

Modelling the dynamics of decision making

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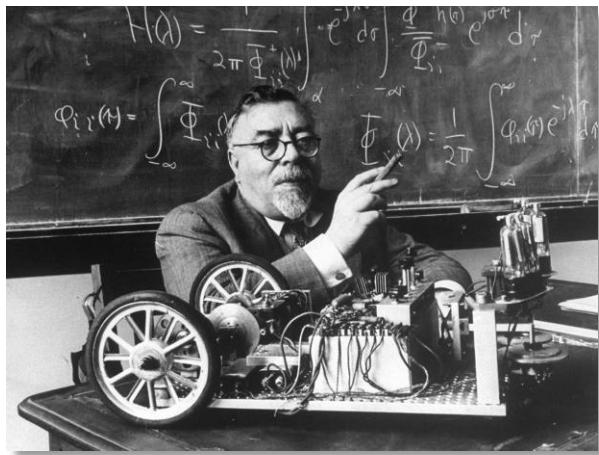
Content:

- **Neural network dynamics (with some cognitive processing applications)**
(introductory)
- **Modelling decision dynamics**
- **Applications to intelligent systems**
(briefly)

Computational view of cognition

Cybernetics (1940's) and Artificial intelligence (AI) (1950's)

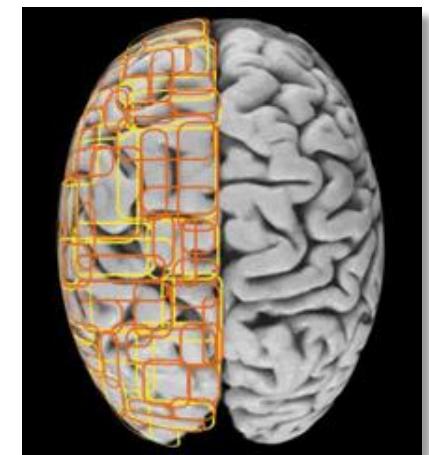
Computational
Neuroscience (1980's)



Mathematician Norbert Wiener
(with his cybernetic moth-bedbug)



Artificial neural networks
& learning algorithms



Biologically based
computational &
mathematical models

Brain functions as computational processing, divided into 3 levels of description (David Marr, 1982).

1st level: Computational theory, which deals with the goal of neural computation involving appropriateness and logic of the strategy in the computation.

2nd level: Representations and algorithms of processing which entails how computation is implemented or realized, what the inputs and outputs are, and the algorithms that process them.

3rd level: “Hardware” implementation, which describes how the representations and algorithms are represented in physical (e.g. biological) systems.

Computational/Theoretical Neuroscience encompasses all these levels of description on brain functions. The level to be employed depends on the research questions and also the availability of data types.

Focus: Network dynamics using the tools in dynamical systems theory (in physics, mathematics, engineering), beginning with simple network models

Representation of neural network models

How do we model neural networks?

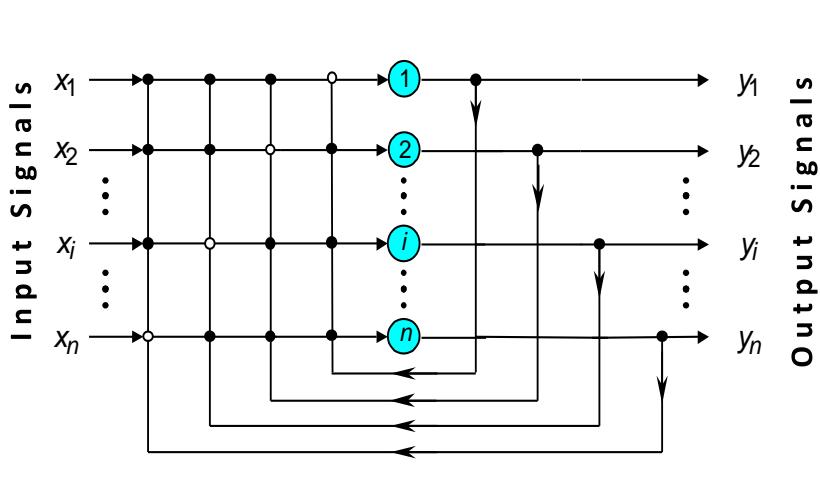
Ordinary/Partial Differential Equations
(ODEs/PDEs), be they:

- biophysical (HH/conductance based) models,
- spiking (IF) neuronal network models, or
- simplified neural network models

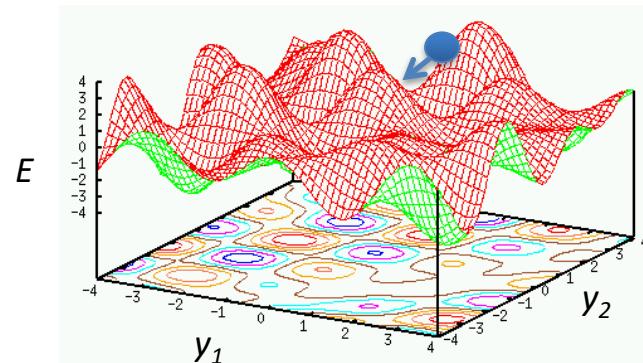
Are there ways to theoretically analyse
and conceptually understand neural
networks?

Can we use certain network behaviour to
model and understand (certain) cognitive
processing or observable behaviour?

Recall Hopfield network model (for memory)



$$Energy, E = -\frac{1}{2} \sum_{i,j} W_{ij} y_i y_j$$



Discretized updating of states (p^{th} iteration)

$$y_i(p+1) = \text{sign} \left(\sum_j w_{ij} x_j(p) - q_i \right)$$

Continuous updating of states

$$\frac{dy_i}{dt} = -\frac{y_i}{\tau} + \sum_j w_{ij} F(y_j)$$

Nonlinear map

or $y_{p+1} = G(y_p)$

(1st order) nonlinear DE

or $\frac{dy}{dt} = F(y)$

Generic Representation & Behaviour of Dynamical Systems

Dynamical systems have generic behaviour.

Can be represented in the general forms*:

Differential equations: $dx/dt = F(x, \pi, t)$ for continuous dynamics

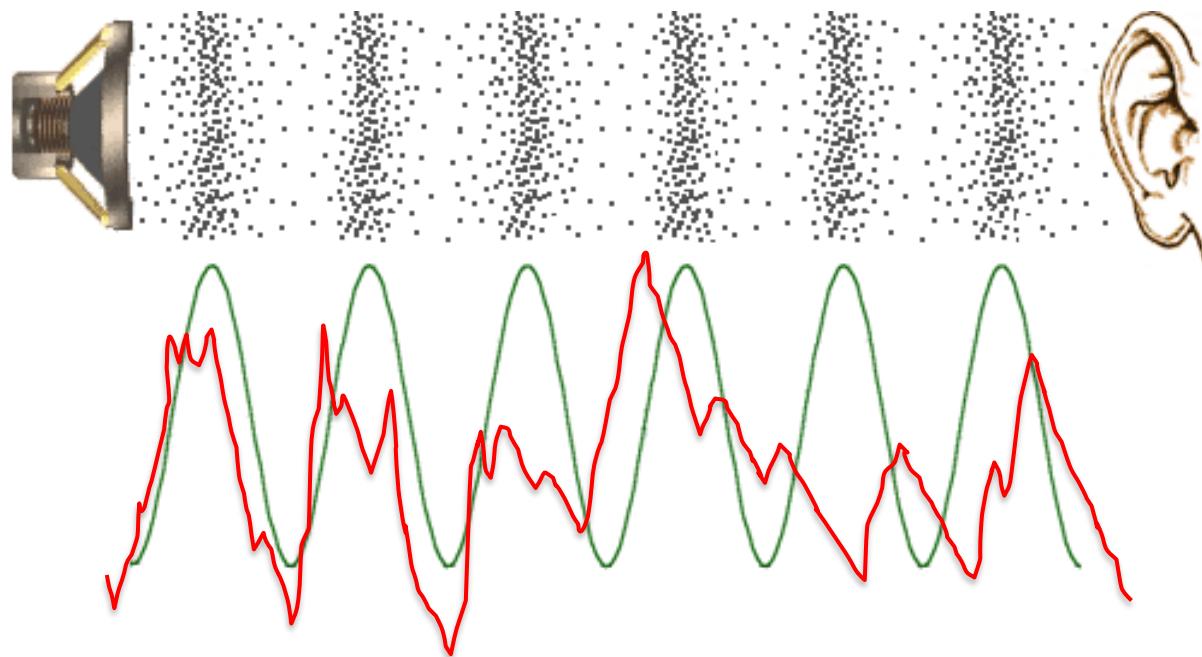
Discrete maps: $x_{p+1} = G(x_p, \pi)$ for discrete dynamics

where state vector $x = (x_1, x_2, \dots, x_n)$, and a set of parameters $\pi = (\pi_1, \pi_2, \dots, \pi_n)$.

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

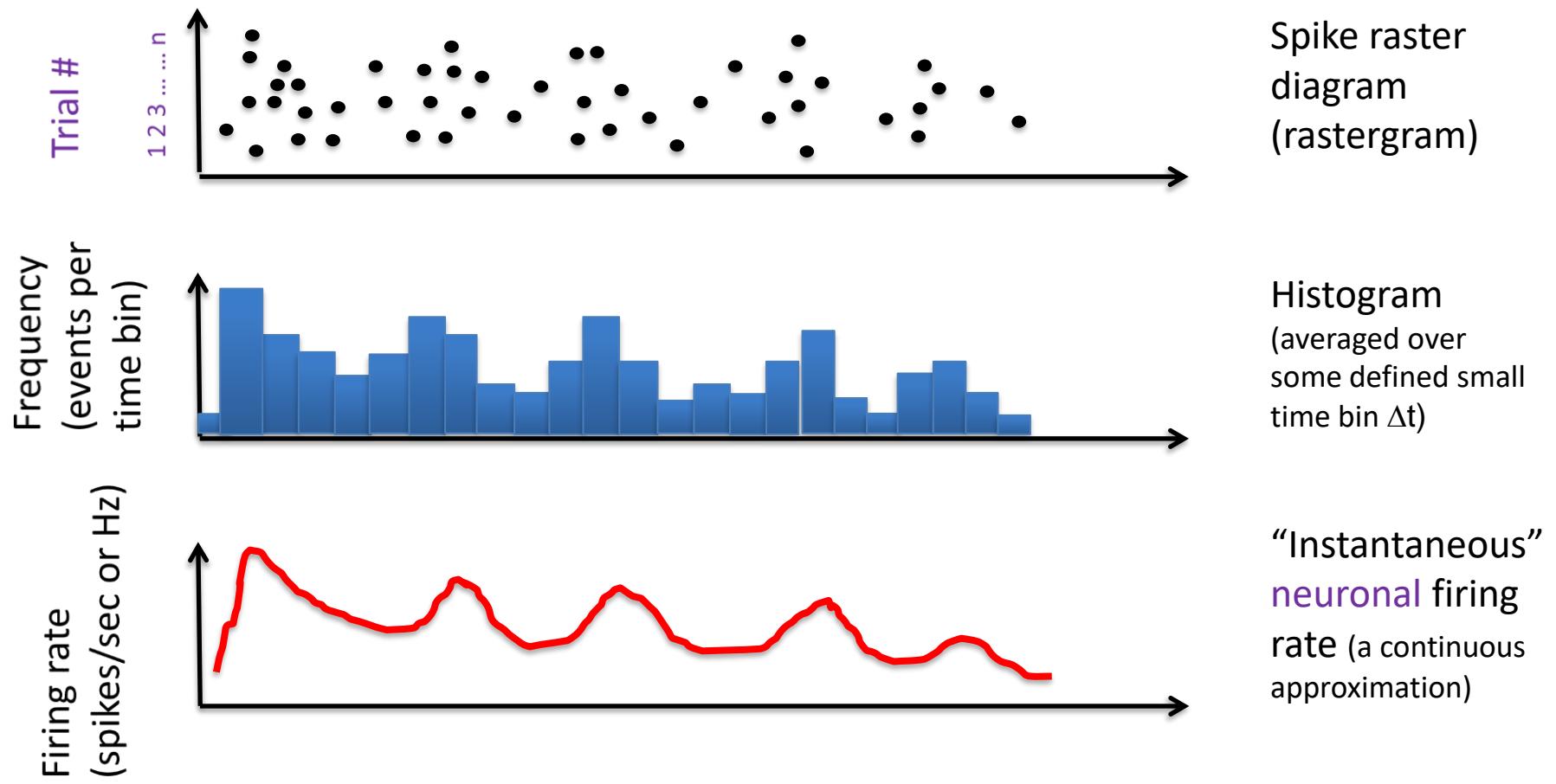
Wait a minute... But we've previously learned that the activity of neurons come in the form of discrete action potentials or spikes. How can we relate that to a continuous stream of activities of a system of neurons, as in the Hopfield model?

Transforming from discretized to continuous activity

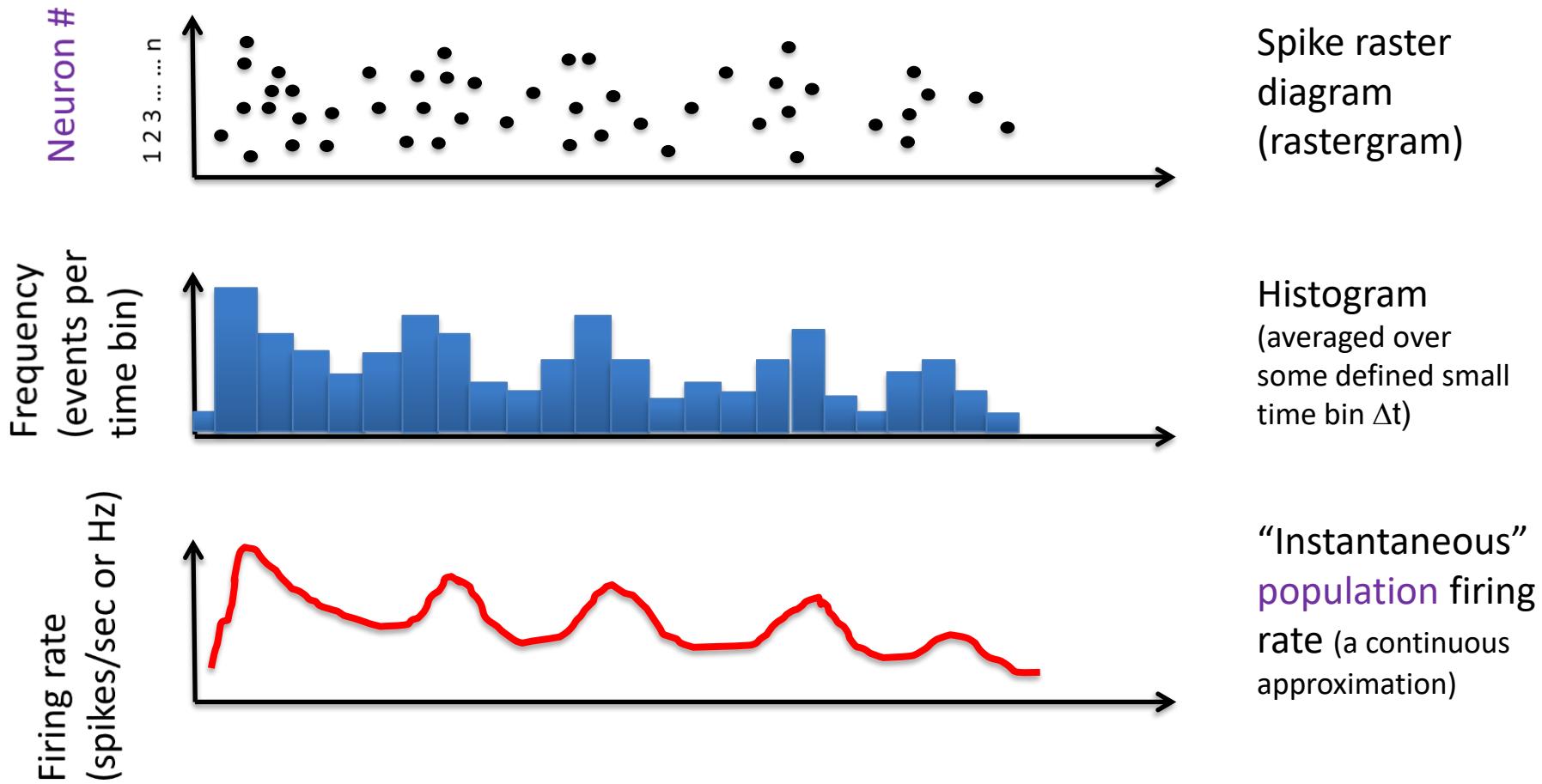


An analogy: from air particle movement to (approximate) continuous sound wave

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



We can also do it for multiple (noisy) neurons by averaging over the neuronal activities



Rate coding – mean, instantaneous firing rates

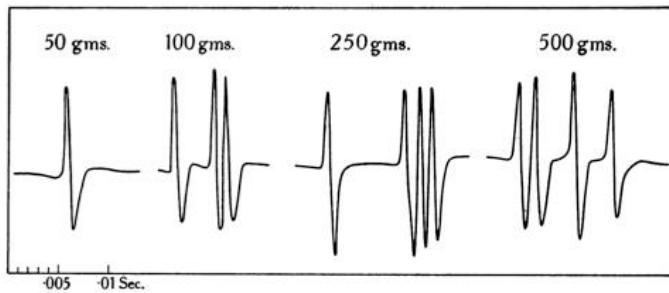
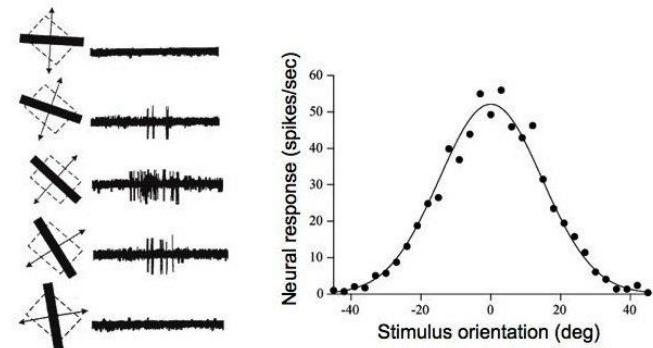
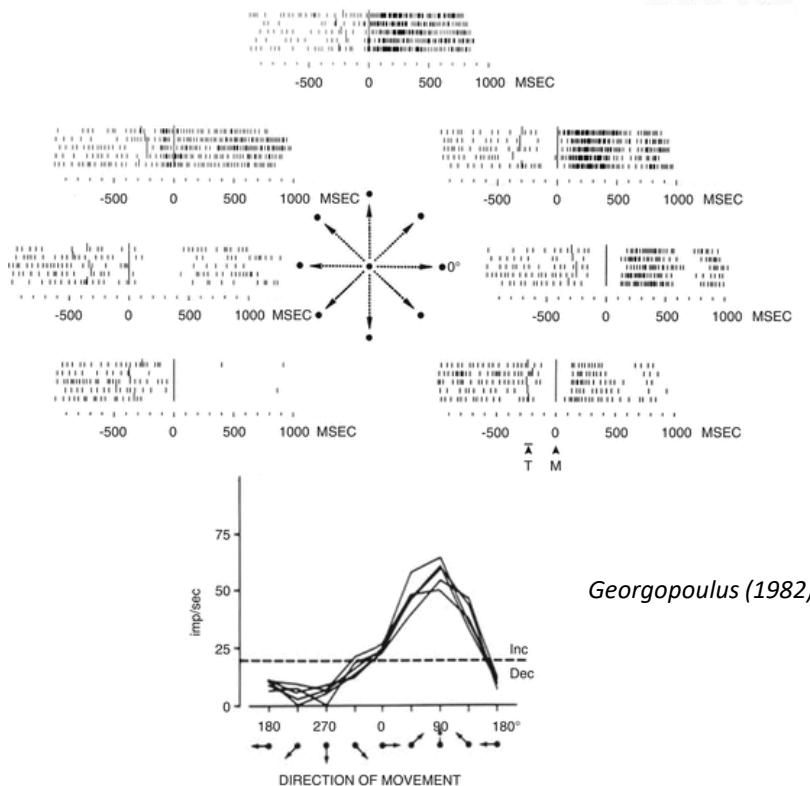


Fig. 5. Analysis of electrometer records, *Exp. 2*, showing that the size of individual impulses does not vary with the stimulus.

Adrian (1926)



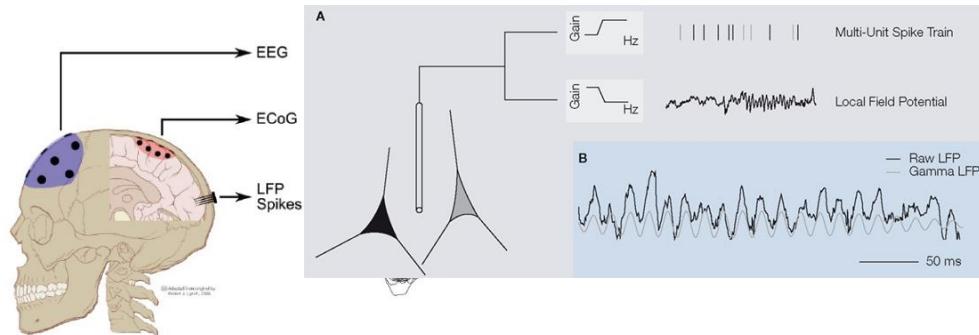
- “Tuning” curves of primary visual cortex (Hubel and Wiesel)
- Motor preparation, movement, reaching (Georgopoulos, 1982)
- Oculomotor movement
- Head direction
- Decision-making
- Various forms of memory encoding and retrieval
- Many more ...



