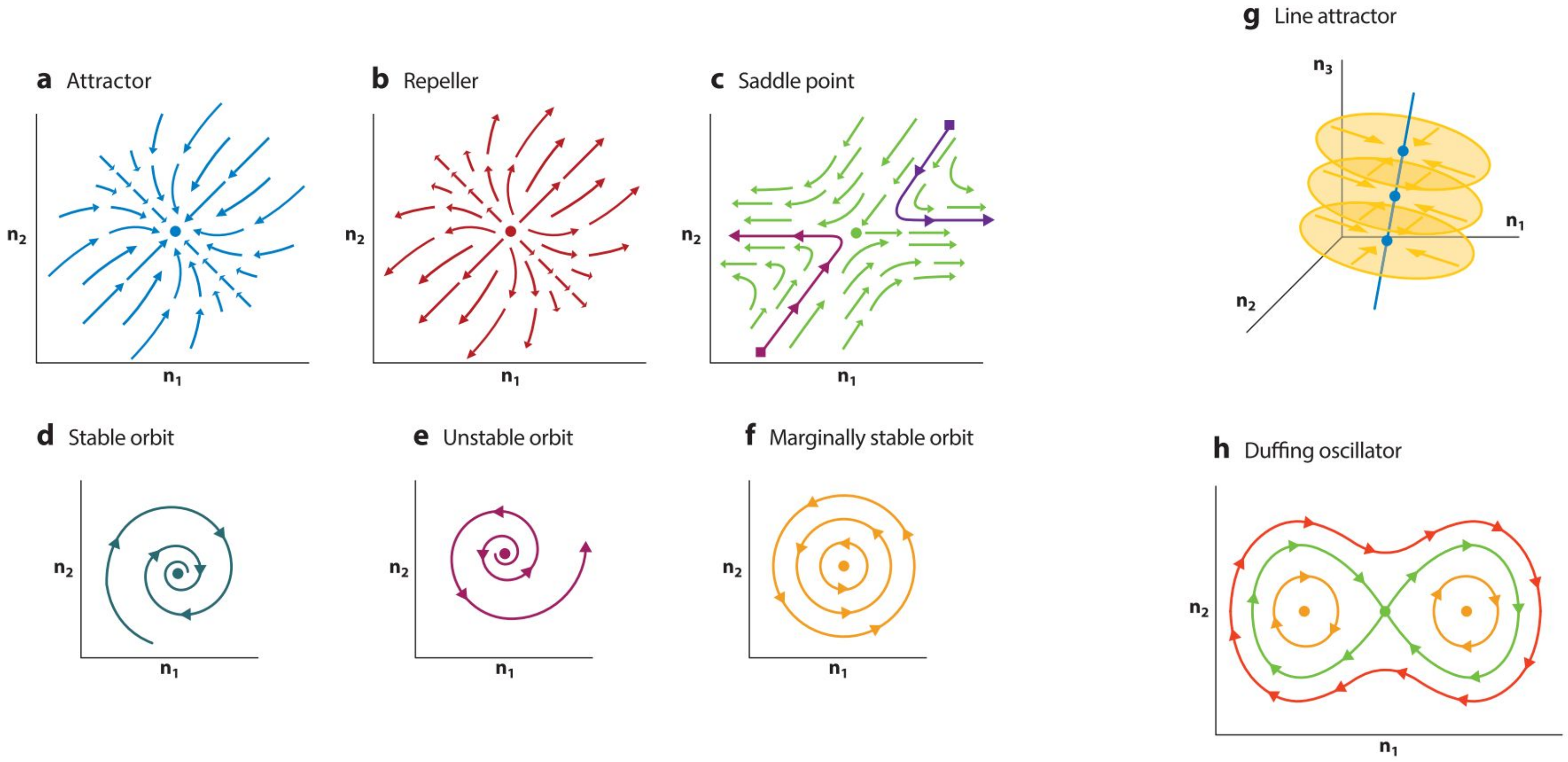




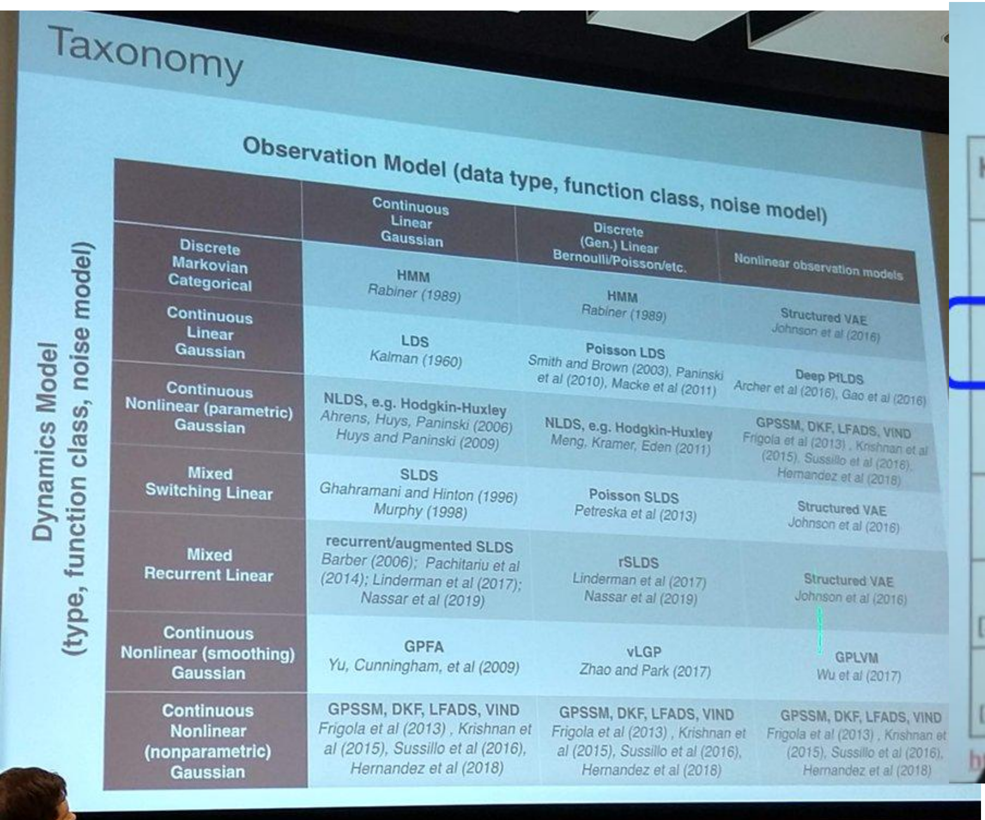
Gatsby Theoretical Neuro. Course notes (2018) Menendez

twitter link - Ella Batty

Patterns of flow within dynamical systems

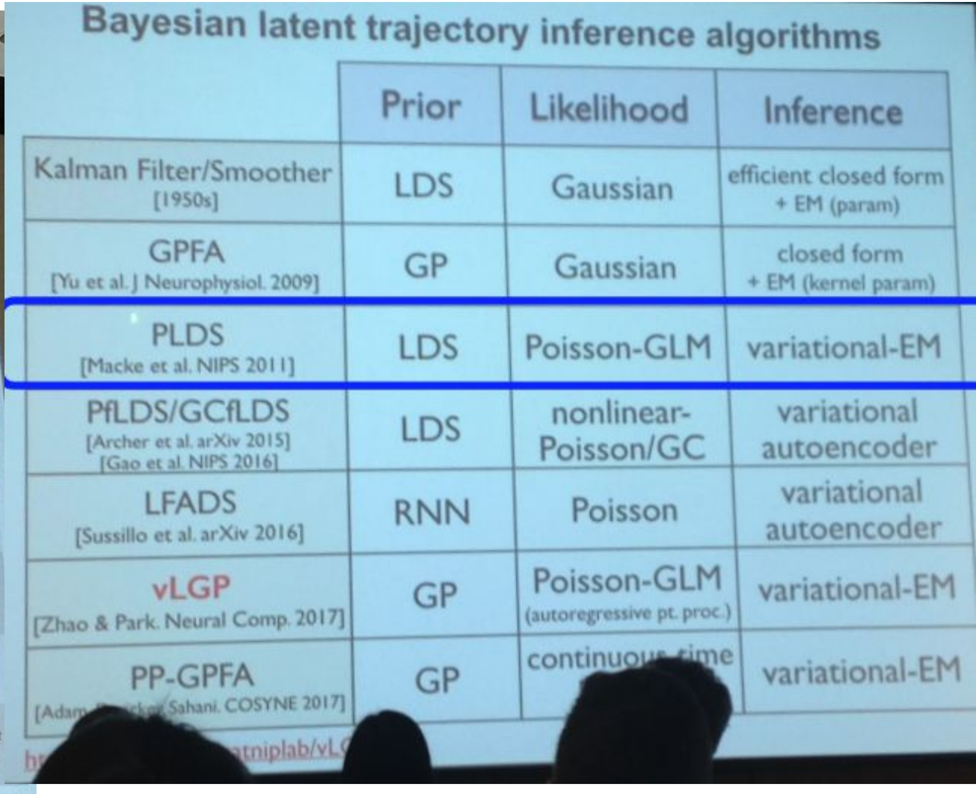


Taxonomy of latent dynamics models in neuroscience



Taxonomy

Dynamics Model (type, function class, noise model)	Continuous Linear Gaussian	Discrete (Gen.) Linear Bernoulli/Poisson/etc.	Nonlinear observation models
Discrete Markovian Categorical	HMM *Rabiner (1989)*	HMM *Rabiner (1989)*	Structured VAE *Johnson et al (2016)*
Continuous Linear Gaussian	LDS *Kalman (1960)*	Poisson LDS *Smith and Brown (2003), Paninski et al (2010), Macke et al (2011)*	Deep PfLDS *Archer et al (2016), Gao et al (2016)*
Continuous Nonlinear (parametric) Gaussian	NLDS, e.g. Hodgkin-Huxley *Ahrens, Huys, Paninski (2006) Huys and Paninski (2009)*	NLDS, e.g. Hodgkin-Huxley *Meng, Kramer, Eden (2011)*	GPSSM, DKF, LFADS, VIND *Frigola et al (2013), Krishnan et al (2015), Sussillo et al (2016), Hernandez et al (2018)*
Mixed Switching Linear	SLDS *Ghahramani and Hinton (1996) Murphy (1998)*	Poisson SLDS *Petreska et al (2013)*	Structured VAE *Johnson et al (2016)*
Mixed Recurrent Linear	recurrent/augmented SLDS *Barber (2006); Pachitariu et al (2014); Linderman et al (2017); Nassar et al (2019)*	rSLDS *Linderman et al (2017) Nassar et al (2019)*	Structured VAE *Johnson et al (2016)*
Continuous Nonlinear (smoothing) Gaussian	GPFA *Yu, Cunningham, et al (2009)*	vLGP *Zhao and Park (2017)*	GPLVM *Wu et al (2017)*
Continuous Nonlinear (nonparametric) Gaussian	GPSSM, DKF, LFADS, VIND *Frigola et al (2013), Krishnan et al (2015), Sussillo et al (2016), Hernandez et al (2018)*	GPSSM, DKF, LFADS, VIND *Frigola et al (2013), Krishnan et al (2015), Sussillo et al (2016), Hernandez et al (2018)*	GPSSM, DKF, LFADS, VIND *Frigola et al (2013), Krishnan et al (2015), Sussillo et al (2016), Hernandez et al (2018)*



Bayesian latent trajectory inference algorithms

	Prior	Likelihood	Inference
Kalman Filter/Smoother [1950s]	LDS	Gaussian	efficient closed form + EM (param)
GPFA [Yu et al. J Neurophysiol. 2009]	GP	Gaussian	closed form + EM (kernel param)
PLDS [Macke et al. NIPS 2011]	LDS	Poisson-GLM	variational-EM
PfLDS/GCfLDS [Archer et al. arXiv 2015] [Gao et al. NIPS 2016]	LDS	nonlinear-Poisson/GC	variational autoencoder
LFADS [Sussillo et al. arXiv 2016]	RNN	Poisson	variational autoencoder
vLGP [Zhao & Park. Neural Comp. 2017]	GP	Poisson-GLM (autoregressive pt. proc.)	variational-EM
PP-GPFA [Adam [illegible] Sahani. COSYNE 2017]	GP	continuou[illegible]ime	variational-EM