Neural recordings

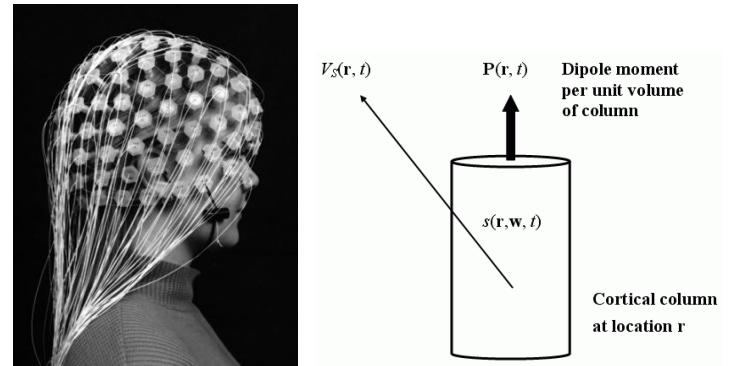
- Local field potential (LFP; electrical field in extracellular space)

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



- Electrical signals from electroencephalogram (EEG)

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

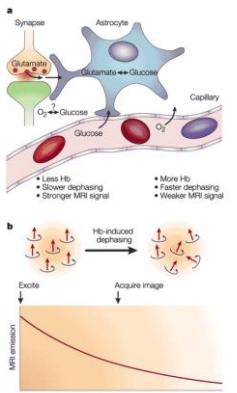
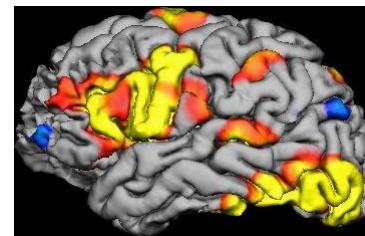


(Or magnetic signals with MEG)

- Functional MRI (fMRI) BOLD signals

Heeger and Ress, Nat. Rev. Neurosci., 2002.

BOLD: Blood oxygen level dependent



Firing (rate) models are:

- computationally more efficient – do not have to simulate every single neuronal spiking. Just treat activity as continuous function and averaged over population of neurons
- used in most artificial neural networks (easier to train)
- more analytically tractable, 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 :

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

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

Wilson and Cowan, 1972; 1973

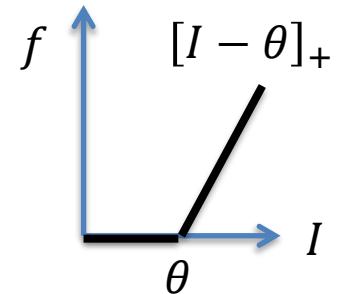
Sometimes, the mean membrane potential $\langle V_i \rangle$ is used instead of current I_i .

Among the most influential theoretical neuroscience papers:

Wilson and Cowan (1972) Excitatory and inhibitory interactions in localized populations of model neurons. Biophysical Journal 12:1-24.
Wilson and 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) function, or rectifier (ReLU) activation function,

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



For $I_i > \theta_i$,

$$\begin{aligned} \tau_i \frac{df_i}{dt} &= -f_i + I_i \\ &= -f_i + \sum_i w_{ij} f_j + I_{i,ext} \end{aligned} \quad \textit{Fully linear}$$

or in matrix/linear algebraic form

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

where \mathbf{f} and \mathbf{I}_{ext} are vector columns, and \mathbf{W} is $(-\mathbb{I} + w_{ij})$ a matrix.

What timescale τ_i to use? Neurons? Synapses?

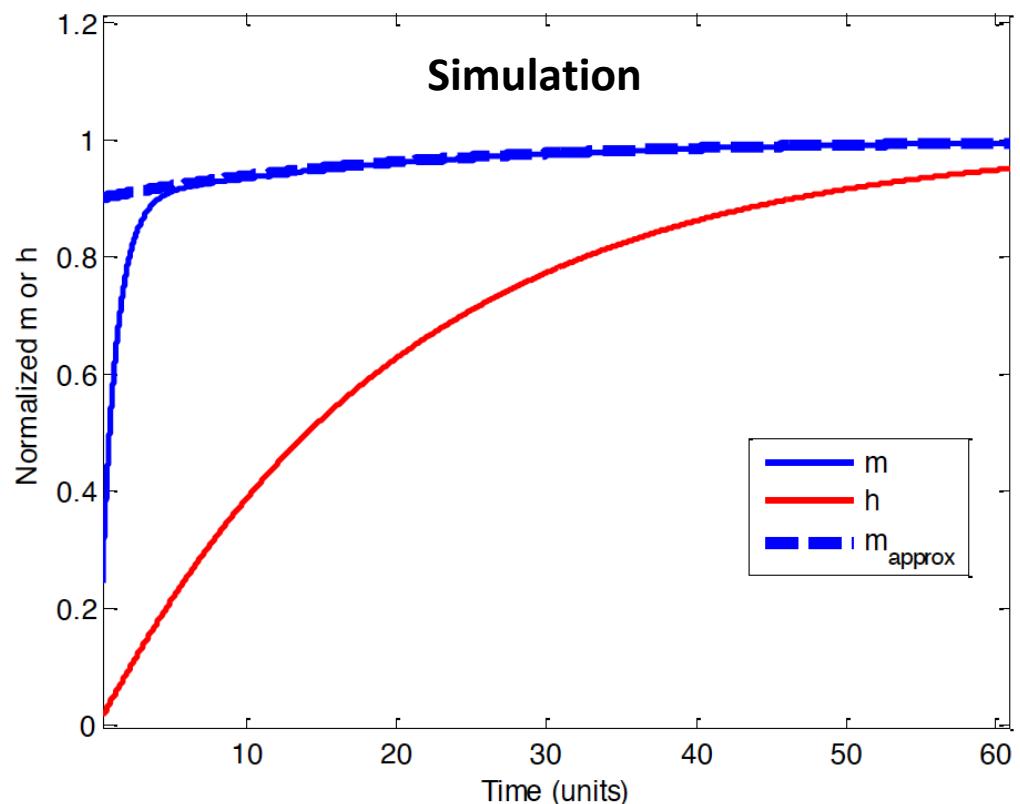
Multiple timescale system

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

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

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

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 .



Method: Separation of timescales

Multiple timescale system

In firing-rate models

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

$$I_{syn,ij} = g_{syn,ij} \sum_j \delta(t - t_j)$$

Instantaneous synapses

$$\langle I_{syn,ij} \rangle \sim g_{syn,ij} f_j$$

Averaged over neurons

$$\tau_{m,i} \frac{df_i}{dt} = -f_i + F_i(\langle I_{syn,ij} \rangle)$$

Governed by membrane potential dynamics (Wilson-Cowan)

Case II: For $\tau_m \ll \tau_{syn}$

we *cannot* ignore synaptic dynamics

$$\frac{dI_{syn,ij}}{dt} = -\frac{I_{ij}}{\tau_{syn,ij}} + g_{syn,ij} \sum_j \delta(t - t_j)$$

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

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

Hold on! But where is the driving force ($V - E$) in the synaptic currents? 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):

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

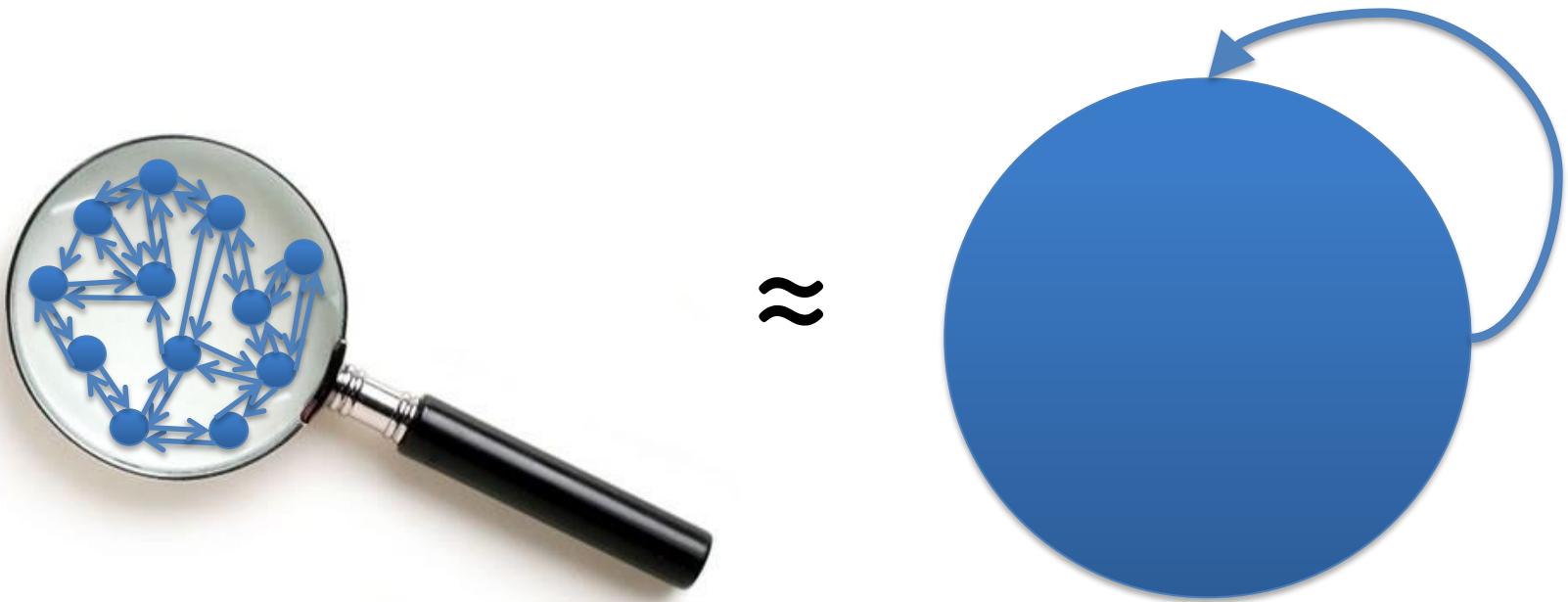
The qualitative coarser network effects can still be captured.

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

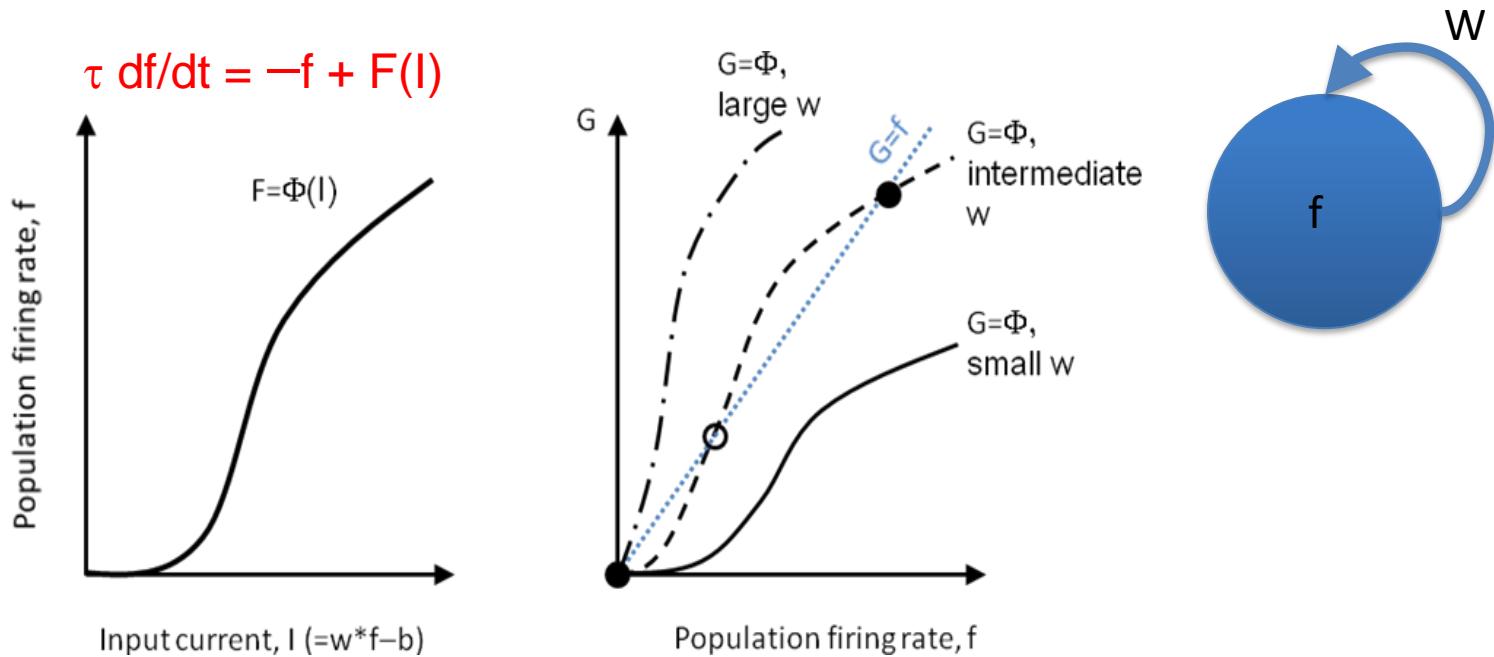
The simplest recurrent neural network model



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

Multi-stability for memory encoding

Categorical (discretized) memory



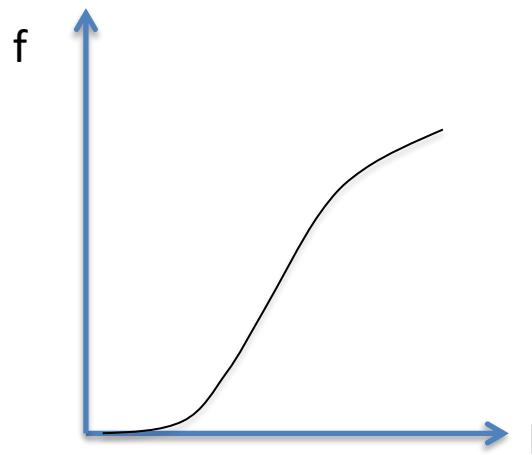
Suppose F is a nonlinear input-output function Φ (e.g. a sigmoidal function) [left]. At steady state, $df/dt = 0$, which means the firing rate $f = F(Wf - b)$.

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 of the system – by definition.

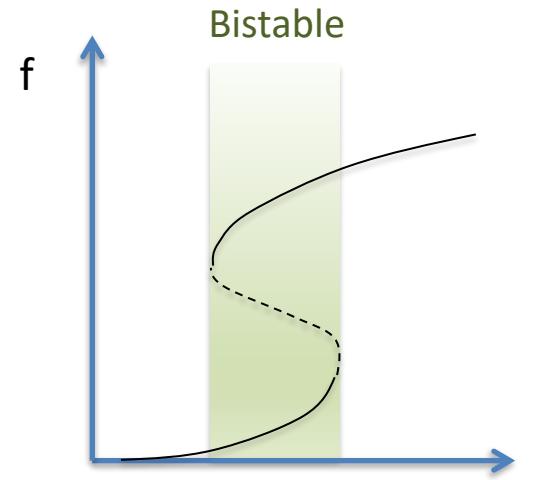
“Working” memory: remembering a brief stimulus

Effective input-output function:

Weak recurrent self-excitation

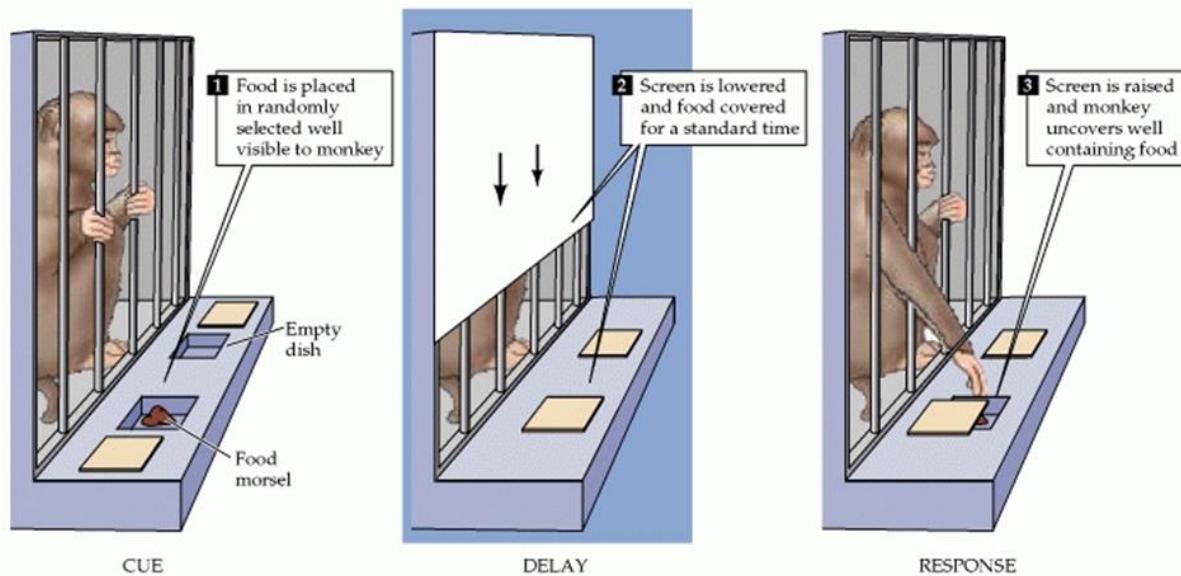


Sufficiently strong recurrent self-excitation → “kinks”

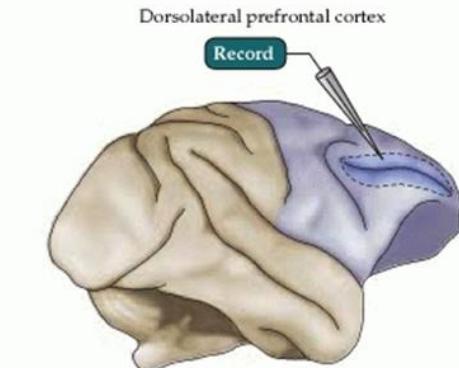


Persistent activity during delay period

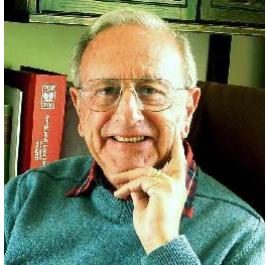
(A)



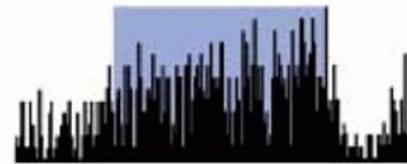
(B)



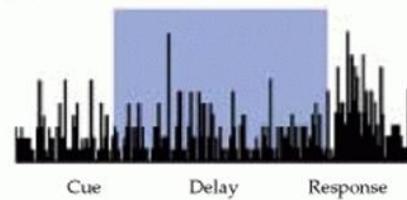
Joaquin Fuster



(C) Stimulus (food morsel) presented



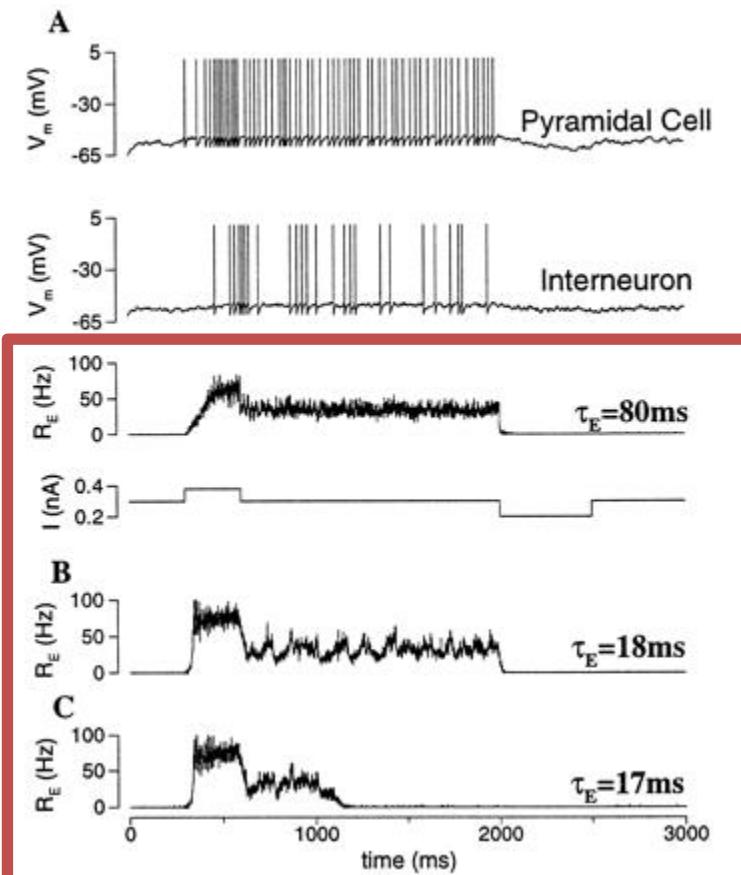
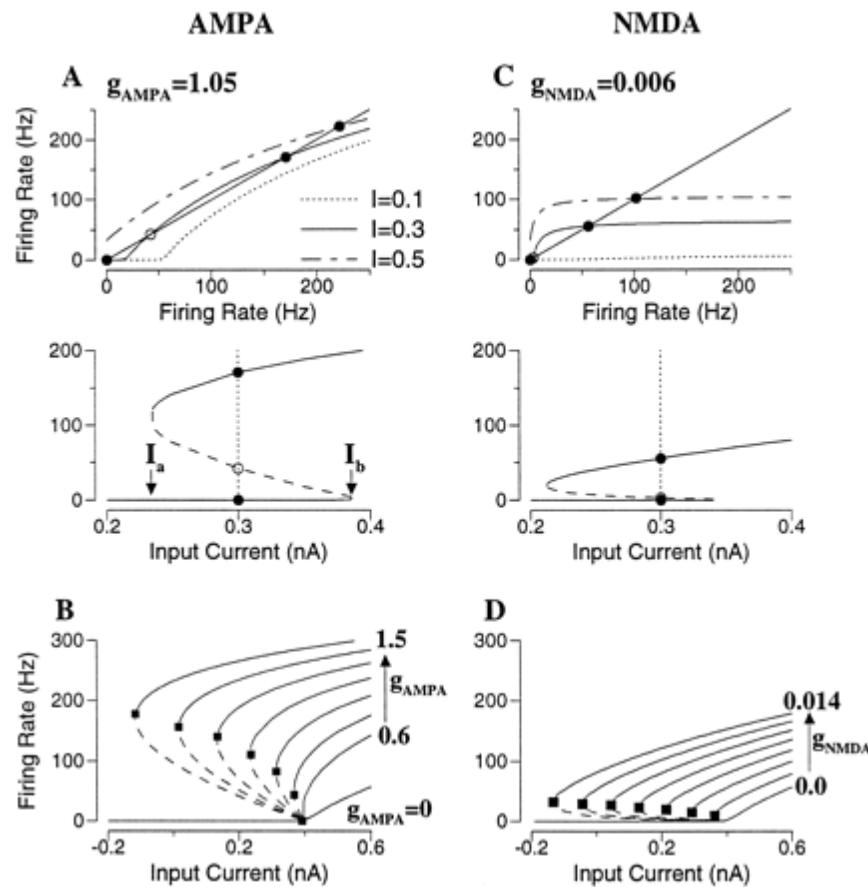
(D) No stimulus presented