Dynamical models of neurons

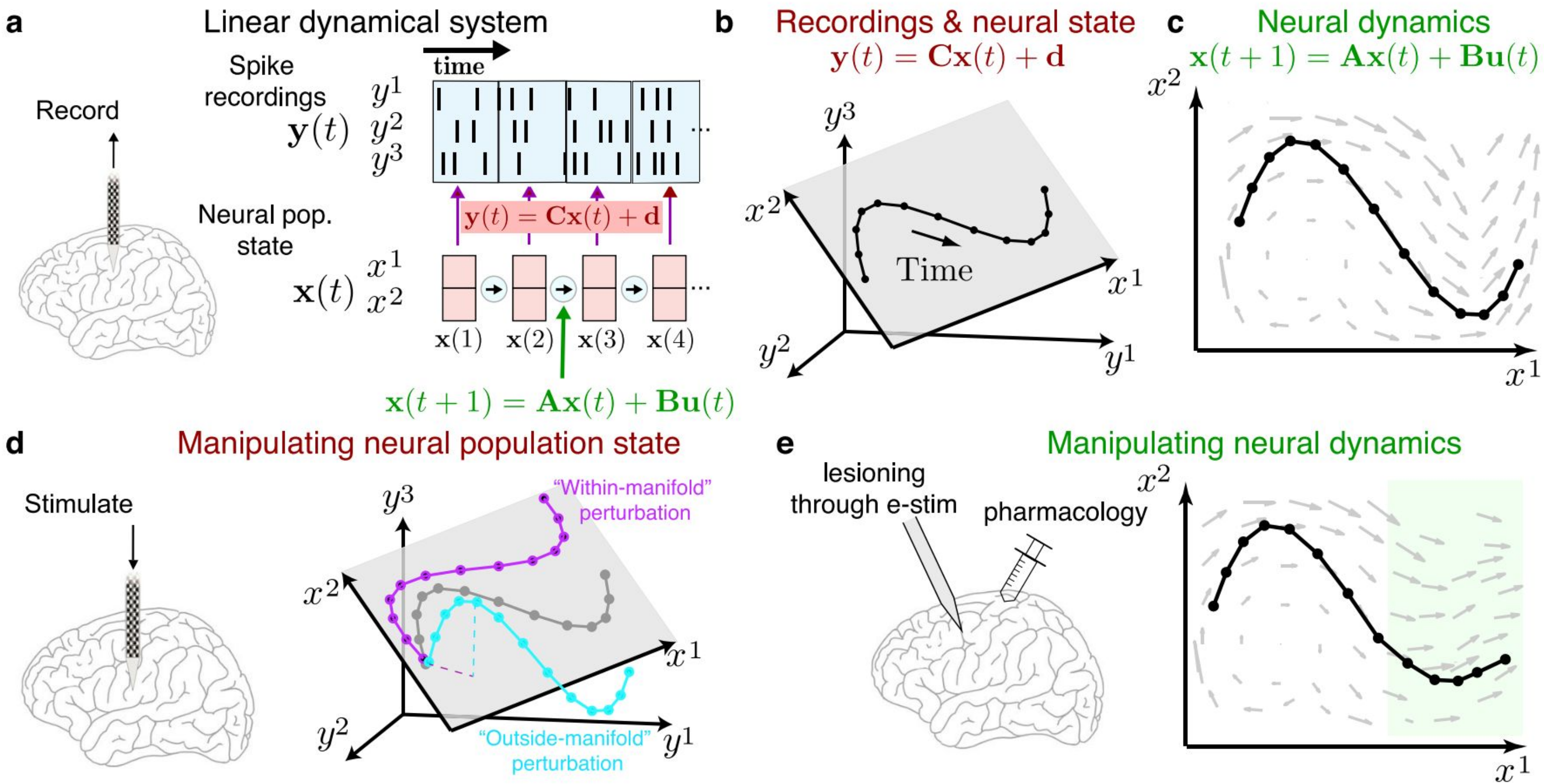
Model	Example	Variables	Remarks	Ref.
Integrate-and-fire neurons	$\frac{dv(t)}{dt} = \begin{cases} -\frac{v(t)}{\tau} + I_{\text{ext}} + I_{\text{syn}}(t) & 0 < v(t) < \theta \\ v(t_0^+) = 0 & v(t_0^-) = \theta \end{cases}$ $I_{\text{syn}}(t) = g \sum_{\text{spikes}} f(t - t_{\text{spike}})$ and $f(t) = A\left[\exp(-t/\tau_1) - \exp(-t/\tau_2)\right]$	$v(t)$ is the neuron membrane potential; θ is the threshold for spike generation. I_{ext} is an external stimulus current, I_{syn} is the sum of the synaptic currents, and τ_1 and τ_2 are time constants characterizing the synaptic currents.	A spike occurs when the neuron reaches the threshold θ in $v(t)$ after which the cell is reset to the resting state.	(Lapicque, 1907)
Rate models	$\dot{a}_i(t) = F_i(a_i(t))\left[G_i(a_i(t)) - \sum_j \rho_{ij} Q_j(a_j(t))\right]$	$a_i(t) > 0$ is the spiking rate of the ith neuron or cluster, ρ_{ij} is the connection matrix, and F, G, Q are polynomial functions.	This is a generalization of the Lotka-Volterra model (see eq. 9).	(Fukai and Tanaka, 1997; Lotka, 1925; Volterra, 1931)
McCulloch and Pitts	$\begin{aligned} x_i(n+1) &= \Theta(\textstyle\sum_j g_{ij} x_j(n) - \theta) \\ \Theta(x) &= 1,\ x > 0 \\ &= 0,\ x \leq 0 \end{aligned}$	θ is the firing threshold; $x_j(n)$ are synaptic inputs at the discrete 'time' n; $x_i(n+1)$ is the output. Inputs and outputs are binary (ones or zero); the synaptic connections g_{ij} are 1, -1, or 0.	The first computational model for an artificial neuron; it is also known as a linear threshold device model. This model neglects the relative timing of neural spikes.	(McCulloch and Pitts, 1943)
Hodgkin-Huxley (H-H)	$\begin{aligned} C\dot{v(t)} &= g_L(v_L - v(t)) \\ &+ g_{Na} m(t)^3 h(t)(v_{Na} - v(t)) \\ &+ g_K\, n(t)^4 (v_K) - v(t)) + I, \\ \dot{m(t)} &= \frac{m_\infty(v(t)) - m(t)}{\tau_m(v(t))} \\ \dot{h(t)} &= \frac{h_\infty(v(t)) - h(t)}{\tau_h(v(t))} \\ \dot{n(t)} &= \frac{n_\infty(v(t)) - n(t)}{\tau_n(v(t))} \end{aligned}$	$v(t)$ is the membrane