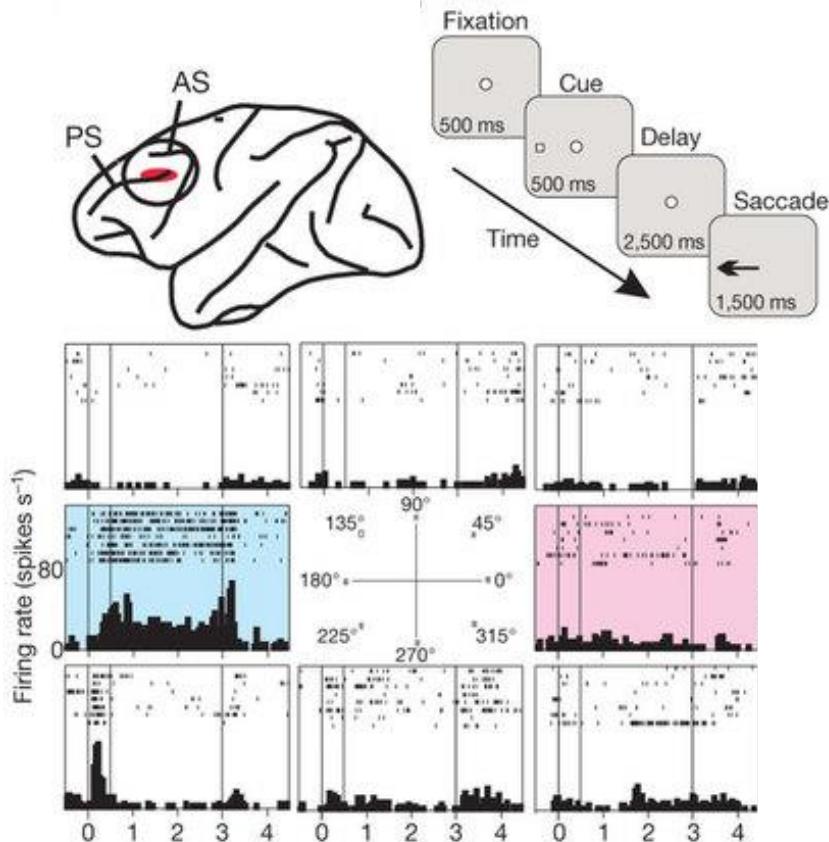
Patricia Goldman-Rakic



Importance of slow (NMDA-mediated) synapses for reliable, low-firing persistent activity



X-J Wang, *J. Neurosci.*, 1999

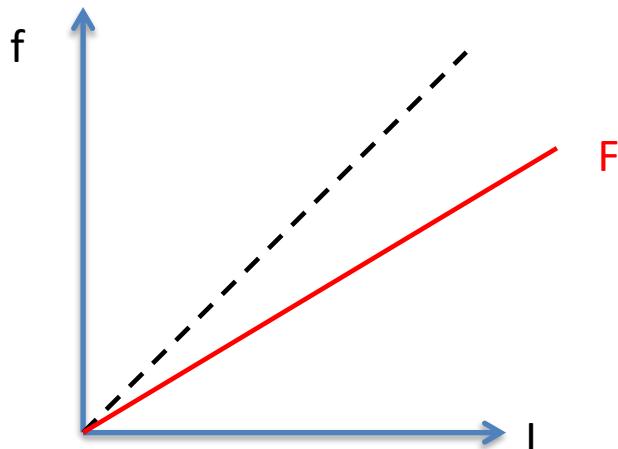


Spatial working memory

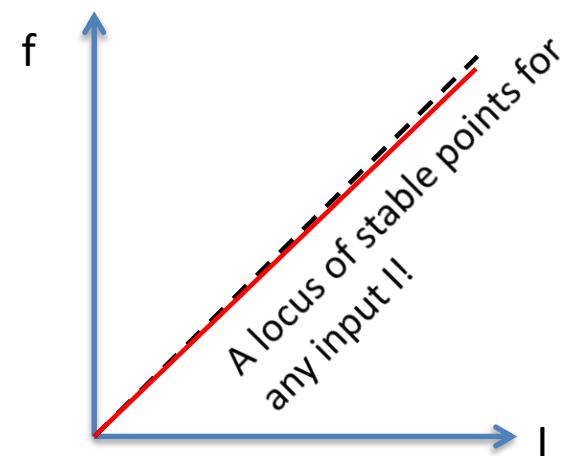
What if the input-output function F is linear?

Parametric (continuous) memory

Weak recurrent excitation

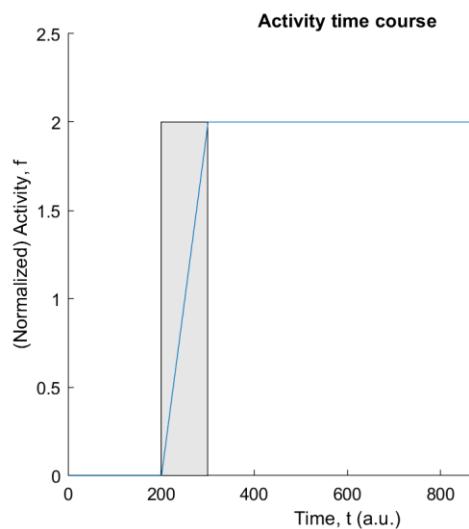


Sufficiently strong recurrent excitation, i.e. memorise continuous values perfectly

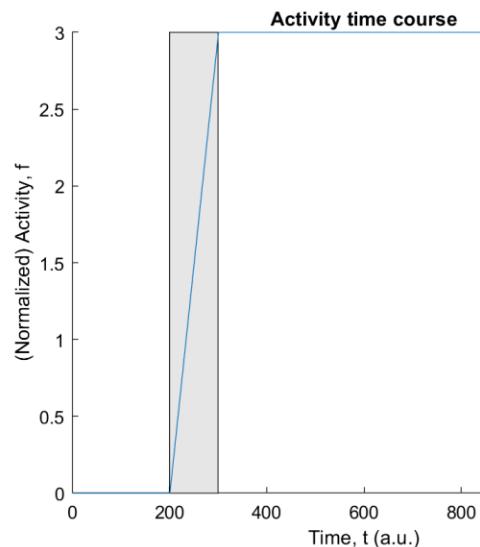


What if the input-output function F is linear?

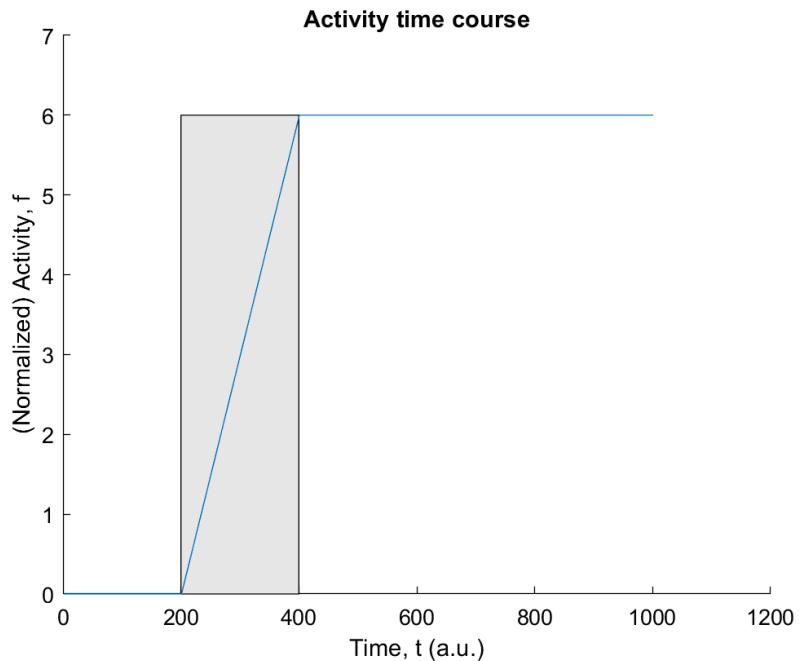
Parametric (continuous) memory



*Input: 0.2
Duration: 100*



*Input: 0.3
Duration: 100*



*Input: 0.3
Duration: 200*

Stability and effective temporal dynamics controlled by synaptic weight W

Parametric memory

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

- If $W > 1$, then $(W - 1) > 0$, and the solution f amplifies exponentially without any upper bound, i.e. f keeps growing.
- If $W < 1$, then $(W - 1) < 0$, and the solution f can reach a certain stable steady state, obtained by setting $df/dt = 0$: $(1 - W)f = b$ 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 is closed to but smaller than 1. Furthermore, the time (constant) to reach this steady state is also dependent on W . Rewriting the equation,

$$\tau/(1 - W) \frac{df}{dt} = f + b/(1 - W)$$

one can see that the effective time constant

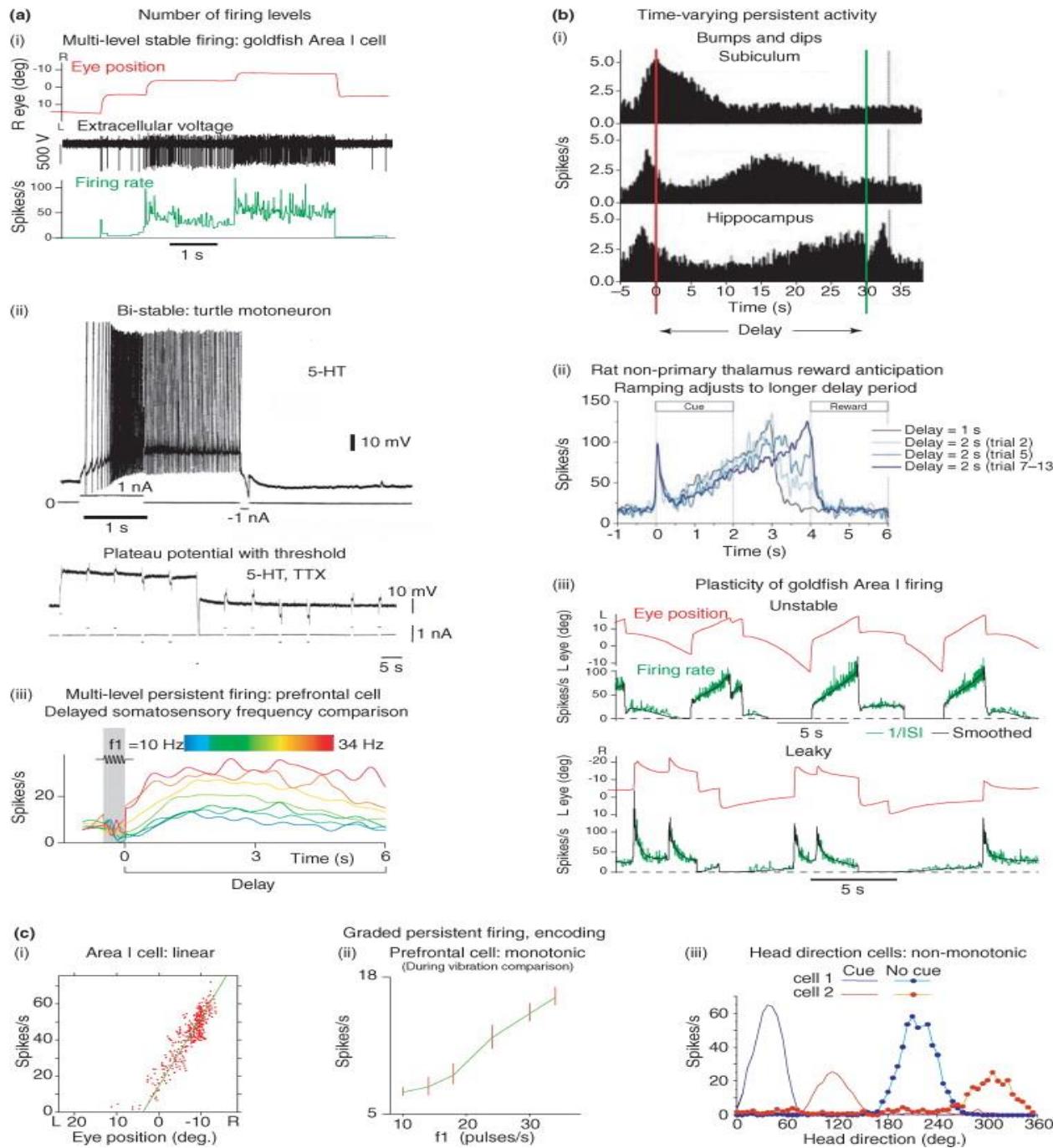
$$\tau_{\text{eff}} = \tau/(1 - W),$$

and if W is closed to 1, the dynamics will be very slow.

- If $W = 1$, then $(W - 1) = 0$, and the solution f can *integrate information* (in the form of afferent/biased input b) *perfectly* (i.e. *no loss of information*):

$$\tau \frac{df}{dt} = b \text{ or } f = (b/\tau)t + \text{constant}$$

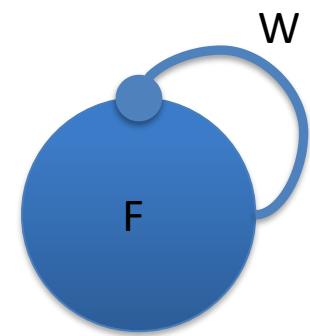
Different kinds of persistent neural activity



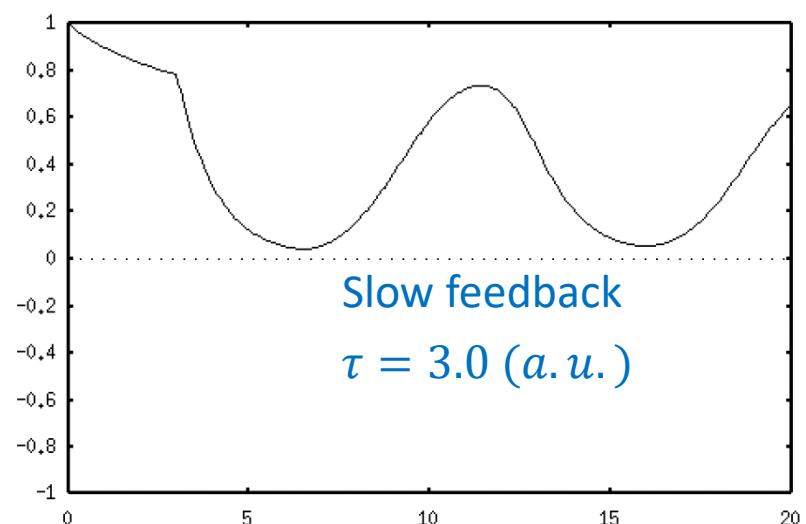
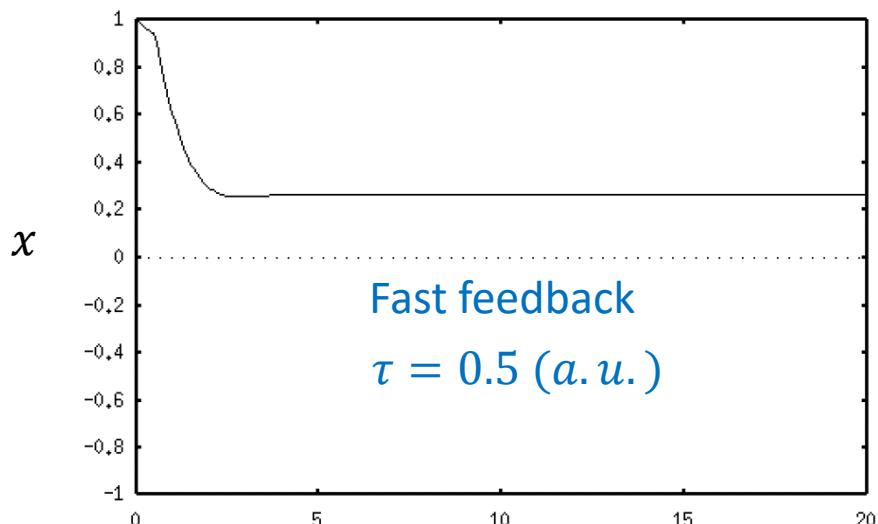
Example: A simple self-feedback population of neurons with time delay

$$\frac{dx}{dt} = -x + F(4x - 0.8 - \tau)$$

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



For different feedback delay time τ



Time t (a.u.)

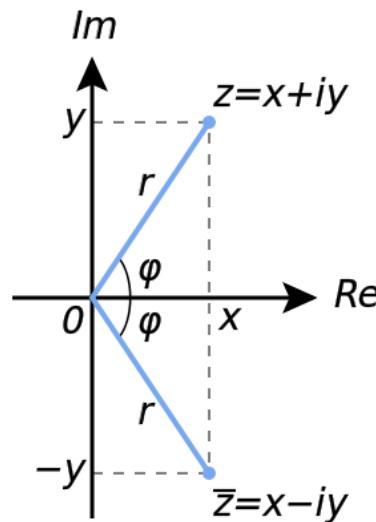
**What if we have 2
neural populations/units
interacting?**

Refresher: Complex numbers

$$i^2 = -1 \text{ or } i = \sqrt{-1} \quad \text{i.e. if } i^2 = -y \text{ or } i = \sqrt{-1 \times y} = i \ y$$

In general: $x + iy$ where x is real (Re) while iy is imaginary (Im)

Re Im

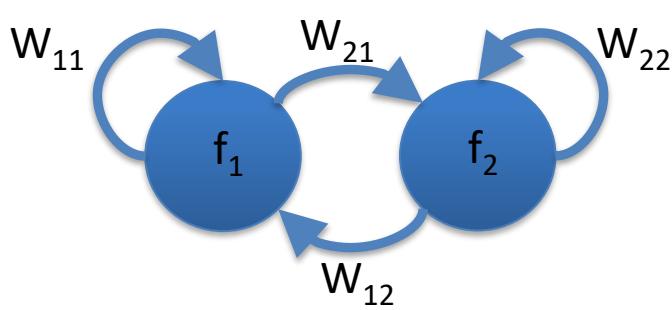


Geometric
representation:
Complex plane

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: Stability and state space in 2-dimensional *linear* systems.

$\frac{df}{dt} = \mathbf{W} \bullet \mathbf{f} + \mathbf{B}$, where $\mathbf{f} = (f_1, f_2)$, absorbing the leak term and the time constant.



$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix} \quad \text{2 coupled equations in matrix form}$$

$$\text{Jacobian matrix, } J = \begin{bmatrix} \frac{\partial F_1}{\partial f_1} & \frac{\partial F_1}{\partial f_2} \\ \frac{\partial G_2}{\partial f_1} & \frac{\partial G_2}{\partial f_2} \end{bmatrix}$$

evaluated at steady state (f_1^*, f_2^*)

For linear coupled equations in matrix form

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

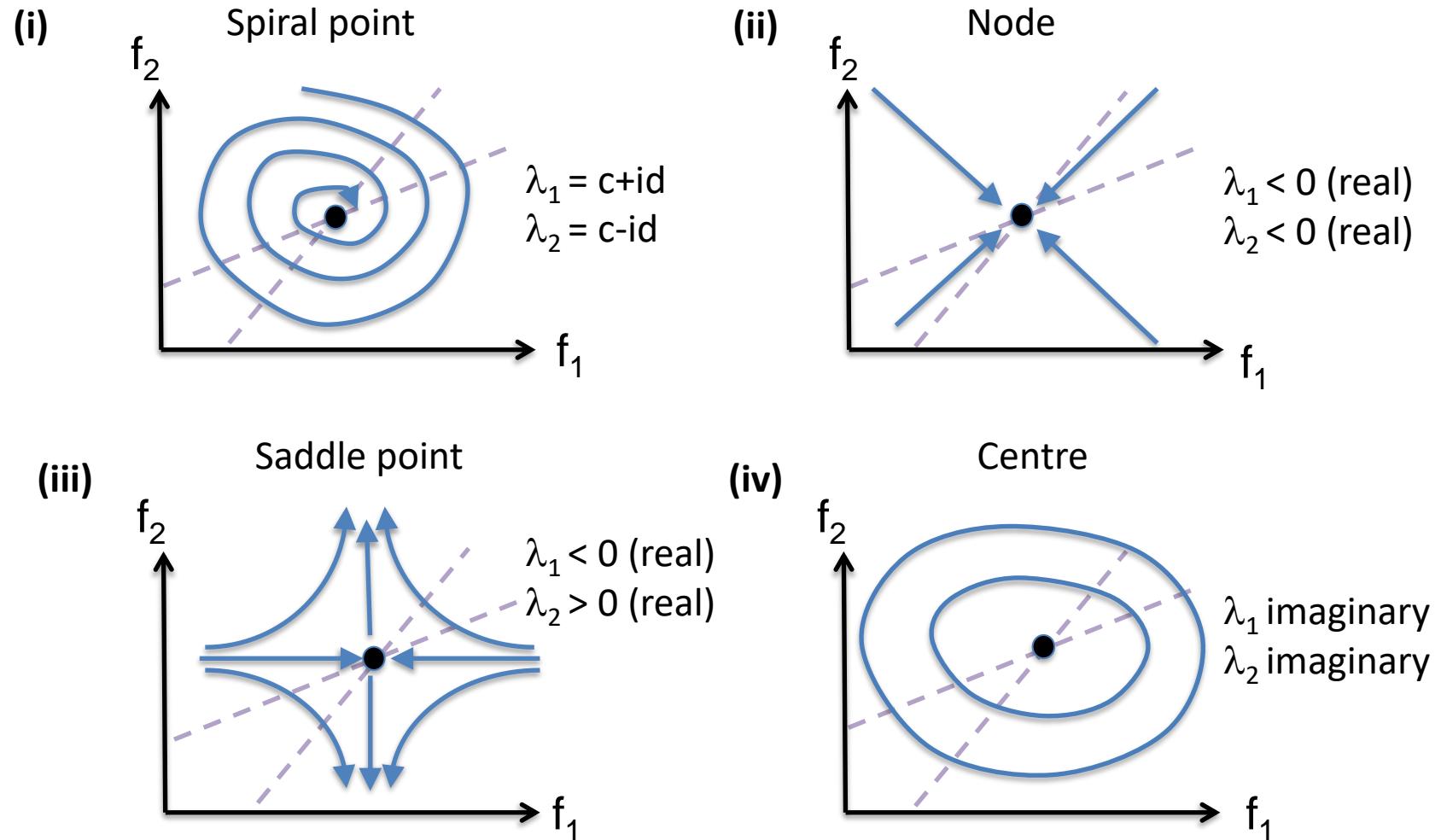
$$J = \begin{bmatrix} \frac{\partial(W_{11}f_1 + W_{12}f_2)}{\partial f_1} & \frac{\partial(W_{11}f_1 + W_{12}f_2)}{\partial f_2} \\ \frac{\partial(W_{21}f_1 + W_{22}f_2)}{\partial f_1} & \frac{\partial(W_{21}f_1 + W_{22}f_2)}{\partial f_2} \end{bmatrix}$$

First note that we can always define a new set of coordinates such that the “origin” lies on (b_1, b_2) . This simplifies the equation to $\frac{df}{dt} = \mathbf{W} \bullet \mathbf{f}$. Then determine the steady states of the system by setting $\frac{df}{dt} = 0$. Next, find the Jacobian matrix J of matrix \mathbf{W} at the steady state. The (local) stability of the system will depend on the characteristics of the eigenvalues of this Jacobian matrix at that steady state.

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

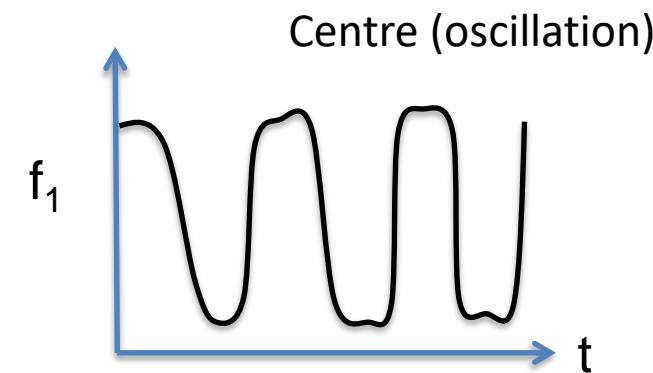
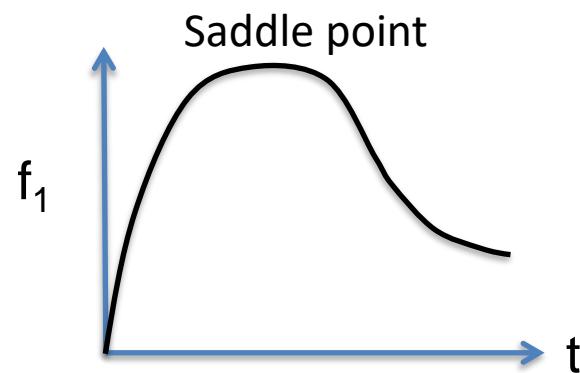
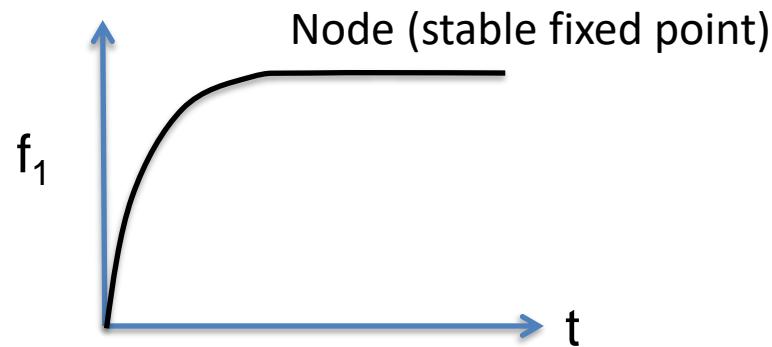
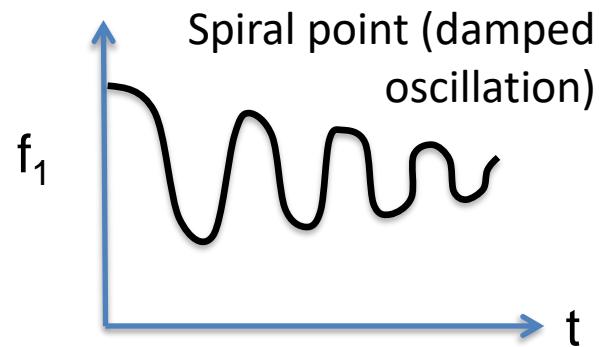
- (i) **Spiral point**, which can result in damped (or amplifying) oscillation of the system. Requires eigenvalues to be *both real (both negative for damped, and positive for amplifying) and non-zero imaginary parts*;
- (ii) **Node**, which can result in strictly attracting towards (or repelling away) 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*.

Stability and state space in 2-dimensional linear systems.
 $\frac{df}{dt} = \mathbf{W} \bullet \mathbf{f} + \mathbf{B}$, $\mathbf{f} = (f_1, f_2)$. 2-D systems have 2 eigenvalues and 2 eigenvectors.



Typical phase plane trajectories for the 4 characteristics equilibrium points (steady states)

Examples of *activity time courses* for one of the neural units f_1



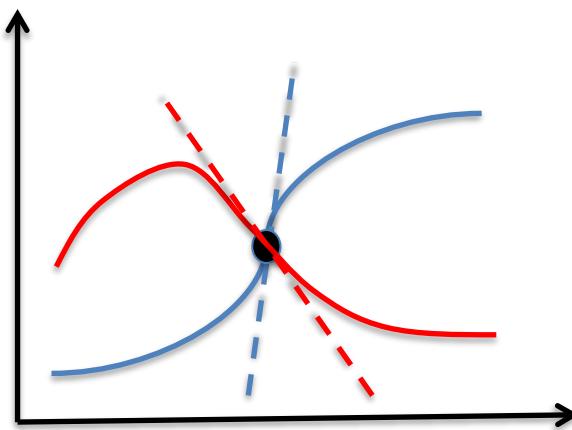
Possible functions?

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

**Technique can be extended to $N > 2$
dimensional coupled systems**

What if the system is nonlinear?

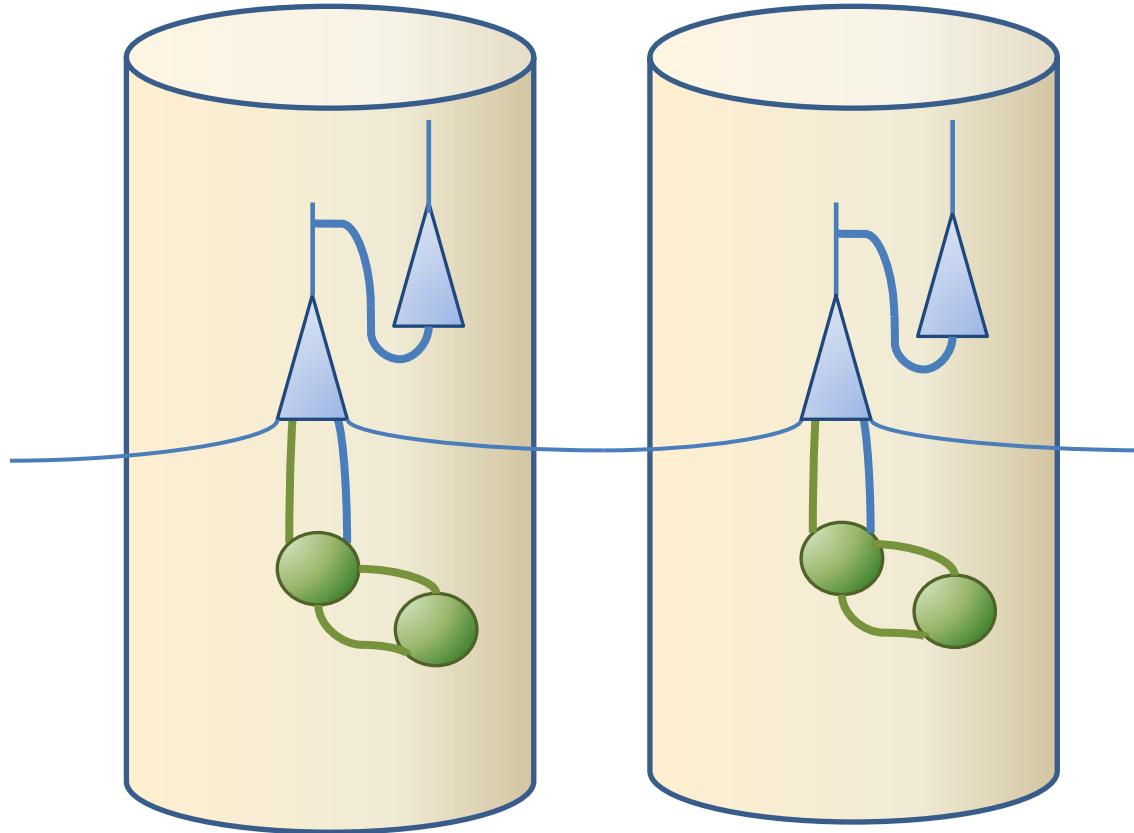
We can still use the same technique (linear stability analysis) as for linear system – It turns out that according to a mathematical theorem, the stability of a nonlinear system's dynamics *sufficiently near a steady state* is the **same** as the linear system near the *same* steady state!



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

Example: Excitatory-inhibitory networks

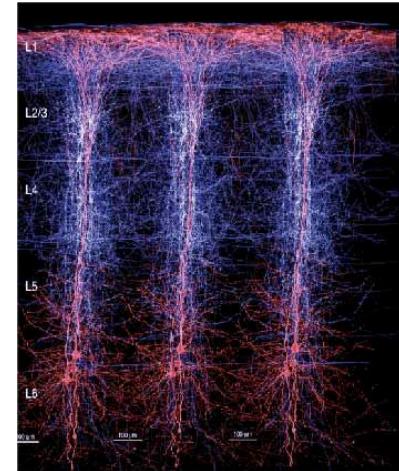
Cartoon representation of cortical “columns”



Excitatory
neuron

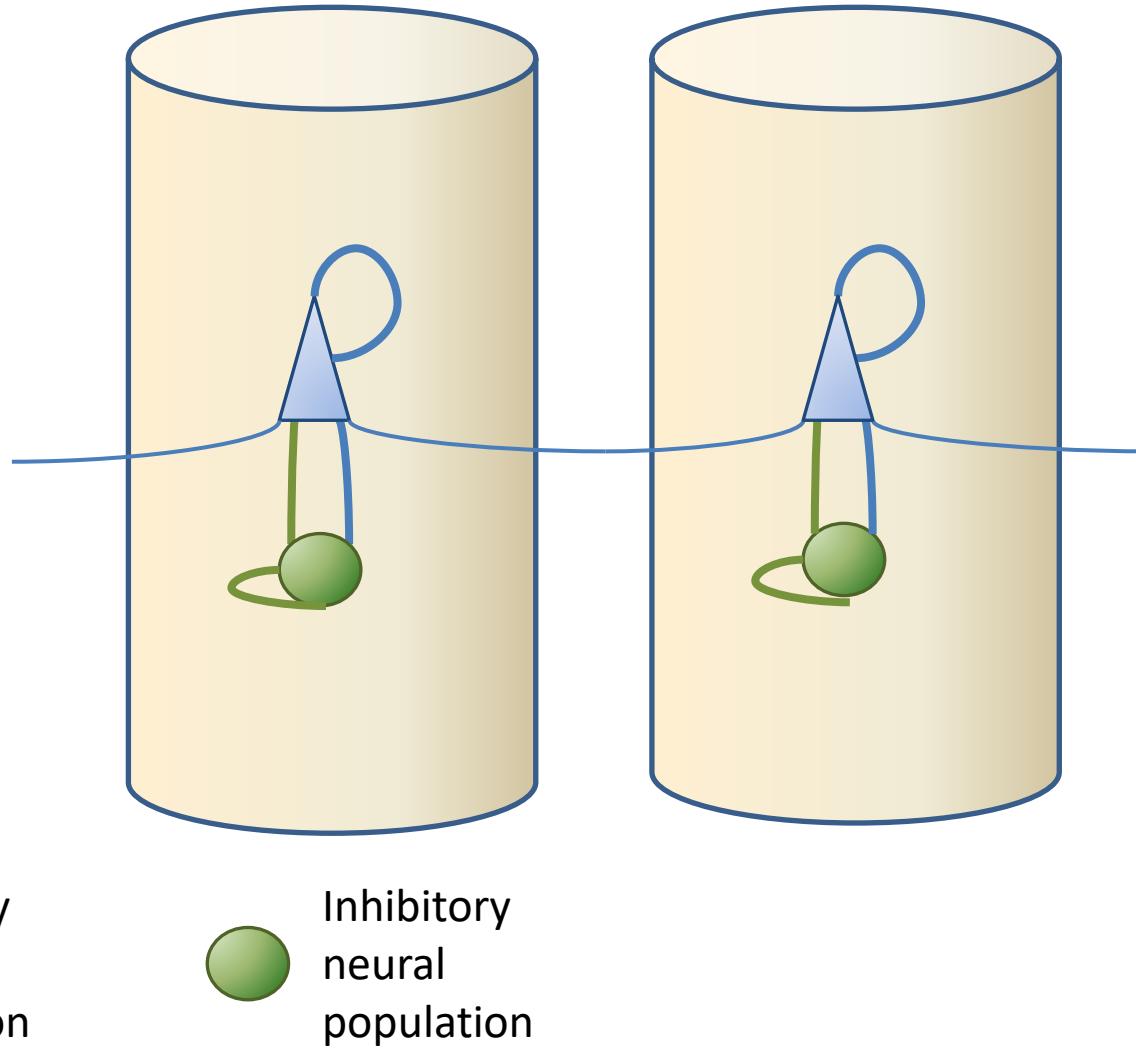


Inhibitory
neuron

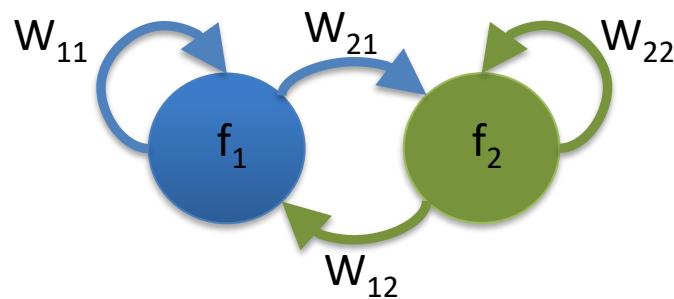


Example: Excitatory-inhibitory networks

A simplified network architecture (assuming homogenous neurons)



What kind of dynamics can an excitatory-inhibitory coupled network produce?



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

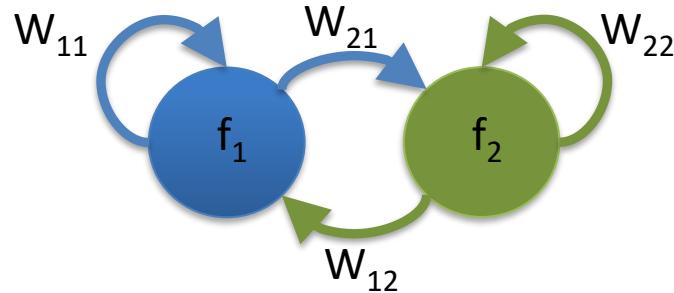
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} w_{11} & w_{12} \\ w_{21} & w_{22} \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

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

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

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

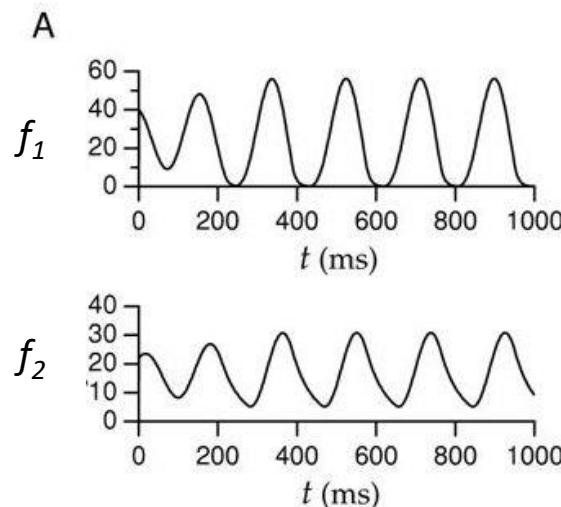
What kind of dynamics can an excitatory-inhibitory coupled network produce?



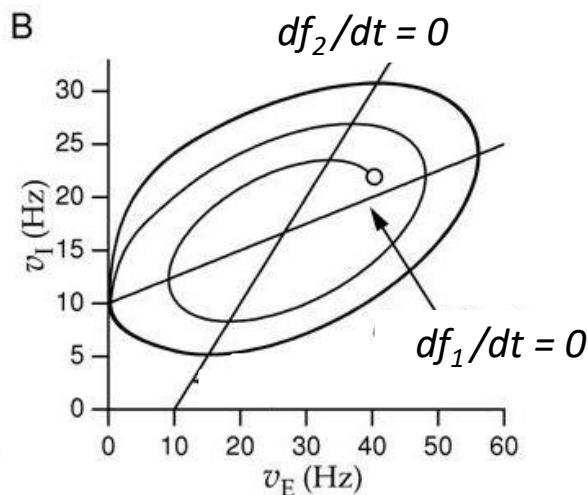
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix}$$

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

Temporal behavior



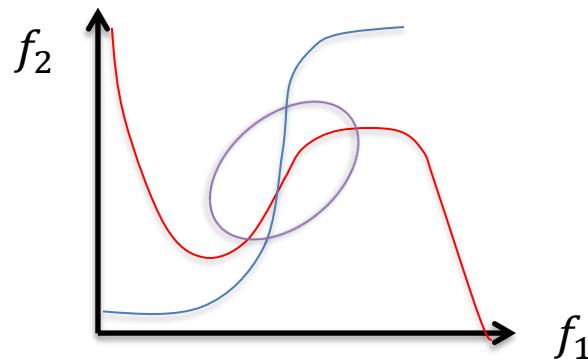
Unstable fixed point – limit cycle



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

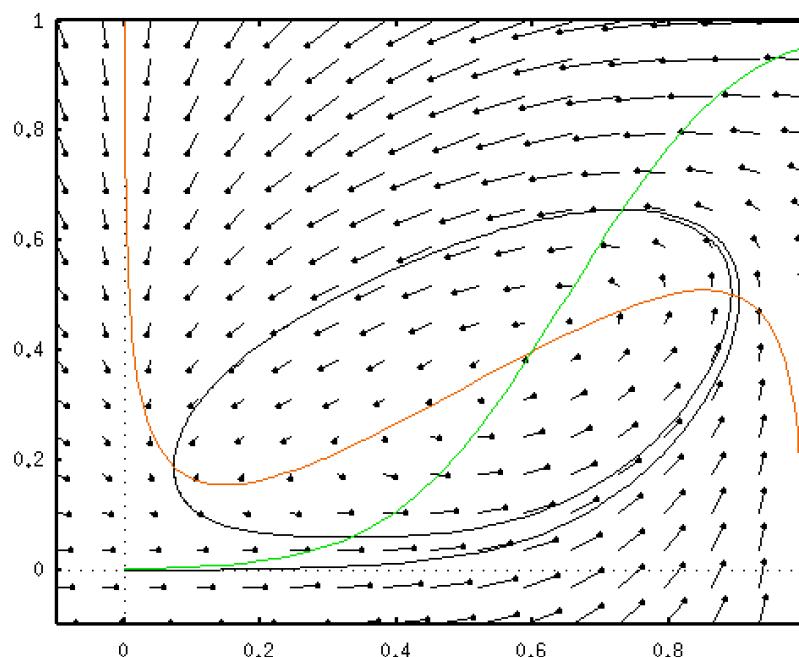
$$W_{21} > 0, W_{12} < 0$$

$$\text{Weak } W_{11} > 0, W_{22} < 0$$



*Nonlinear nullclines
(blue and red lines):*

Excitatory-inhibitory network (Wilson-Cowan type)



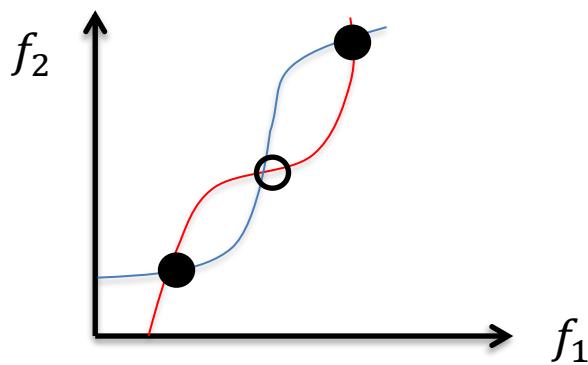
*With vector field
(using XPPAUT software)*

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

Mutually inhibitory neural units

$W_{12} > 0, W_{21} > 0$

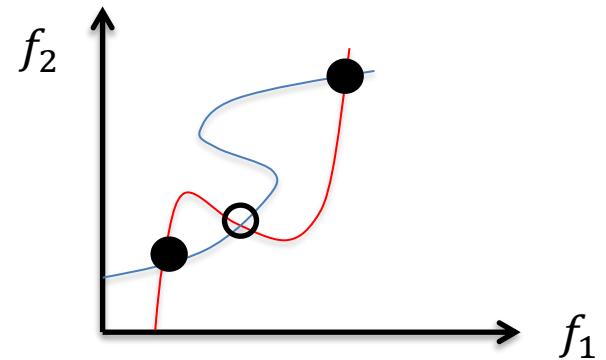
Weak $W_{11} > 0, W_{22} > 0$



Mutual excitation with weak self-connections

$W_{12} > 0, W_{21} > 0$

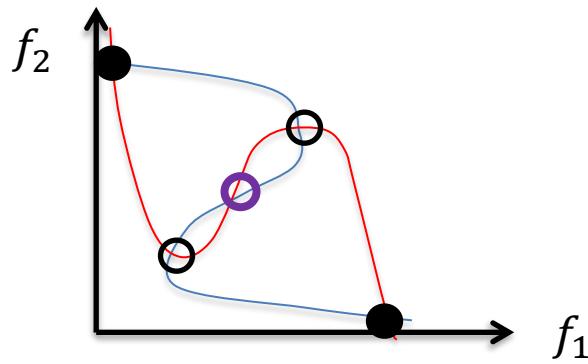
Strong $W_{11} > 0, W_{22} > 0$



Mutual excitation with strong self-connections

$W_{12} < 0, W_{21} < 0$

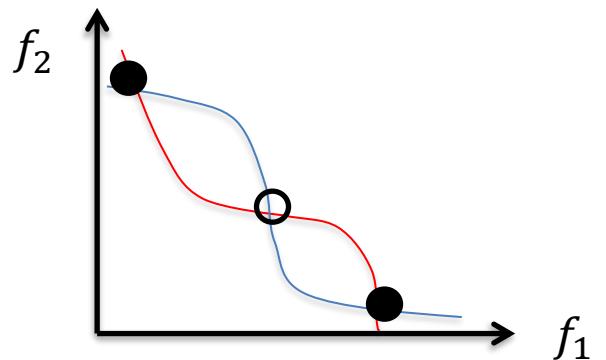
Strong $W_{11} > 0, W_{22} > 0$



Mutual inhibition with strong self-connections

$W_{12} < 0, W_{21} < 0$

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

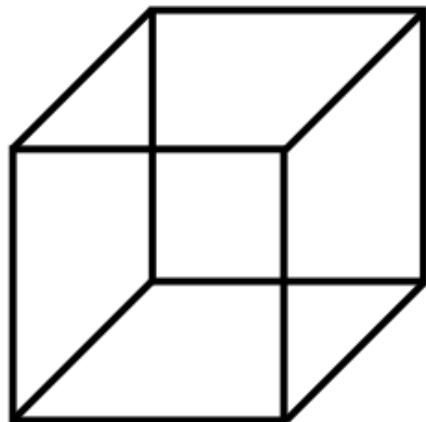


Mutual inhibition with weak self-connections

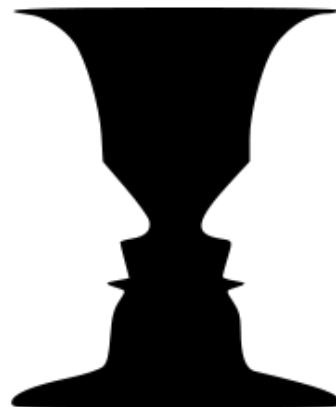
Note: The right balance of input currents and connection weights are required.