potential, $m(t), h(t)$ and $n(t)$ represent empirical variables describing the activation and inactivation of the ionic conductances; I is an external current. The steady state values of the conductance variables $m_\infty, h_\infty, n_\infty$ have a nonlinear voltage dependence, typically through sigmoidal or exponential functions.	These ODEs represent point neurons. There is a large list of models derived from this one, and it has become the principal tool in computational neuroscience. Other ionic currents can be added to the right hand side of the voltage equation to better reproduce the dynamics and bifurcations observed in the experiments.	(Hodgkin and Huxley, 1952)
Fitz-Hugh-Nagumo	$\begin{aligned} \dot{x} &= x - c\,x^3 - y + I, \\ \dot{y} &= x + b\,y - a \end{aligned}$	$x(t)$is the membrane potential, and $y(t)$ describes the dynamics of fast currents; I is an external current. The parameter values a, b and c are constants chosen to allow spiking.	A reduced model describing oscillatory spiking neural dynamics including bistability.	(FitzHugh, 1961; Nagumo *et al.*, 1962)
Wilson-Cowan	$\mu \frac{\partial E(x,t)}{\partial t} = -E(x,t) + (1 - rE(x,t))\mathcal{L}_e\left(E(x,t) \otimes w_{ee}(x) - I(x,t) \otimes w_{ei}(x) + I_e(x,t)\right)$ $\mu \frac{\partial I(x,t)}{\partial t} = -I(x,t) + (1 - rI(x,t))\mathcal{L}_i\left(E(x,t) \otimes w_{ie}(x) - I(x,t) \otimes w_{ii}(x) + I_i(x,t)\right),$	$\{E(x,t), I(x,t)\}$ are the number density of active excitatory and inhibitory neurons at location x of the continuous neural media. $(w_{ee}(x), w_{ie}(x), w_{ei}(x), w_{ii}(x))$ are connectivity distributions among the populations of cells. $\{\mathcal{L}_e, \mathcal{L}_i\}$ are nonlinear responses reflecting different populations of thresholds. The operator $\otimes$ is a convolution involving the connectivity distributions.	The first 'mean field' model. It is an attempt to describe a cluster of neurons to avoid the inherent noisy dynamical behavior of individual neurons; by averaging to a distribution noise is reduced.	(Wilson and Cowan, 1973)