Example: Perceptual oscillations – Binocular rivalry

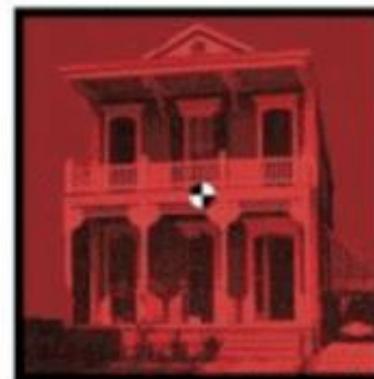
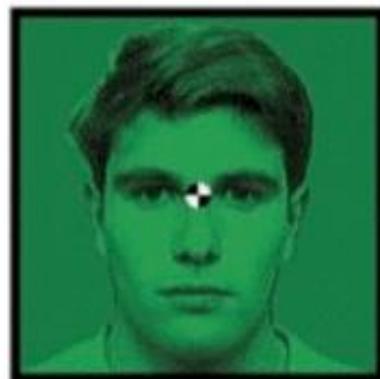
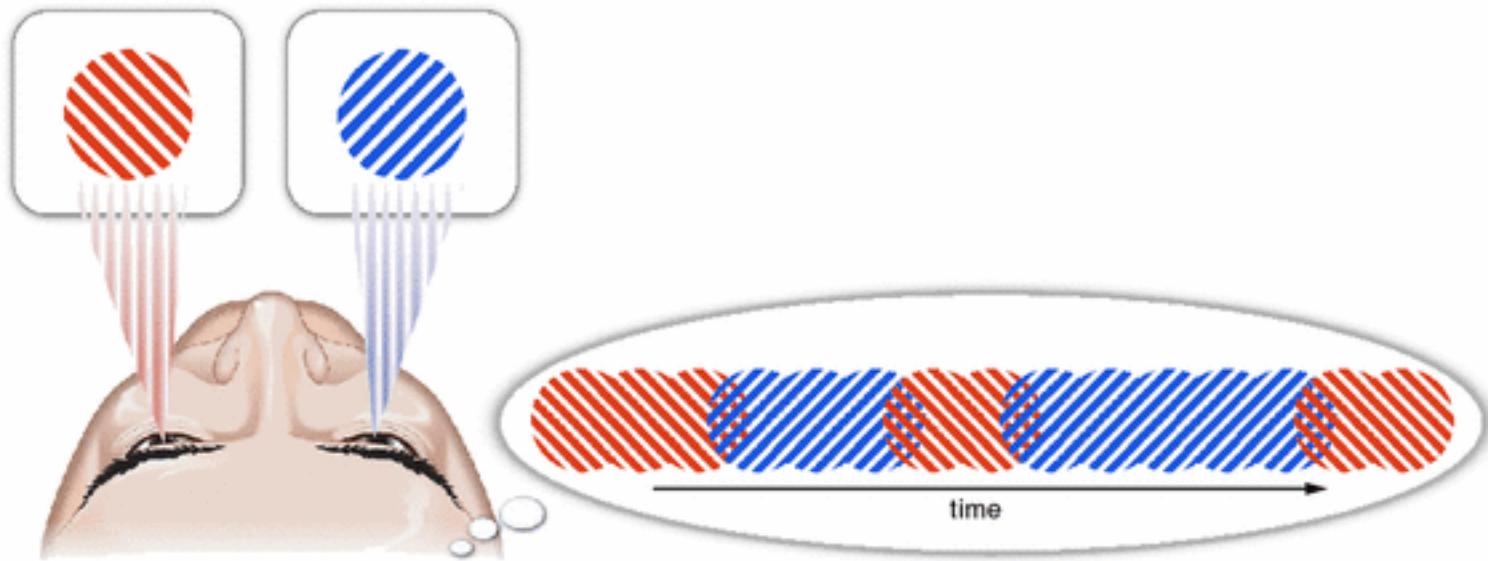
Multiple states of the mind
(for the same stimulus)



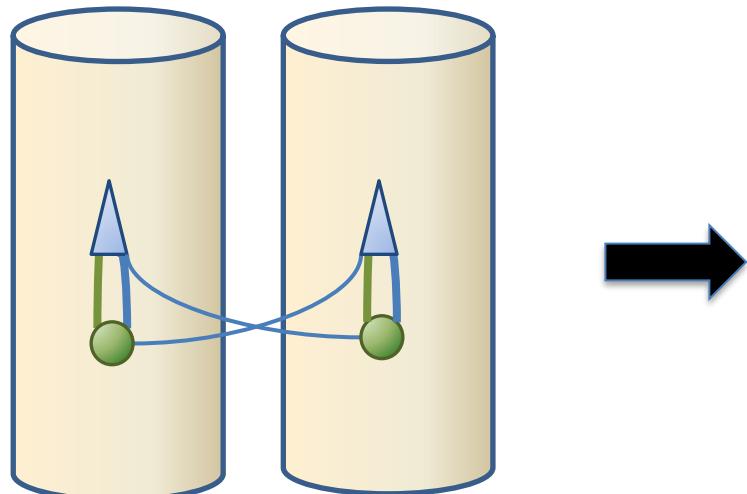
Necker cube



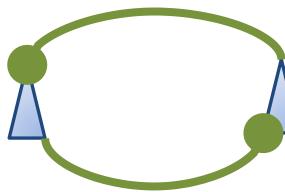
Binocular rivalry: A phenomenon of visual perception in which perception alternates between different images presented to each eye.



A basic model for perceptual alternation phenomenon



Mutual (effectively) inhibitory population
- Implicitly incorporate inhibitory populations

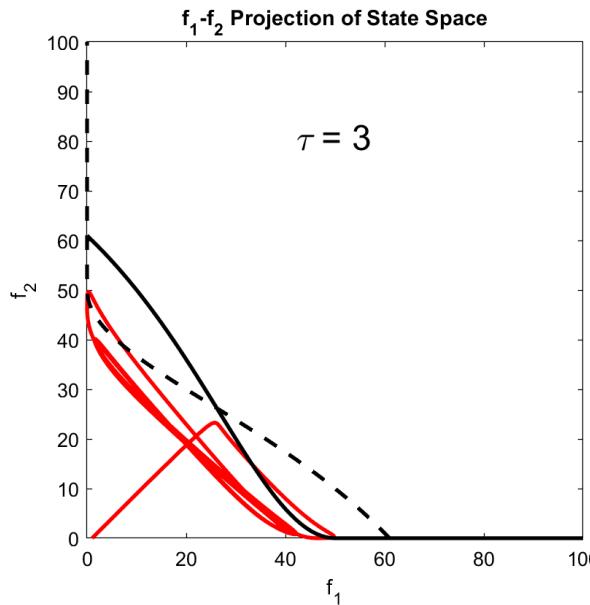
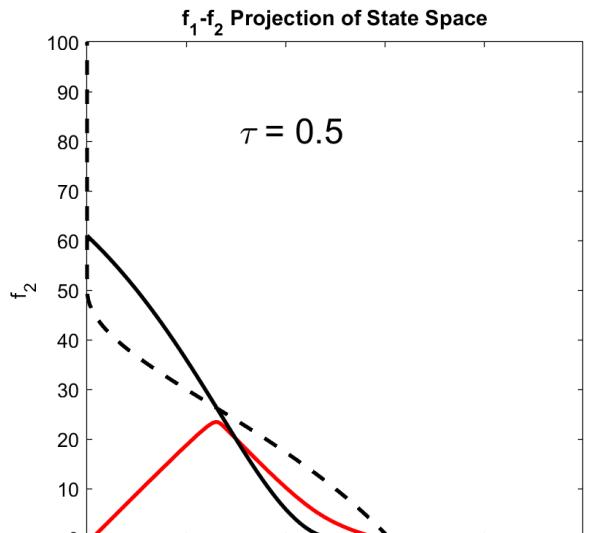
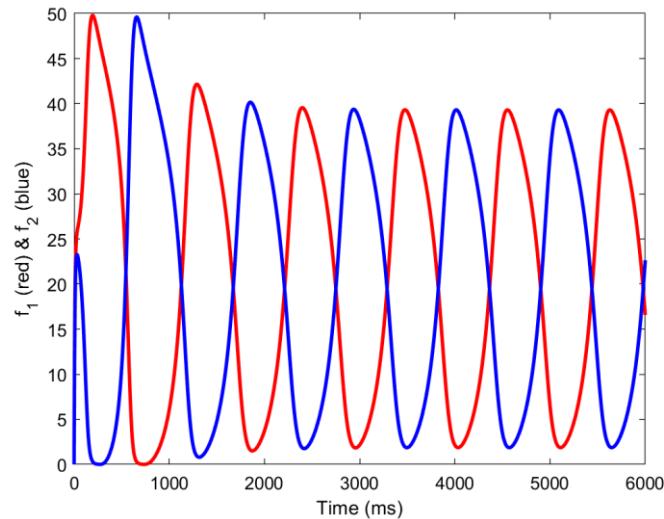
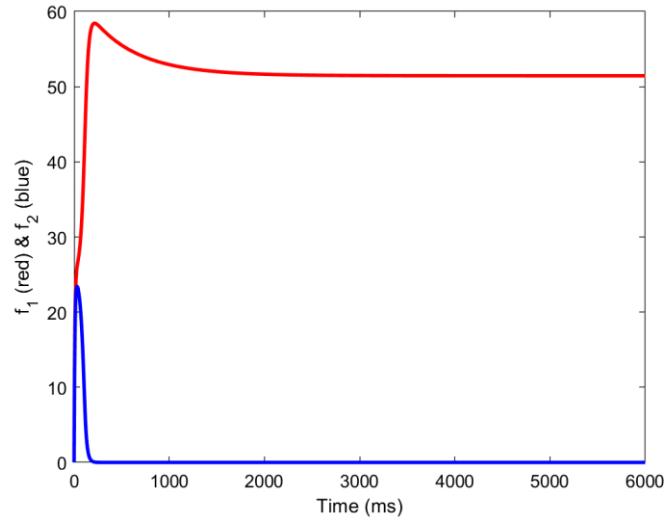


Assume some slow adaption neural mechanism, A (\rightarrow 4 dynamical equations)

$$df/dt = -f + F(W, f, A)$$

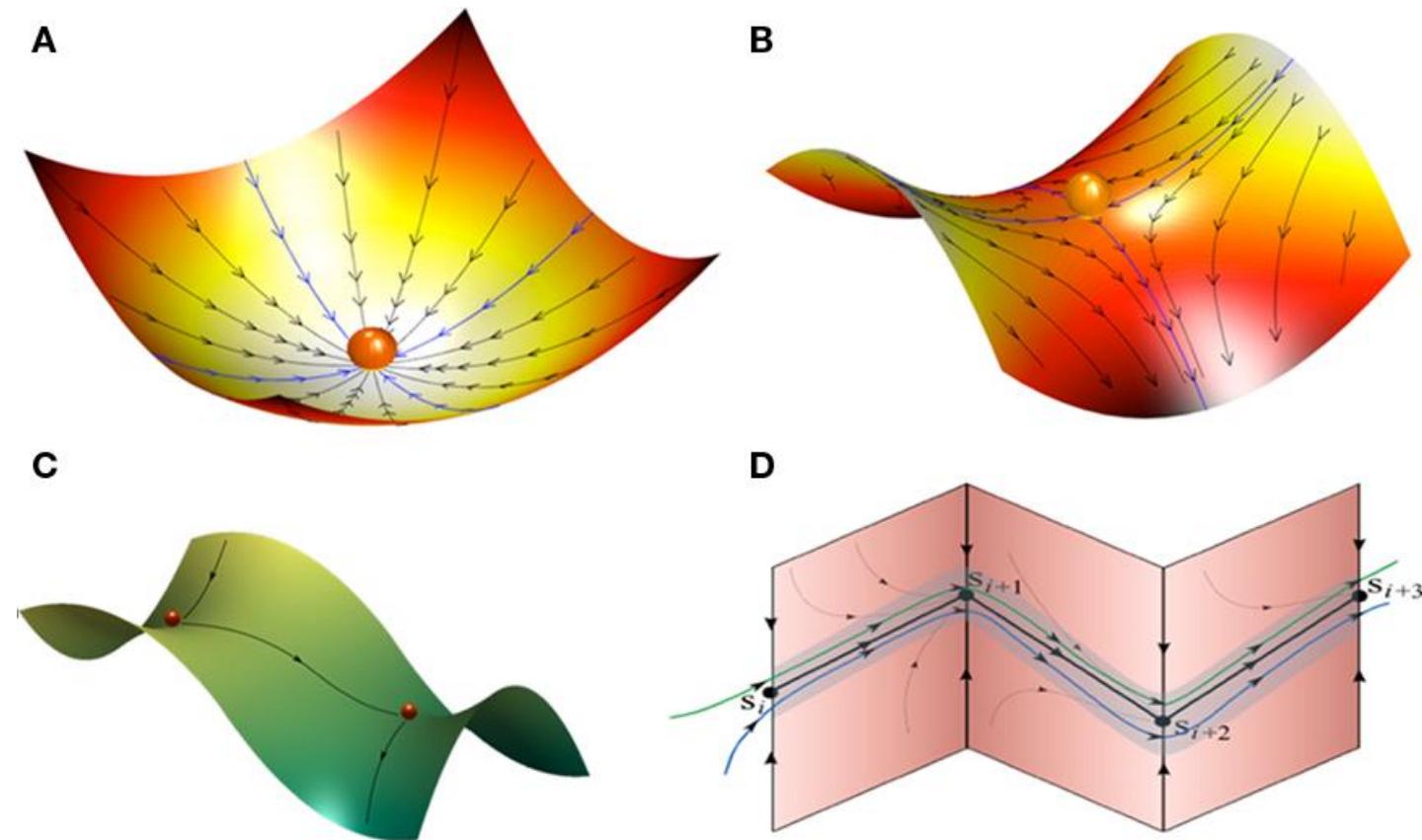
$$\tau dA/dt = -A + \beta f$$

A basic model for perceptual alternation phenomenon

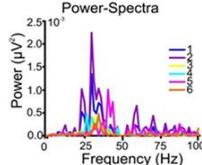
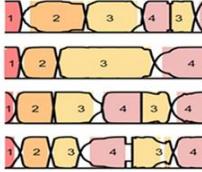
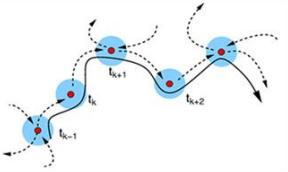
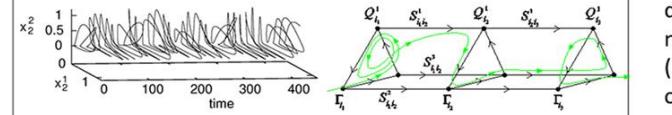
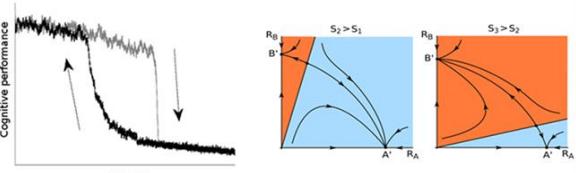
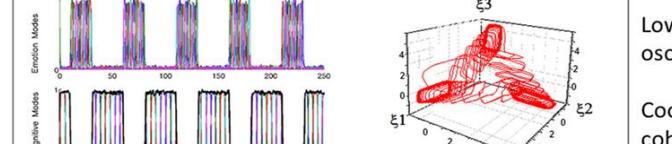
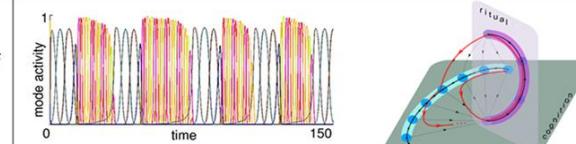


**Are there other types of neural
network dynamics?**

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.



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

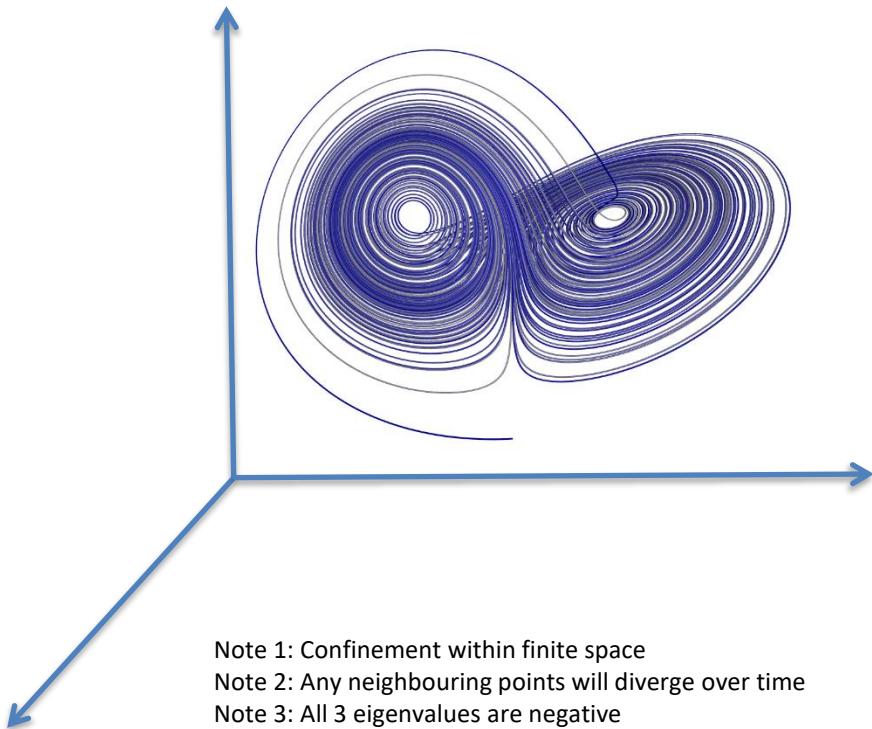
Representative examples of dynamics of possible brain functions

Rabinovich MI and Varona P (2011) Robust transient dynamics and brain functions. *Front. Comput. Neurosci.* 5:24. doi: 10.3389/fncom.2011.00024

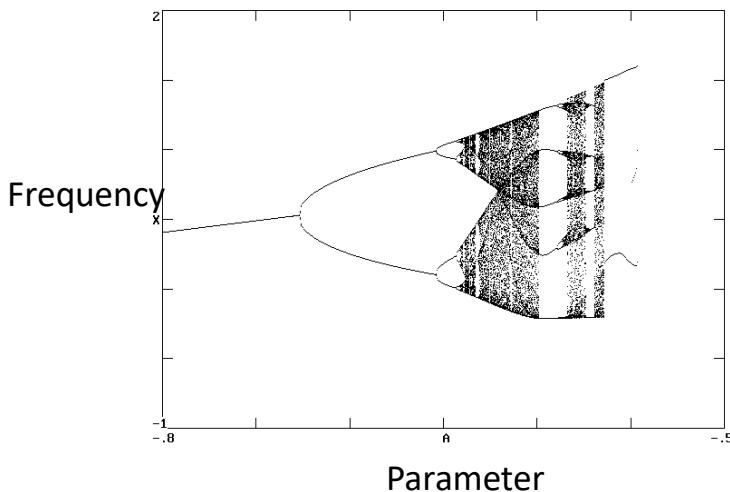
Chaotic (strange) attractor

- Deterministic chaos

Lorenz attractor (3D system)

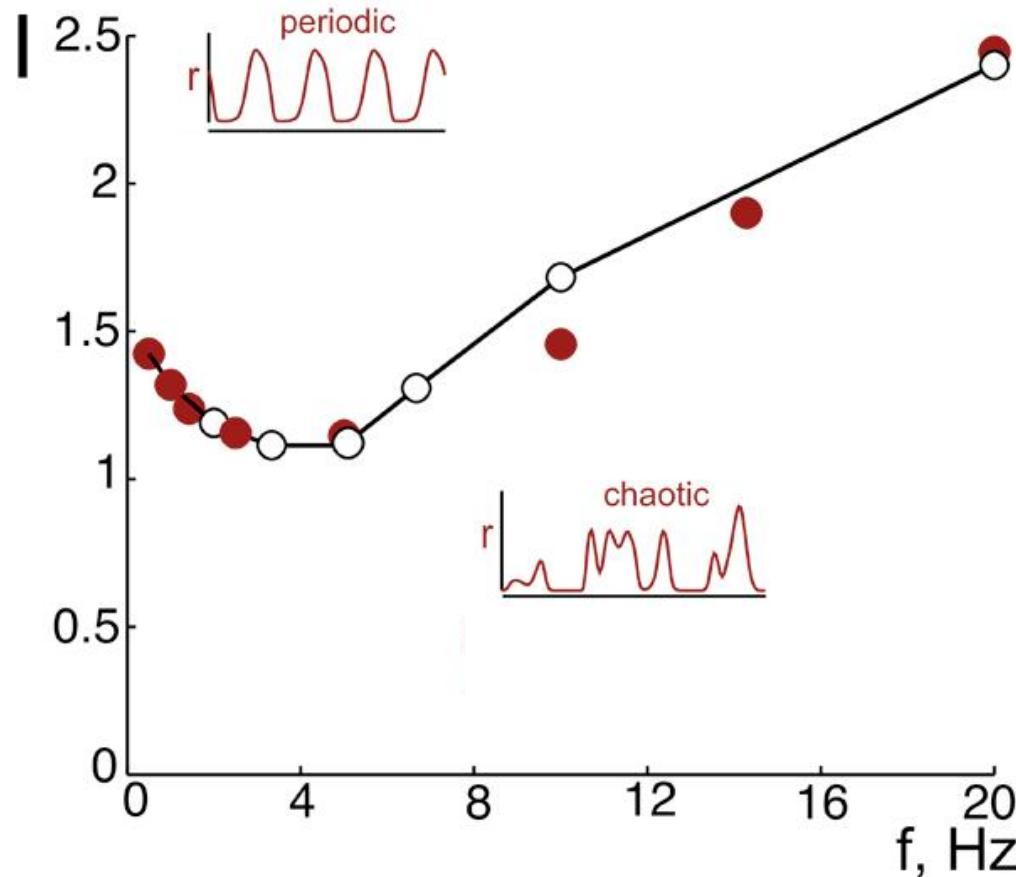


Period doubling leading to chaos



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

Transition between periodic oscillations and chaos in randomly connected recurrent neural networks



*Input current I can suppress, or create
chaotic behaviour*

Rajan, Abbott & Sompolinsky (2010)
Engelken, Wolf & Abbott (2023)

References

- Hugh R. 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, (M. A. Arbib and J. Bonaiuto) *Cambridge, MA: MIT Press* (2016).
- Dayan and Abbott, Theoretical Neuroscience, chapter 7 “Network models”, MIT Press, 2001.
- G. Bard Ermentrout and David H. Terman, Mathematical Foundations of Neuroscience, book chapter 11 “Firing rate models”, Springer, NY, 2010.
- H. S. Seung. Amplification, Attenuation, and Integration. In: The Handbook of Brain Theory and Neural Networks: Second Edition (M. A. Arbib, Editor) Cambridge, MA: MIT Press, pp. 94-97 (2003).
- Brinkman et al. (2021) Metastable dynamics of neural circuits and networks. arXiv:2110.03025.