TABLE I A summary of many frequently used neuronal models.

Model	Equations	Variables	Remarks	Ref.
Morris-Lecar	$\begin{aligned} \dot{v(t)} &= g_L(v_L - v(t)) + n(t) g_n (v_n - v(t)) \\ &+ g_m\, m_\infty(v(t))(v_m - v(t)) + I, \\ \dot{n(t)} &= \lambda(v(t))(n_\infty(v(t)) - n(t)) \\ m_\infty(v) &= \frac{1}{2}\left(1 + \tanh \frac{v - v_m}{v_m^0}\right) \\ n_\infty(v) &= \frac{1}{2}\left(1 + \tanh \frac{v - v_n}{v_n^0}\right) \\ \lambda(v) &= \phi_n \cosh \frac{v - v_n}{2\, v_n^0} \end{aligned}$	$v(t)$ is the membrane potential; $n(t)$ describes the recovery activity of a calcium current; I is an external current.	Simplified model that reduces the number of dynamical variables of the H-H model. It displays action potential generation when changing I leads to a saddle node bifurcation to a limit cycle.	(Morris and Lecar, 1981)
Hindmarsh-Rose	$\begin{aligned} \dot{x(t)} &= y(t) + a\,x(t)^2 - b\,x(t)^3 - z(t) + I, \\ \dot{y(t)} &= C - d\,x(t)^2 - y(t), \\ \dot{z(t)} &= r\left[s(x(t) - x_0) - z(t)\right] \end{aligned}$	$x(t)$ is the membrane potential;$y(t)$ describes fast currents; $z(t)$ describes slow currents; and I is an external current	Simplified model that uses a polynomial approximation to the right hand side of a Hodgkin-Huxley model. This model fails to describe the hyperpolarized periods after spiking of biological neurons.	(Hindmarsh and Rose, 1984)
Phase oscillator models	$\frac{d\theta_i(t)}{dt} = \omega + \sum_j H_{ij}(\theta_i(t) - \theta_j(t))$	$\theta(t)$ is the phase of the ith neuron with approximately periodic behavior, and H_{ij} is the connectivity function determining how neuron i and j interact.	First introduced for chemical oscillators; good for describing strongly dissipative oscillating systems in which the neurons are intrinsic periodic oscillators	(Cohen *et al.*, 1982; Ermentrout and Kopell, 1984; Kuramoto, 1984)
Map models	$\begin{aligned} x_{t+1}(i) &= \frac{\alpha}{1 + x_t(i)^2} + y_t(i) \\ &+ \frac{\epsilon}{N} \textstyle\sum_j x_t(j) \\ y_{t+1}(i) &= y_t(i) - \sigma x_t(i) - \beta \end{aligned}$	x_t represents the spiking activity and y_t represents a slow variable. A discrete time map.	One of a class of simple phenomenological models for spiking, bursting neurons This kind of model can be computationally very fast, but has little biophysical foundation.	(Cazelles *et al.*, 2001; Rulkov, 2002)

TABLE I Continuation: summary of many frequently used neuronal models.

Dynamical systems + perturbations



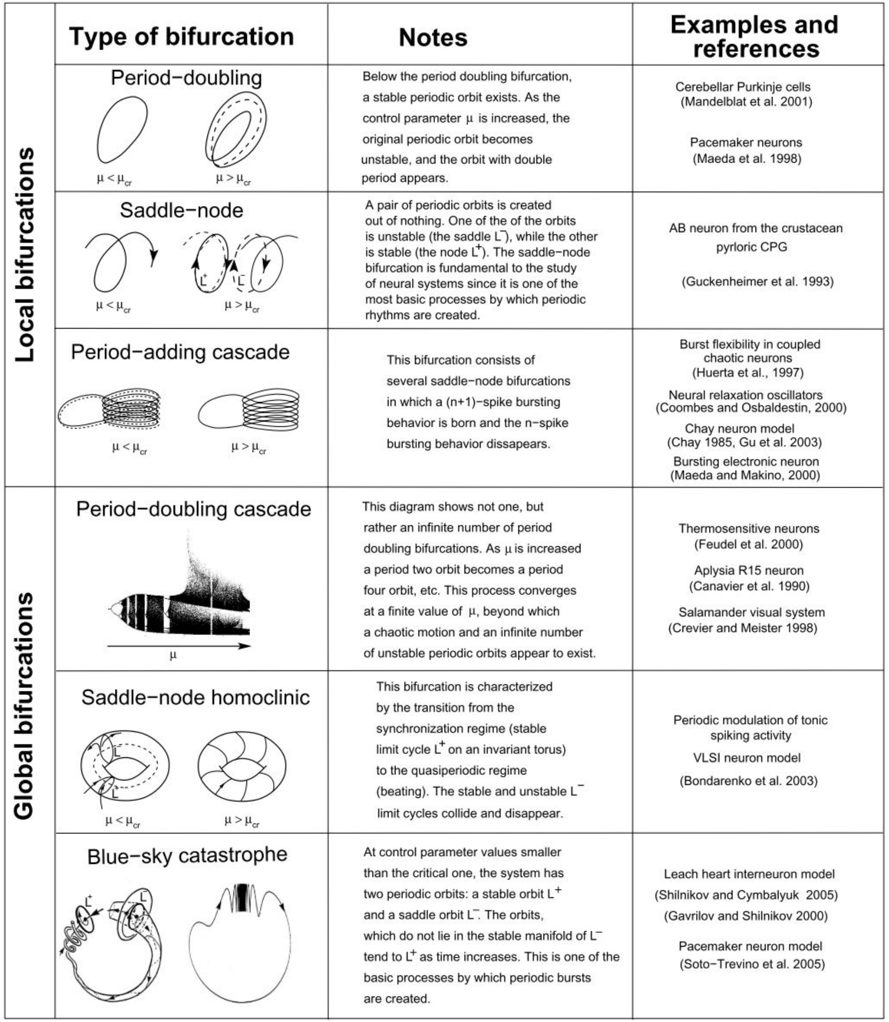
"Measurement, manipulation and modeling of brain-wide neural population dynamics" (2021) Shenoy, Kao