Additional:

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

Modelling decision dynamics



Perceptual decision making (under uncertainty)

Integrate sensory information

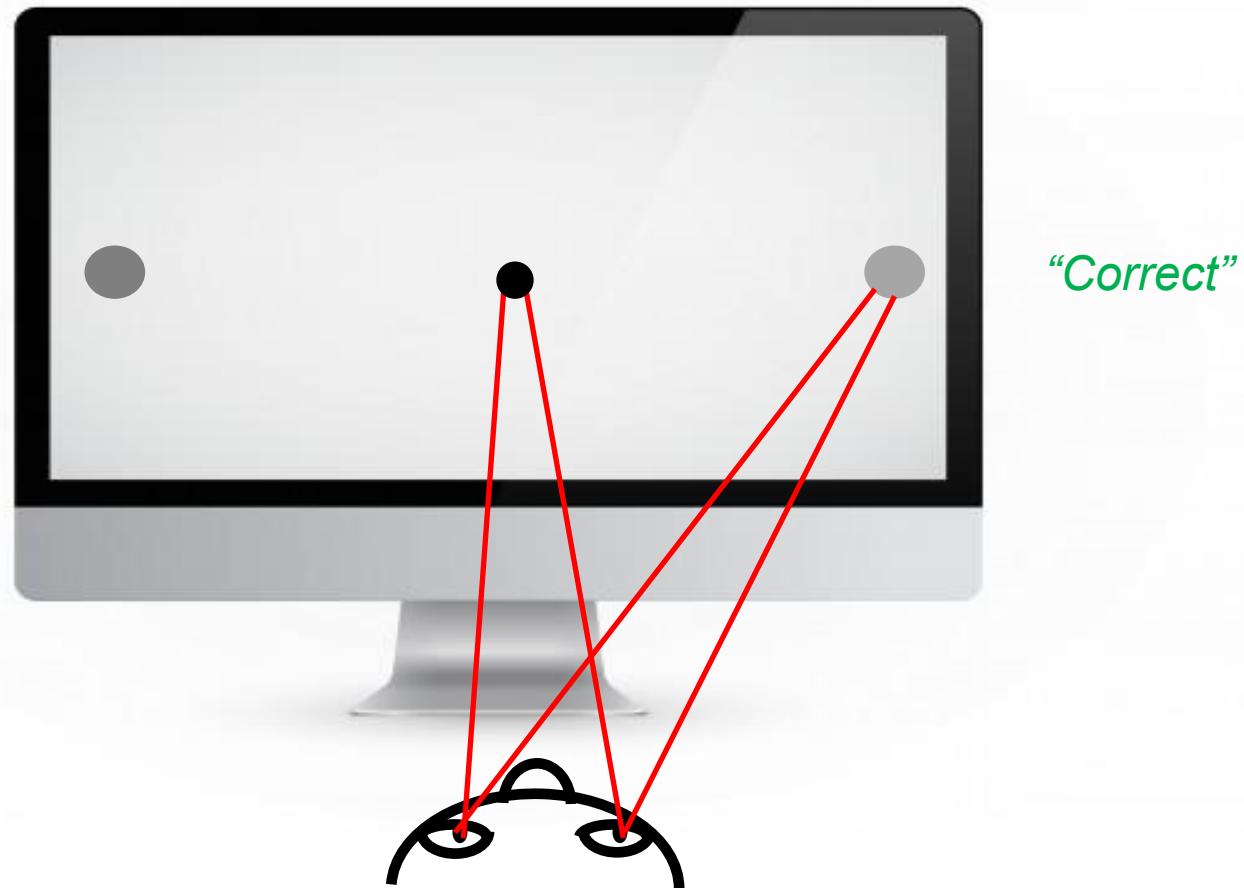
Select an action/choice among alternative competing options

Respond quickly and/or accurately



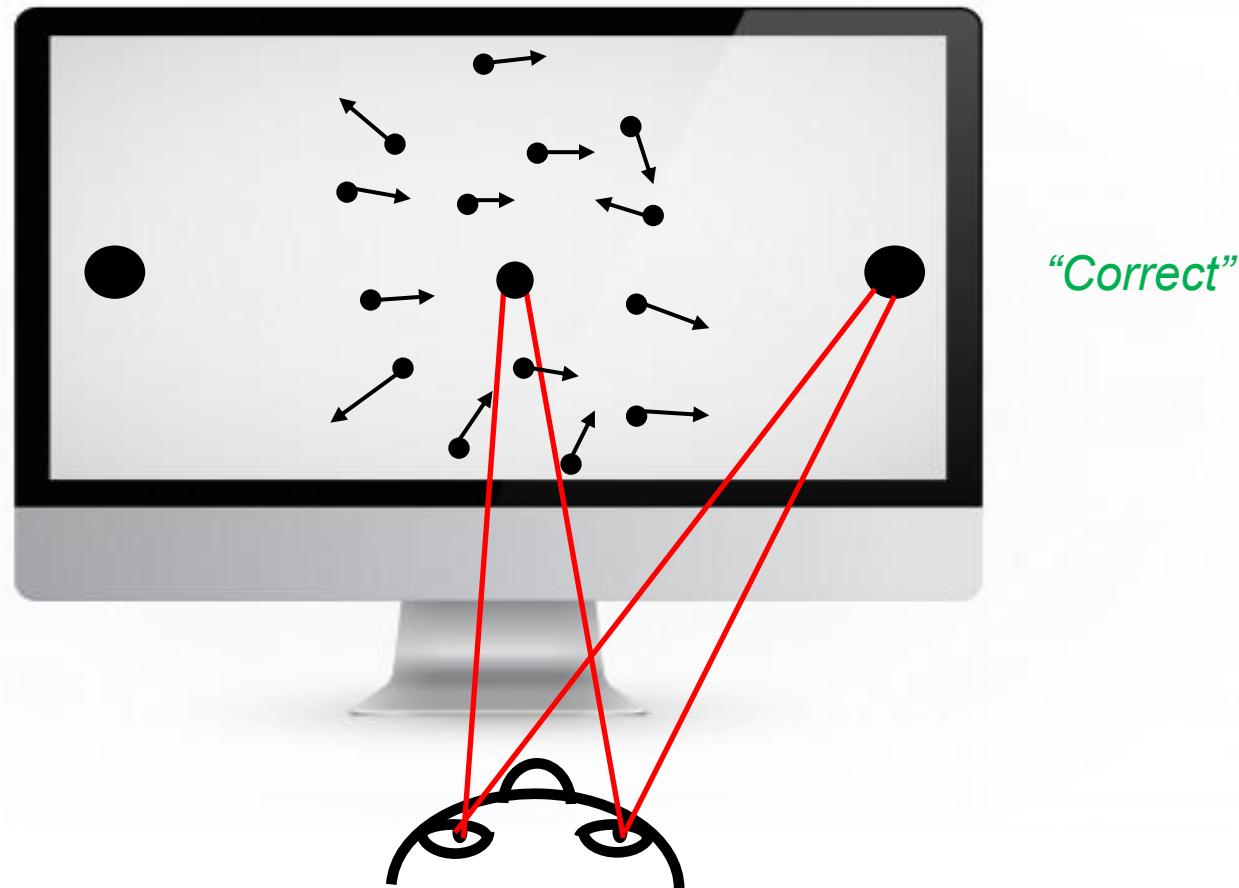
A colour/brightness discrimination task

Experimentalist controls difference in colours/brightness



A visual motion direction discrimination task

Experimentalist controls % of dots moving in the same direction (e.g. more rightward than leftward)



Golden age of Mathematical Psychology

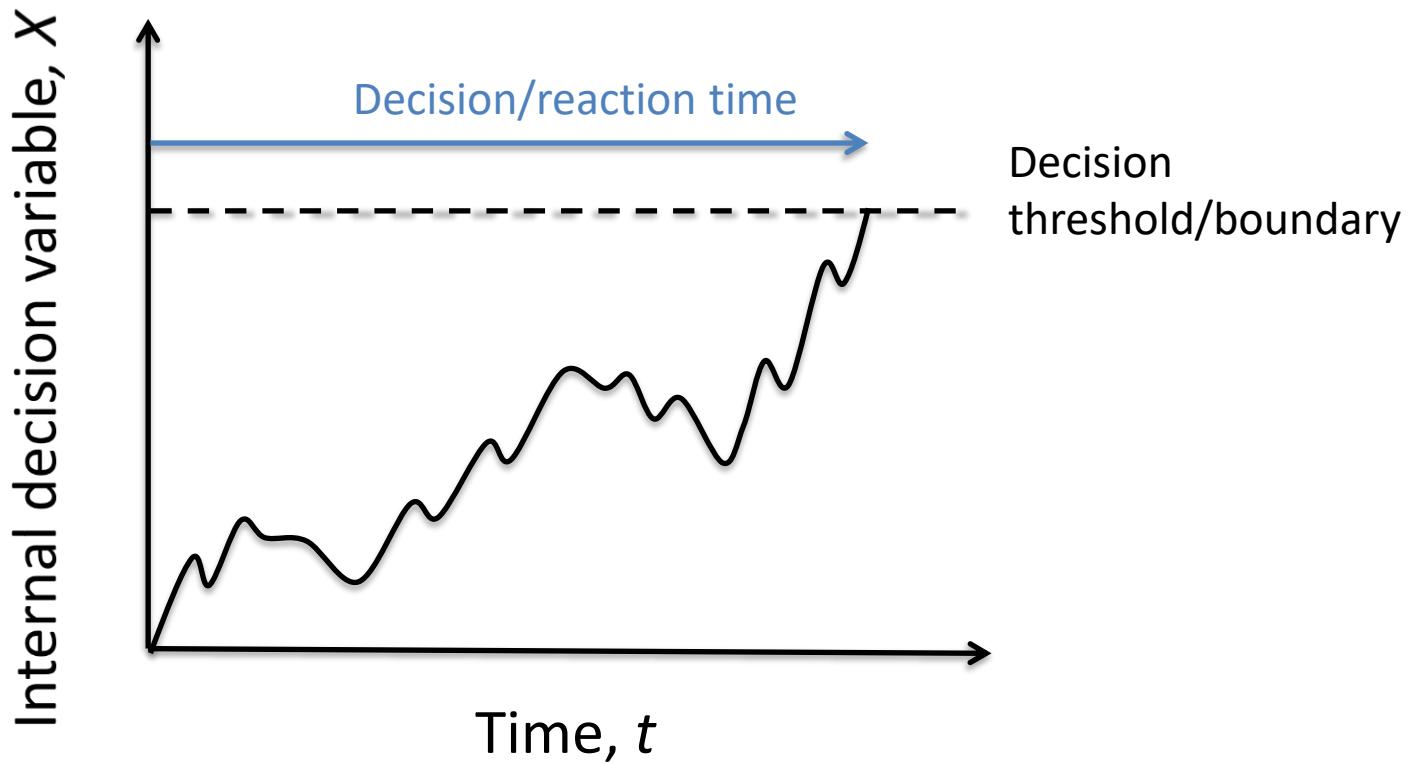
(1940's) ...

Coinciding with the maturation of some mathematical (information-theoretic and probabilistic) frameworks to describe individual's choice behaviour and response times.

... & birth of Decision Sciences

A gradually common feature: Evidence accumulation

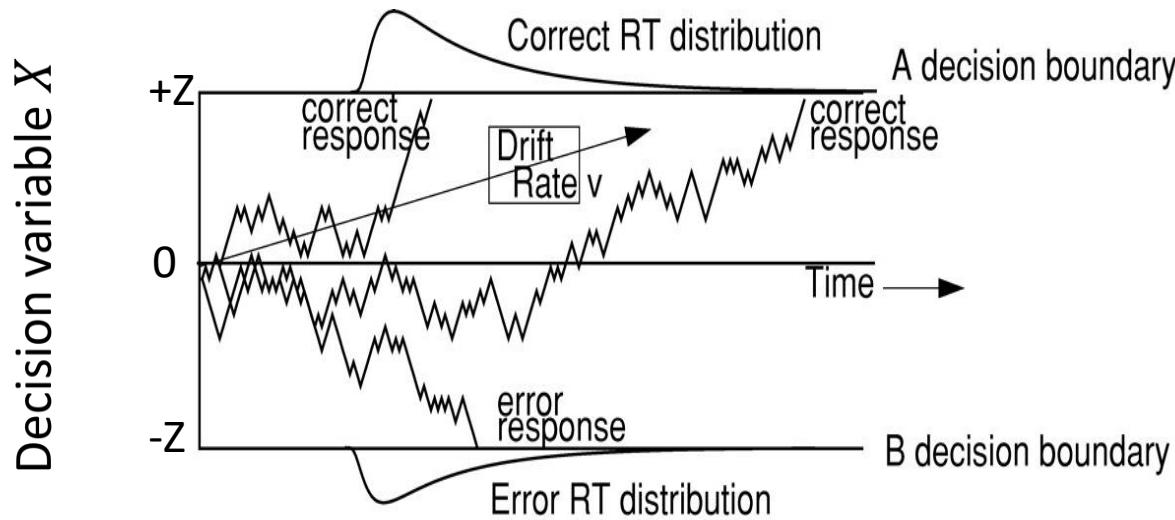
Accumulator models



Sequential sampling model framework

Cognitive model: Drift-diffusion model

Cognitive, mathematical model by Roger Ratcliff (1978) and colleagues

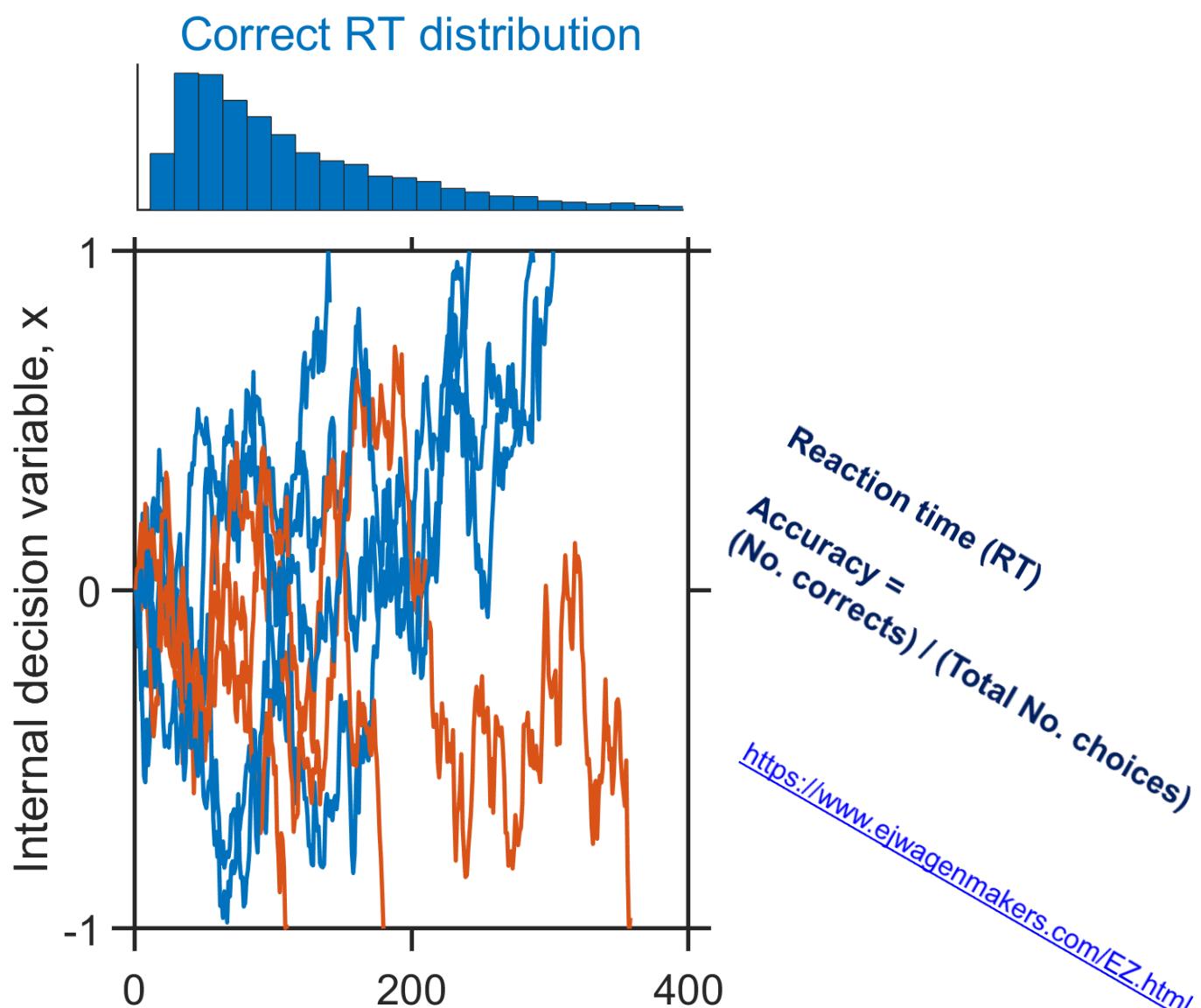


$$\begin{aligned} X = \int dX &= \int v dt + \sigma dW \\ &= \text{signal difference} + \text{noise} \end{aligned}$$

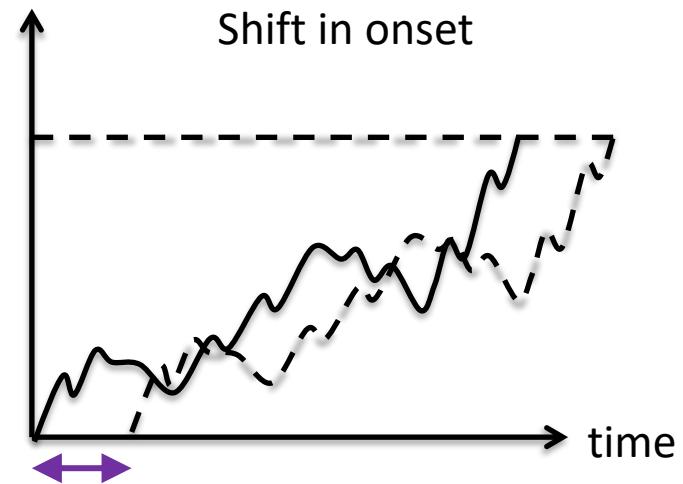
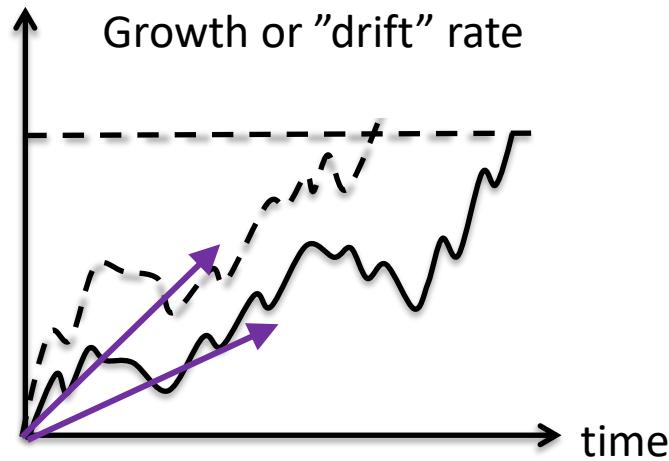
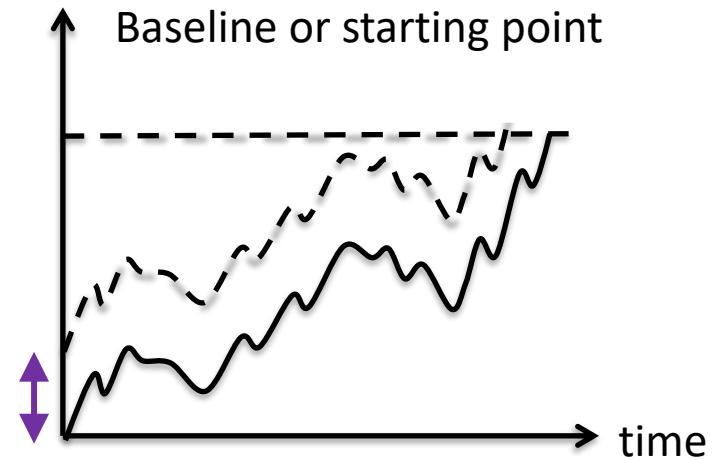
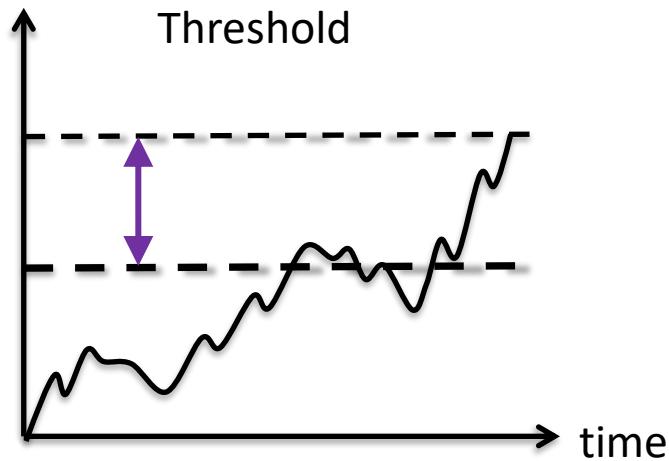
(stochastic) calculus

Computer simulations over several trials

With upward drift rate (signal)



“Biases” or “controls” in decision making



Threshold, drift rate, noise can be time-dependent

Review

Bridging Neural and Computational Viewpoints on Perceptual Decision-Making

Redmond G. O'Connell,^{1,*} Michael N. Shadlen,^{2,3} KongFatt Wong-Lin,⁴ and Simon P. Kelly^{5,*}

Sequential sampling models have provided a dominant theoretical framework guiding computational and neurophysiological investigations of perceptual decision-making. While these models share the basic principle that decisions are formed by accumulating sensory evidence to a bound, they come in many forms that can make similar predictions of choice behaviour despite invoking fundamentally different mechanisms. The identification of neural signals that reflect some of the core computations underpinning decision formation offers new avenues for empirically testing and refining key model assumptions. Here, we highlight recent efforts to explore these avenues and, in so doing, consider the conceptual and methodological challenges that arise when seeking to infer decision computations from complex neural data.