Types of bifurcation

"Dynamical principles in neuroscience" (2006)

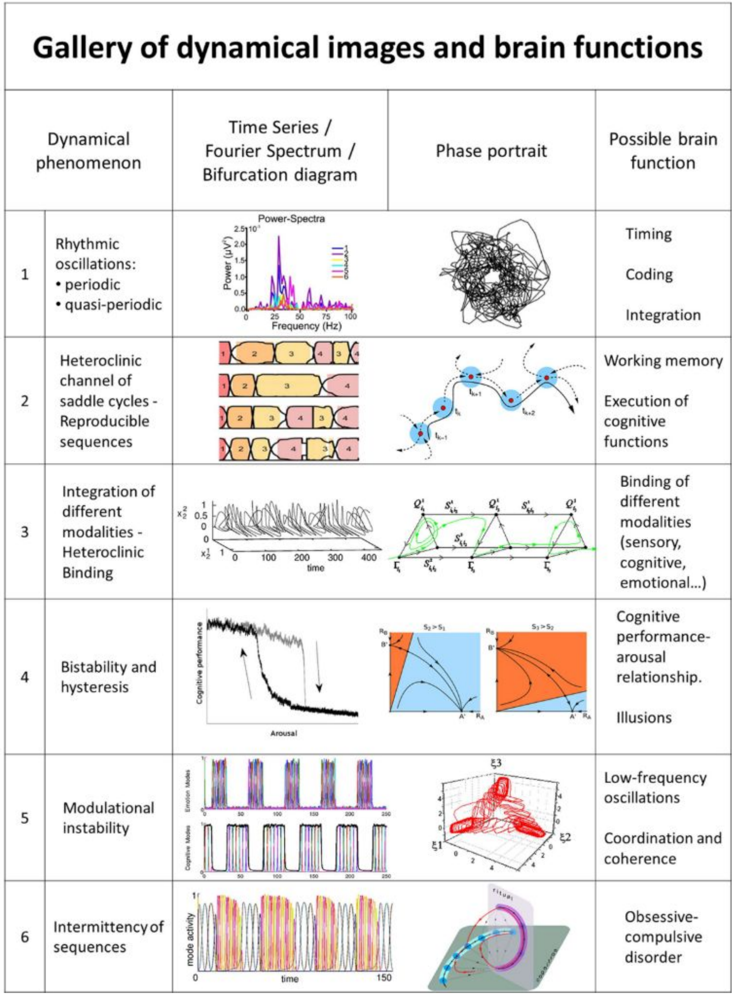
Rabinovich et al.

- *thorough review*



	Type of bifurcation	Notes	Examples and references
Local bifurcations	Period−doubling $\mu < \mu_{cr}$ $\mu > \mu_{cr}$	Below the period doubling bifurcation, a stable periodic orbit exists. As the control parameter μ is increased, the original periodic orbit becomes unstable, and the orbit with double period appears.	Cerebellar Purkinje cells (Mandelblat et al. 2001) Pacemaker neurons (Maeda et al. 1998)
	Saddle−node $\mu < \mu_{cr}$ $\mu > \mu_{cr}$	A pair of periodic orbits is created out of nothing. One of the of the orbits is unstable (the saddle L^-), while the other is stable (the node L^+). The saddle−node bifurcation is fundamental to the study of neural systems since it is one of the most basic processes by which periodic rhythms are created.	AB neuron from the crustacean pyrloric CPG (Guckenheimer et al. 1993)
	Period−adding cascade $\mu < \mu_{cr}$ $\mu > \mu_{cr}$	This bifurcation consists of several saddle−node bifurcations in which a (n+1)−spike bursting behavior is born and the n−spike bursting behavior dissapears.	Burst flexibility in coupled chaotic neurons (Huerta et al., 1997) Neural relaxation oscillators (Coombes and Osbaldestin, 2000) Chay neuron model (Chay 1985, Gu et al. 2003) Bursting electronic neuron (Maeda and Makino, 2000)
Global bifurcations	Period−doubling cascade μ	This diagram shows not one, but rather an infinite number of period doubling bifurcations. As μ is increased a period two orbit becomes a period four orbit, etc. This process converges at a finite value of μ, beyond which a chaotic motion and an infinite number of unstable periodic orbits appear to exist.	Thermosensitive neurons (Feudel et al. 2000) Aplysia R15 neuron (Canavier et al. 1990) Salamander visual system (Crevier and Meister 1998)
	Saddle−node homoclinic $\mu < \mu_{cr}$ $\mu > \mu_{cr}$	This bifurcation is characterized by the transition from the synchronization regime (stable limit cycle L^+ on an invariant torus) to the quasiperiodic regime (beating). The stable and unstable L^- limit cycles collide and disappear.	Periodic modulation of tonic spiking activity VLSI neuron model (Bondarenko et al. 2003)
	Blue−sky catastrophe	At control parameter values smaller than the critical one, the system has two periodic orbits: a stable orbit L^+ and a saddle orbit L^-. The orbits, which do not lie in the stable manifold of L^- tend to L^+ as time increases. This is one of the basic processes by which periodic bursts are created.	Leach heart interneuron model (Shilnikov and Cymbalyuk 2005) (Gavrilov and Shilnikov 2000) Pacemaker neuron model (Soto−Trevino et al. 2005)

FIG. 2 Six examples of limit cycle bifurcations observed in living and model neural systems.



Gallery of dynamical images and brain functions

	Dynamical phenomenon	Time Series / Fourier Spectrum / Bifurcation diagram	Phase portrait	Possible brain function
1	Rhythmic oscillations: • periodic • quasi-periodic			Timing Coding Integration
2	Heteroclinic channel of saddle cycles - Reproducible sequences			Working memory Execution of cognitive functions
3	Integration of different modalities - Heteroclinic Binding			Binding of different modalities (sensory, cognitive, emotional...)
4	Bistability and hysteresis			Cognitive performance-arousal relationship. Illusions
5	Modulational instability			Low-frequency oscillations Coordination and coherence
6	Intermittency of sequences			Obsessive-compulsive disorder

"Robust Transient Dynamics and Brain Functions" (2011) Rabinovich

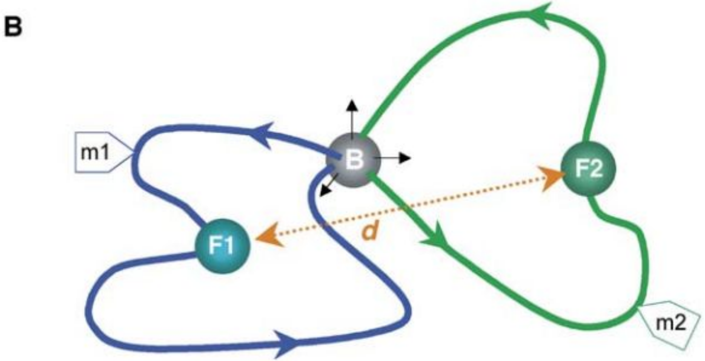


Figure 8. Schematic Diagram of Odor-Evoked PN Activity

(Ai) Idealized odor trajectory in PN space. *B*, baseline; *F*, fixed point; t_i, times corresponding to one oscillation cycle. During the on transient, synchronization is the highest and most spikes occur within a single 10–20 ms period. Activity thus "hops" from one oscillation cycle to the next while the identities of the responding PNs evolve (see [Aii]).

(Aii) Evolving PN activity that underlies the trajectory in (Ai), green squares represent responsive PNs.

(B) Idealized trajectories for two different odors. Odor trajectories differ at their fixed points (*F1* and *F2*) but are maximally distant during the transient response phases (e.g., *m1* and *m2*). (d, Euclidian distance.)

"Transient Dynamics versus Fixed Points in Odor Representations by Locust Antennal Lobe Projection Neurons" (2005) Mazor, Laurent

Why study dynamics?

- Time matters for physical things in the world
  - F = ma is a dynamical system
  - Hopfield was a physicist
  - If the brain is to interface with the world, it better “get” time
- Dynamical models enable forecasting - predicting the future
  - As well as remembering (integration)
- Huge history of successful application -> lots of tools and prior characterization
- Bridges high-dimensional, noisy measurements to low-dimensional interpretable causes
  - Dynamic predictions as a regularizer
- (Dynamical models are intriguing)
  - We’re perhaps drawn to them because of an evolutionary pressure to “care about” water, fire

What makes studying dynamics difficult?

- Often real-world problems are nonlinear
  - Nonstationary / State-dependent
- Feedback
  - potential instability
  - errors compound
- Coupling of relevant variables (“everything” is correlated)
- High dimensionality
- Unobserved variables
- Chaos + stochasticity
- Multiscale dynamics

See also: “What Is Turbulence? Turbulent Fluid Dynamics are Everywhere” Brunton

Additional topics not explored here

- Nonlinear dynamics
- Perturbations / input-driven dynamics
- Chaos, robustness to initial conditions
- Oscillations - rhythmic networks
- Parameter bifurcations
- Spatial dynamics - traveling waves