Decision-Making as a Core Component of Cognition

The term 'decision-making' often calls to mind scenarios such as voting in an election or selecting a course of study. Yet, even simply perceiving our sensory environment relies on a continuous stream of elementary judgments, known as 'perceptual decisions'. In some cases, perceptual decisions can be as consequential as those requiring more abstract judgements (e.g., is the traffic light red or green?). In the highly complex and dynamic environment that we inhabit, making accurate and timely decisions is a considerable challenge for the brain, since

Highlights

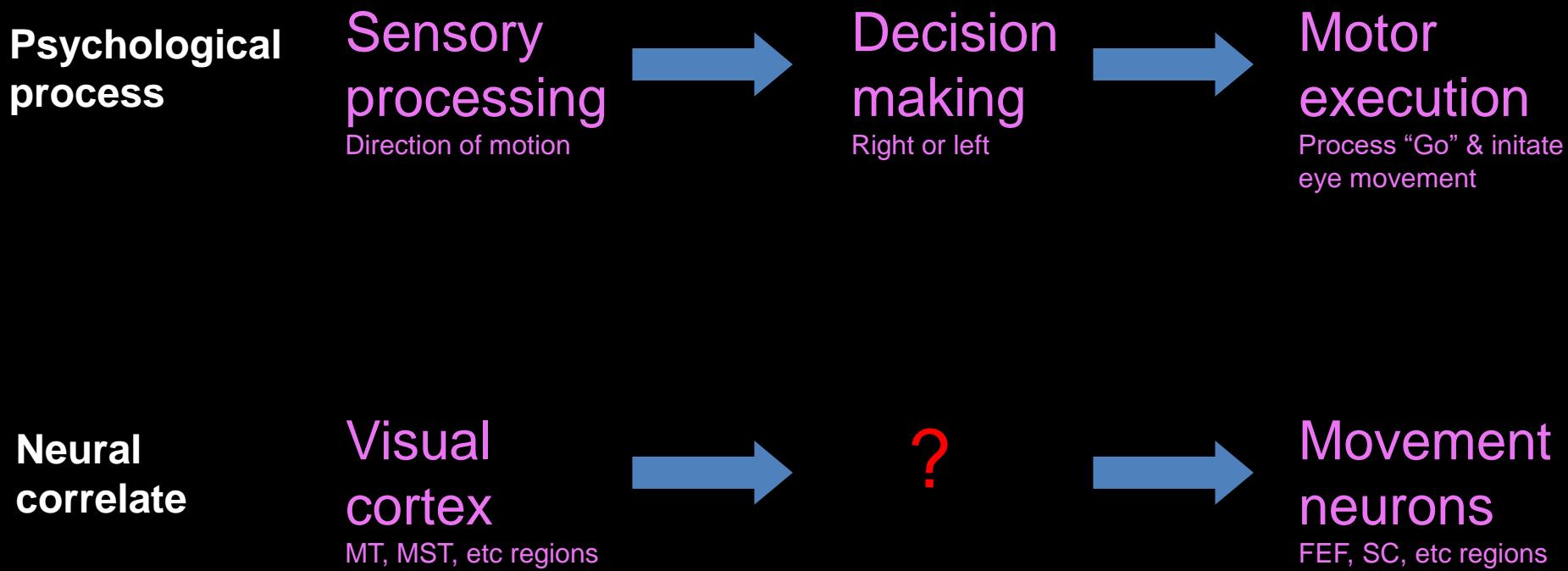
Sequential sampling models have been widely embraced in contemporary decision neuroscience. The models come in many forms that, despite containing fundamentally different algorithmic elements, can make highly similar predictions for behaviour. Consequently, it can be difficult to definitively adjudicate between alternative models based solely on quantitative fits to behaviour.

The discovery of brain signals that reflect key neural computations underpinning decision-making is opening new avenues for empirically testing and refining model predictions.

Neurophysiological research is highlighting the multilayered neural architecture for implementing even the most elementary sensorimotor decisions. We do not yet know how many processing layers are required nor what distinct computations are performed at each layer.

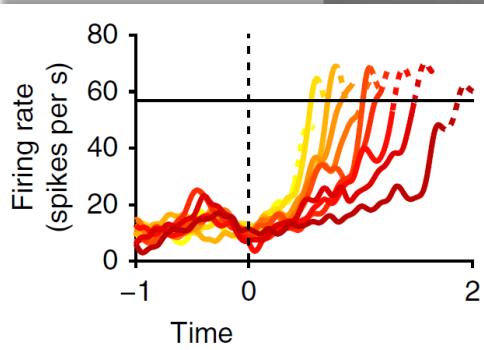
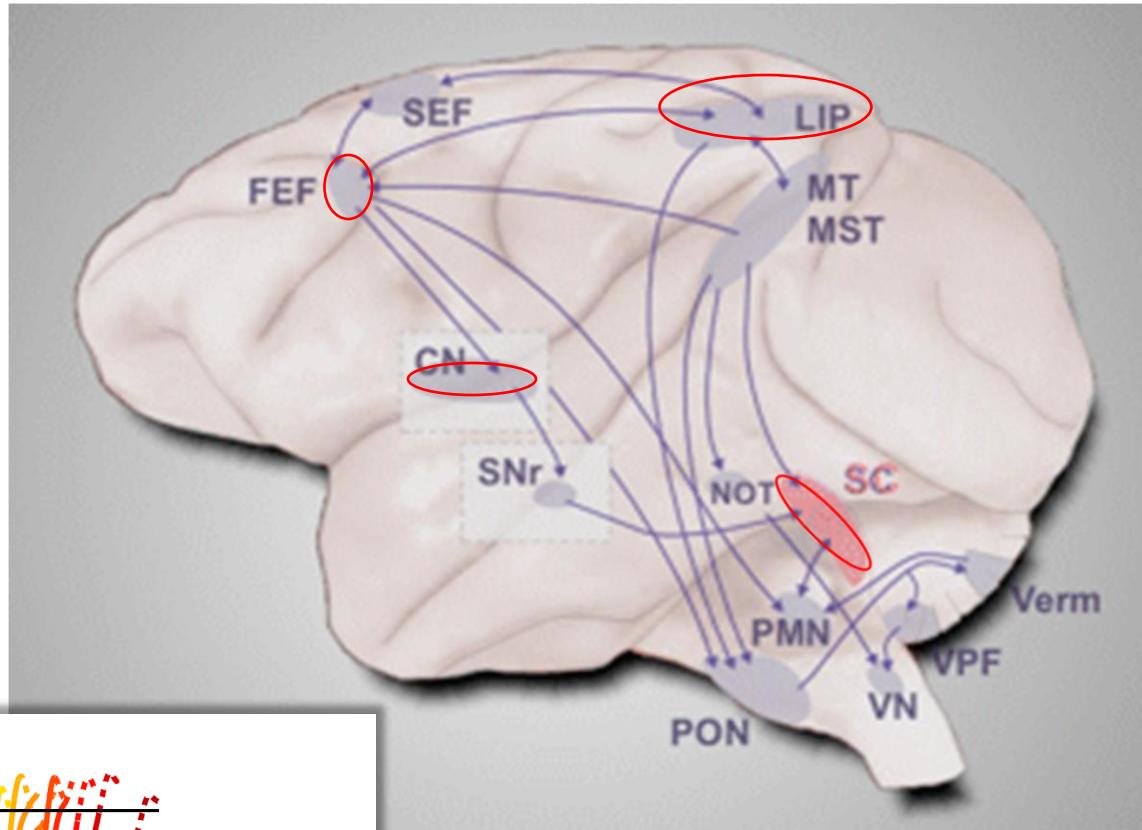
Is there evidence in brain physiology of such processes in perceptual decision-making?

Neural correlates of perceptual decision making



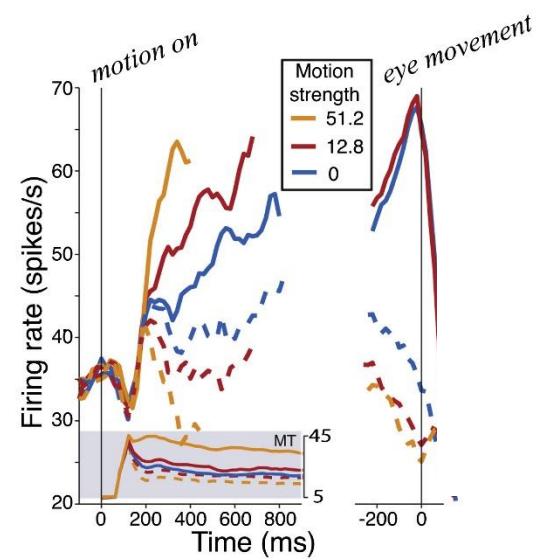
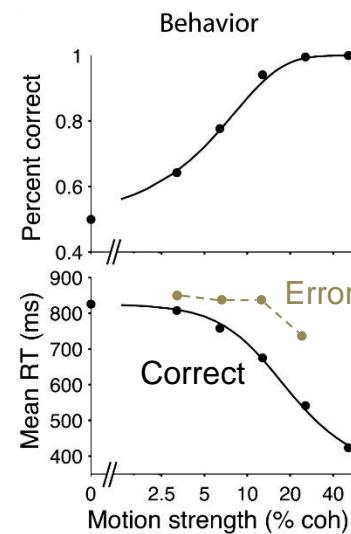
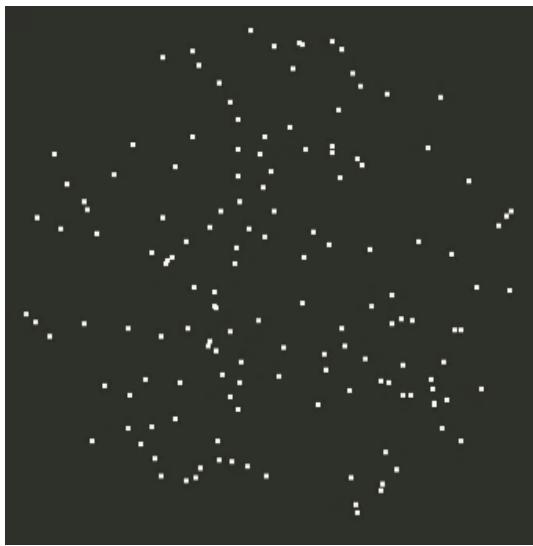
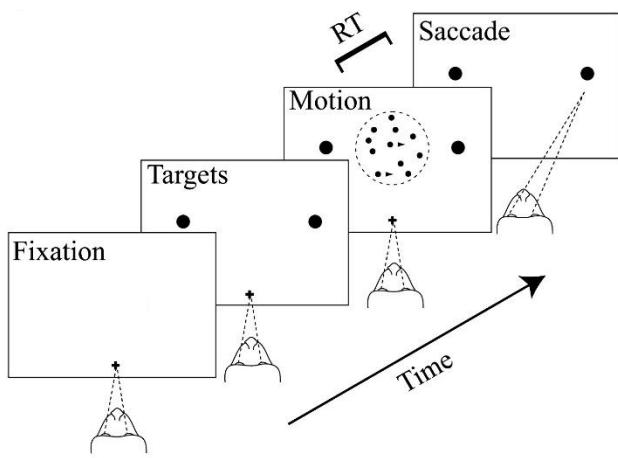
Brain circuitry controlling (saccadic) eye movements

The search for “neural integrators” in the brain



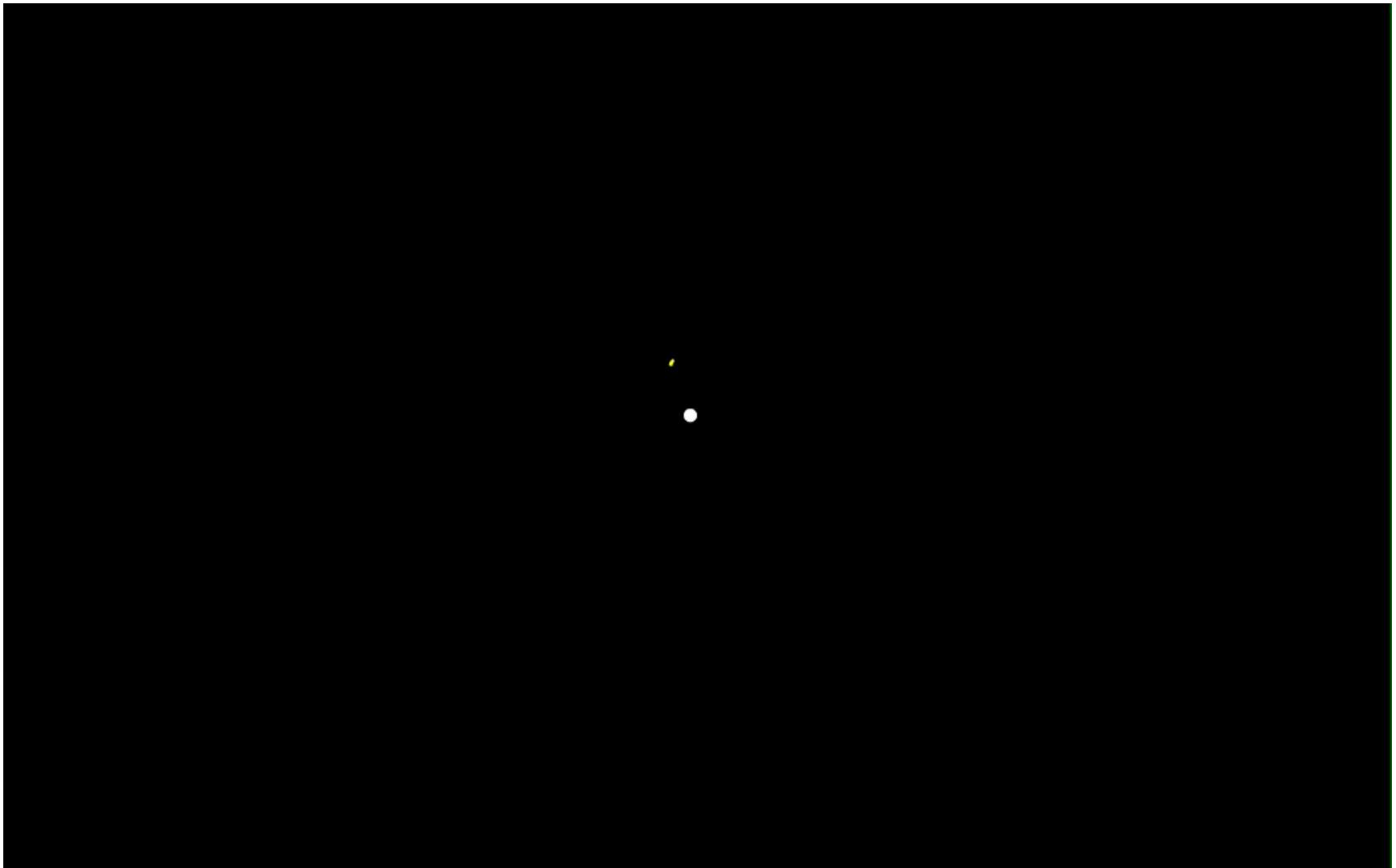
$$\int \dots dt$$

Classic experiment

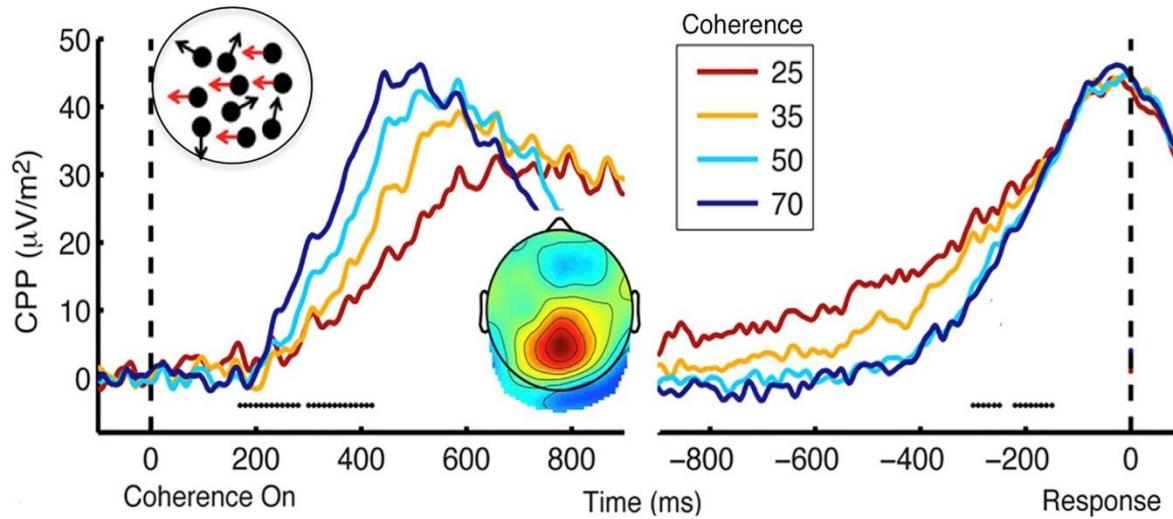


Neuronal population in area LIP (lateral intraparietal area)

Recording of a particular (LIP) brain cell in a non-human primate performing motion discrimination task



Similar macroscale brain activity dynamics in humans



Kelly & O'Connell, J. Neurosci. (2013)

Electroencephalography (EEG) measures ensembles of neural activity with high temporal resolution

How to link cognitive models to elements of the brain, i.e. brain cells (neurons) and their connections (synapses)?

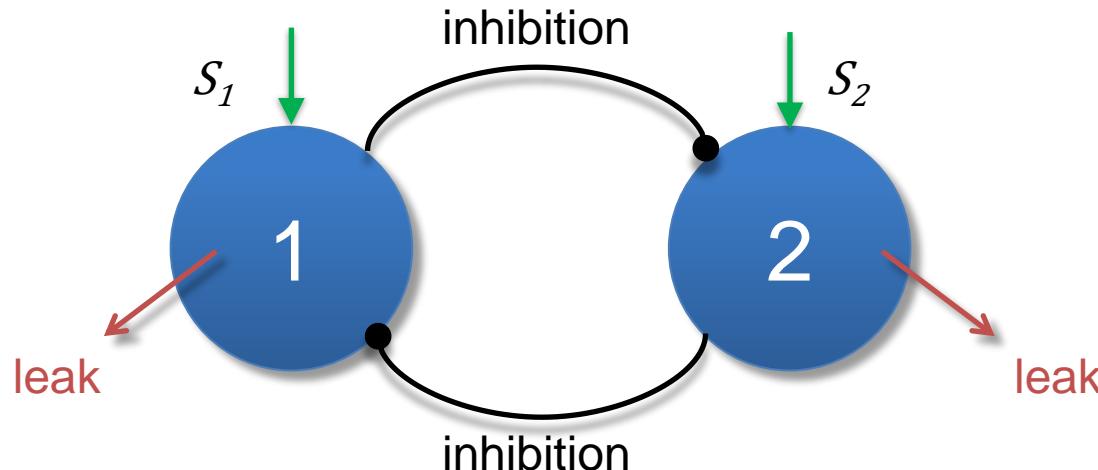
A simple neural network model

Leaky Competing Accumulator (LCA) model

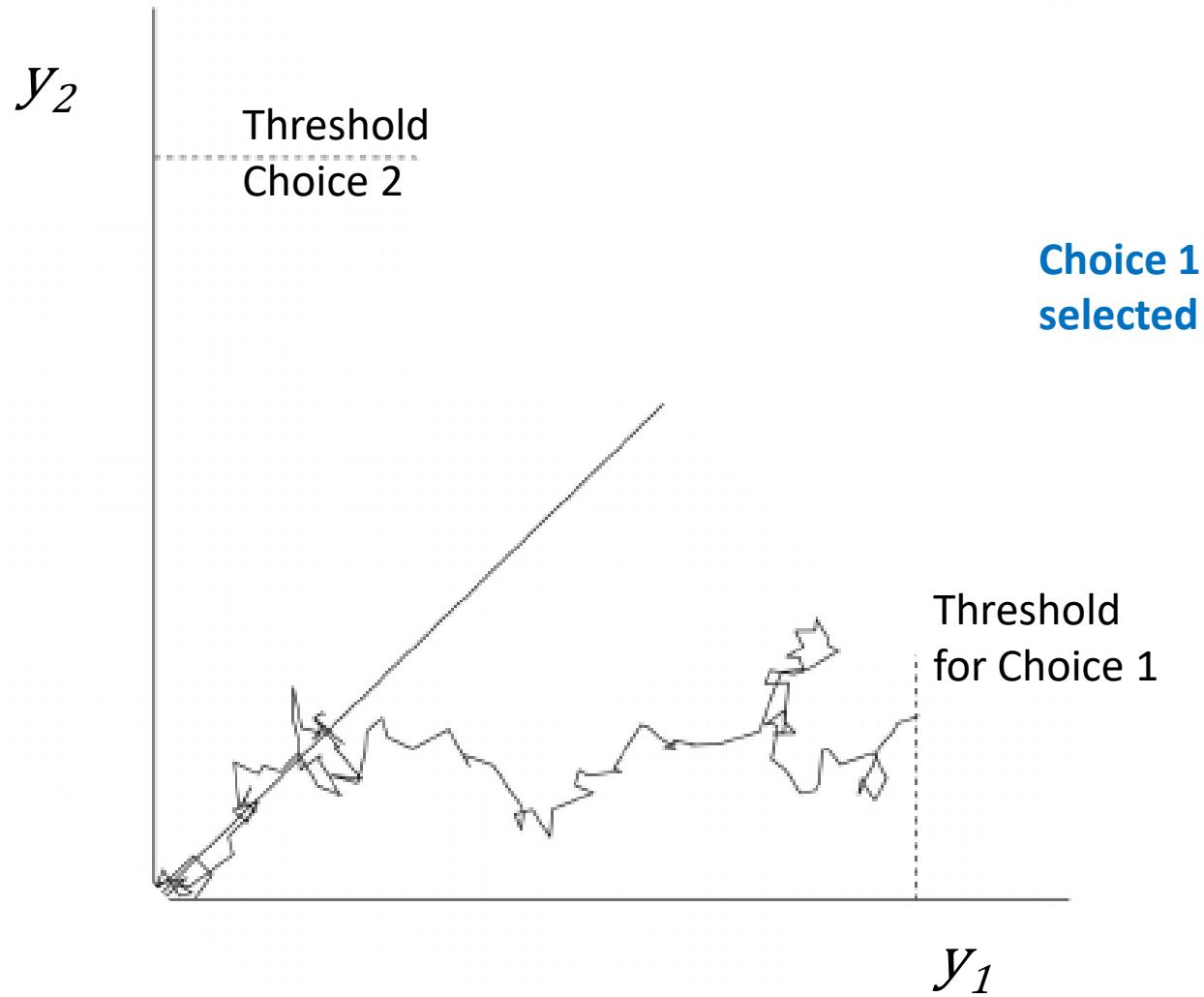
The decision process as the integration of evidence by competing accumulators – *winner-take-all* behaviour is necessary, or there will be conflict and indecisiveness.

$$\begin{aligned} dy_1 &= [-\gamma y_1 + f(-\beta y_2) + s_1] dt + \sqrt{D} dW_1 \\ dy_2 &= [-\underbrace{\gamma y_2}_{\text{leak}} + f(-\underbrace{\beta y_1}_{\text{inhibit}}) + \underbrace{s_2}_{\text{stim}}] dt + \underbrace{\sqrt{D} dW_2}_{\text{noise}} \end{aligned}$$

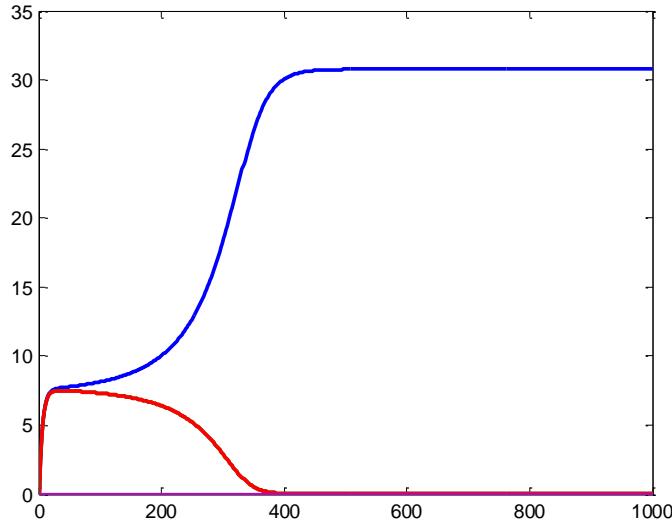
Usher & McClelland (1995, 2001)



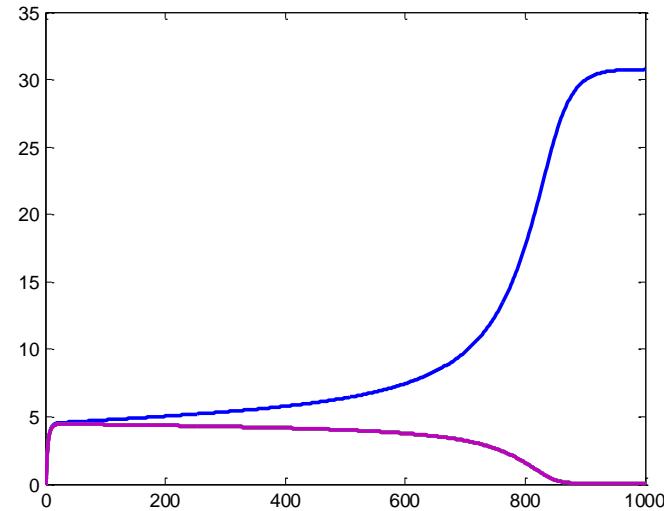
Sample simulated trajectory of nonlinear LCA model in activity (phase/state) space



A multi-population winner-take-all network model



With 2 choices
(short latency or
response time)
Note: The other neural
population follows the
same dynamics as purple

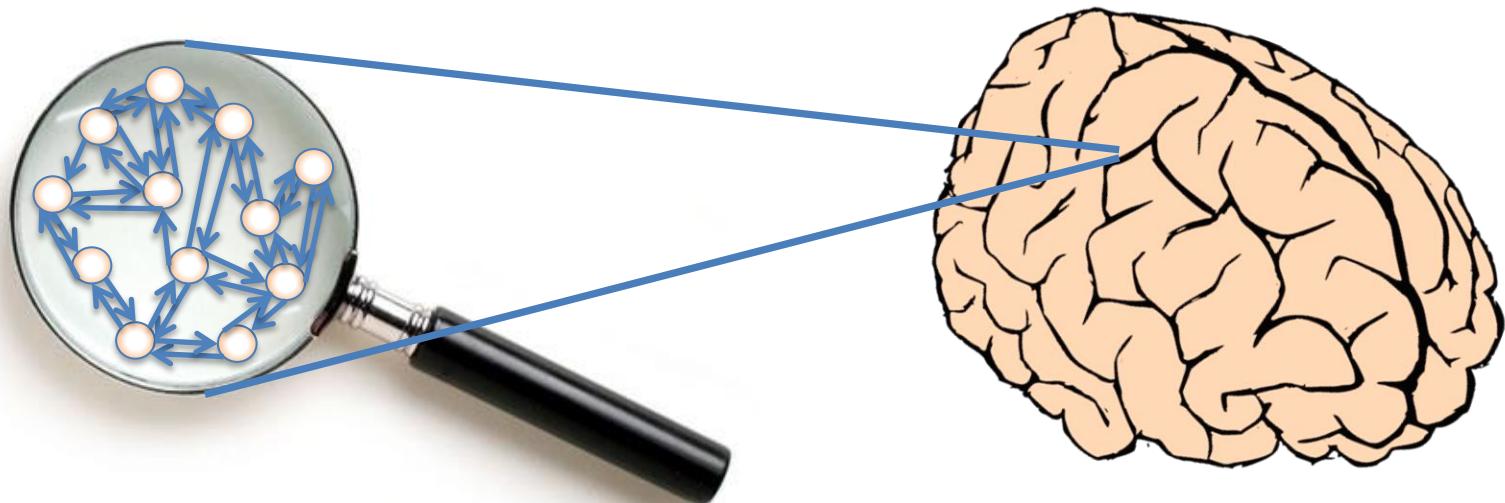


With 5 choices
(long latency or
response time)
Note: The other 3 neural
populations follow the
same dynamics as purple

Hick's or Hick-Hyman law: Describes the time it takes for a person to make a decision as a result of the possible choices: increasing the number of choices will increase the decision time logarithmically

All model parameter values remain the same in both cases.

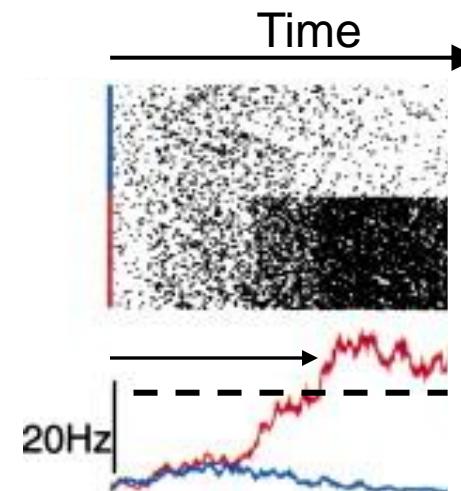
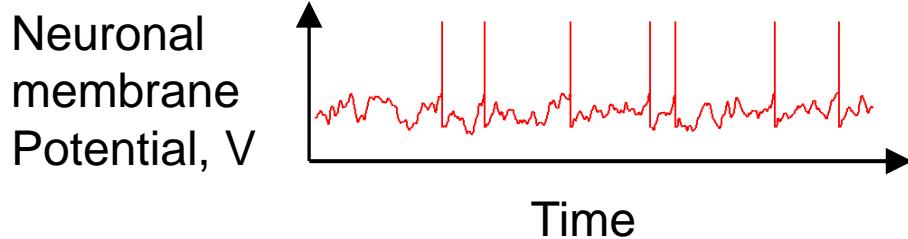
A network of neurons and emergent behaviour



Spiking activity from a single model neuron, and network of connected neurons

Leaky Integrate-and-fire neuronal model
with realistic synaptic dynamics

$$\frac{dV}{dt} = -g_L(V-E_L) + I_e - \sum g_s s(t) (V-E_s)$$



X-J Wang
(2002)
Neuron

A “mean-field” (neural population) approach

Neural population dynamics described by

$$\tau \frac{dr}{dt} = -r + \varphi(I)$$

$$\varphi(I) = \frac{c I - I_0}{1 - \exp(-g(cI - I_0))}$$



an approximation of a first passage time formula for LIF neurons (via Fokker-Planck approach), and I is averaged total input to a neuron,

$$I = W S + I_{stimulus} + I_{noise}$$

where W is the synaptic (connectivity) strength, and

$$\tau_{noise} \frac{dI_{noise}}{dt} = -I_{noise} + \eta \sqrt{\tau_{noise} \sigma_{noise}^2} \quad (\text{Ornstein-Uhlenbeck process})$$

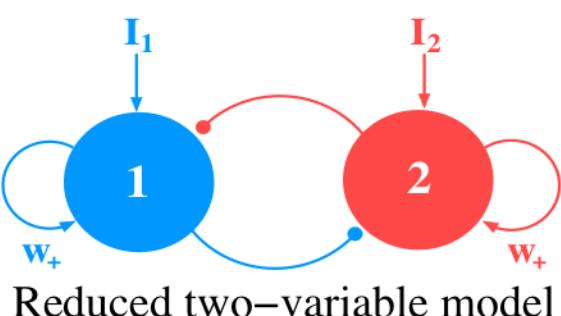
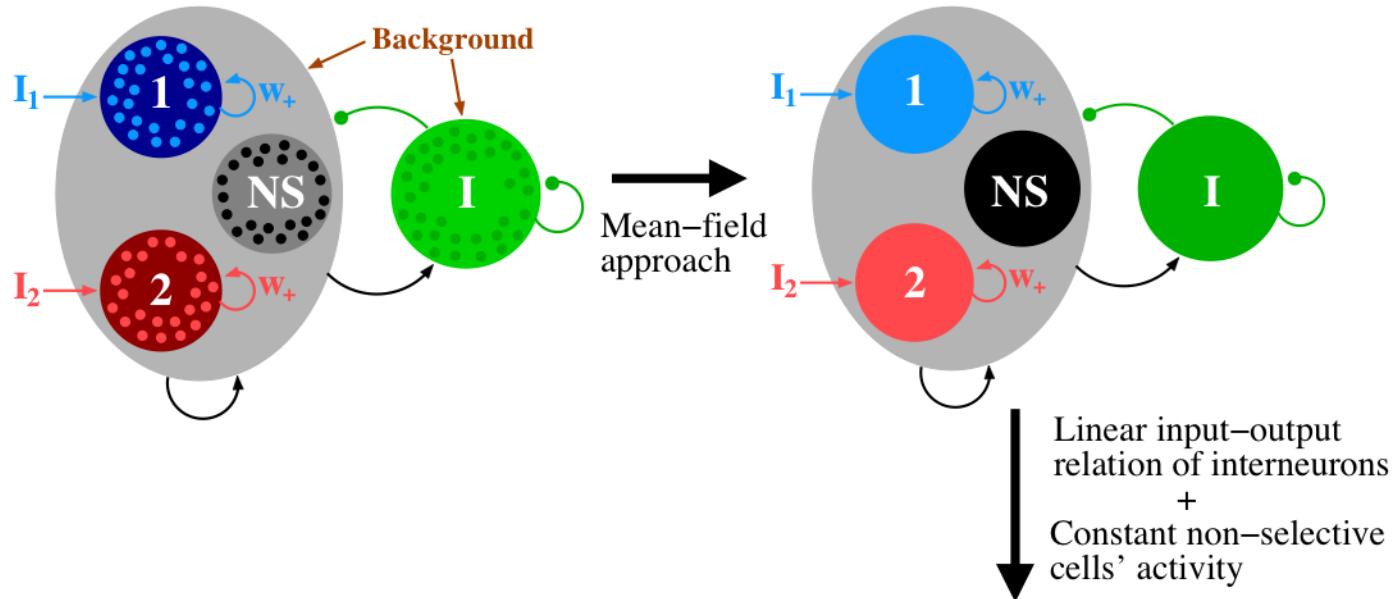
Dynamics describing the averaged (slow) synaptic dynamics for the neural population

$$\frac{dS}{dt} = -\frac{S}{\tau_s} + (1 - S) \gamma r$$

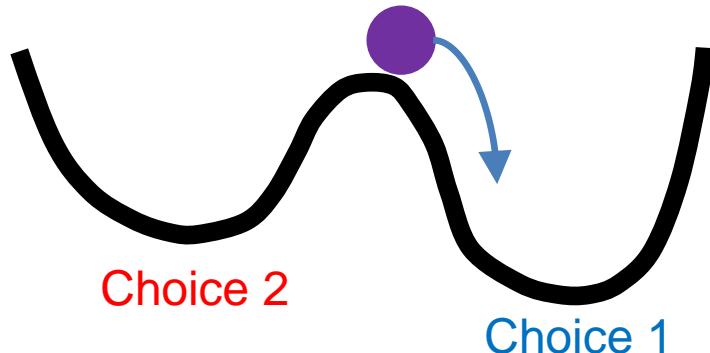
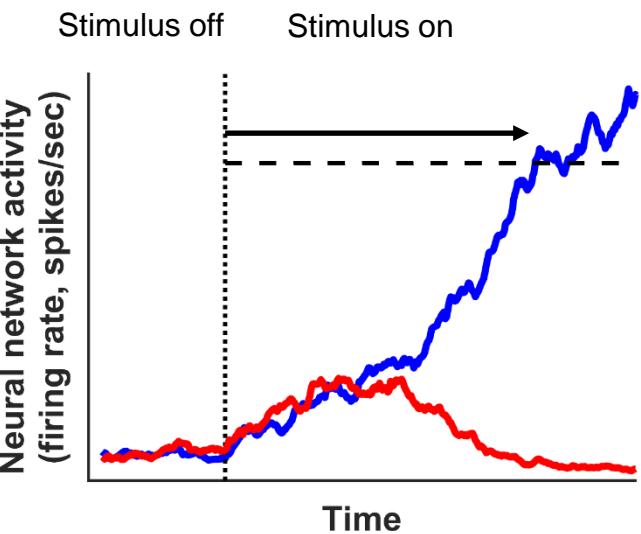
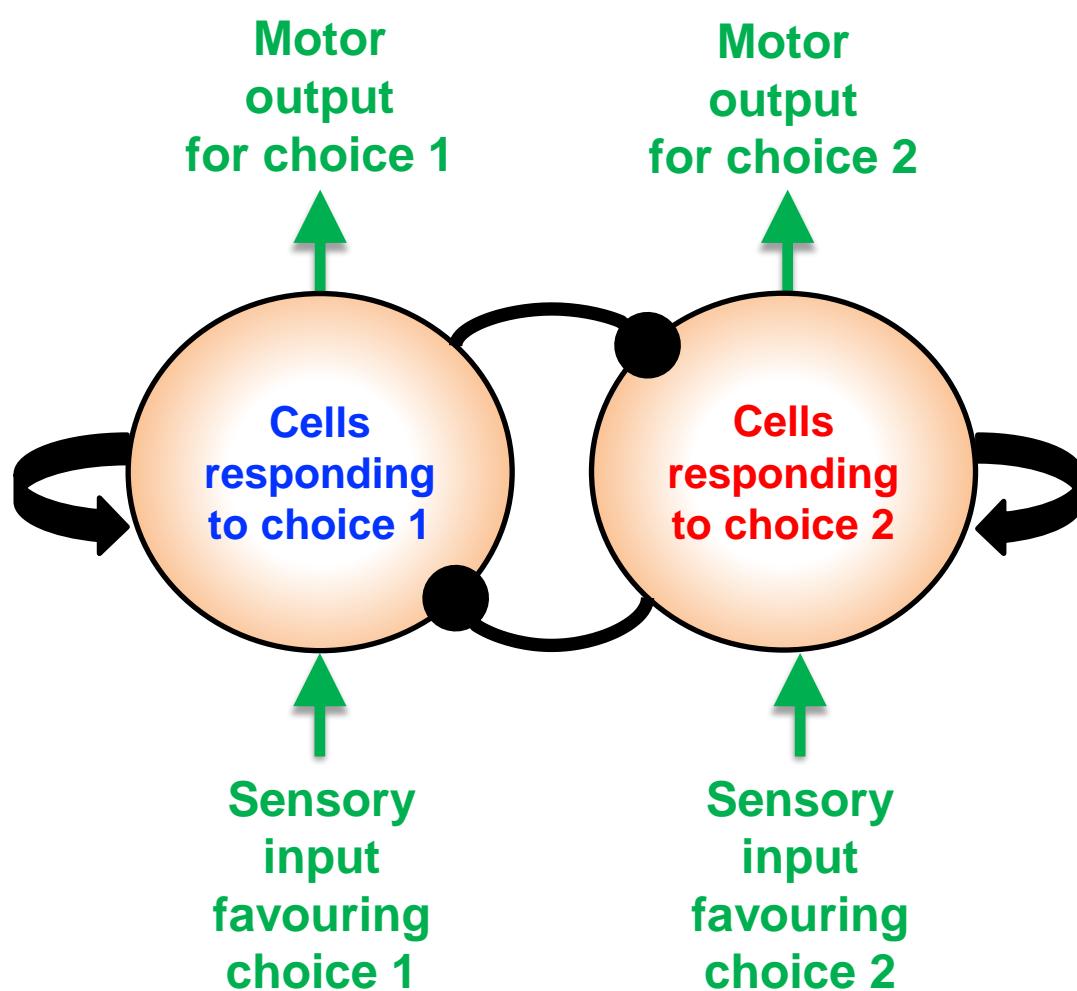
(with interspike interval distribution \sim Poisson)

Reducing a biophysical model of decision-making

Spiking neuronal network model

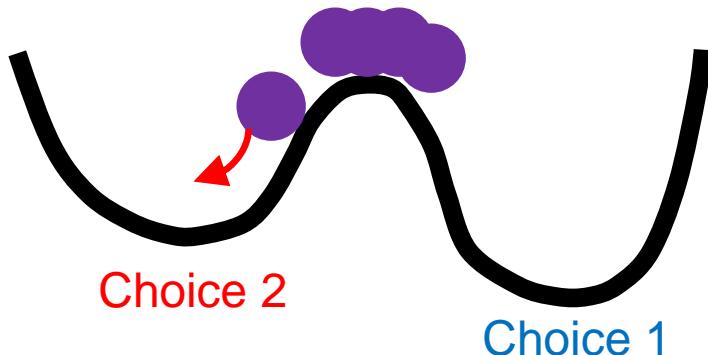
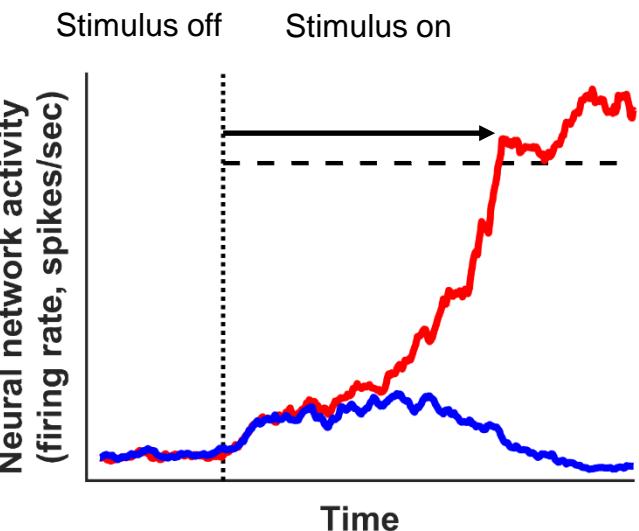
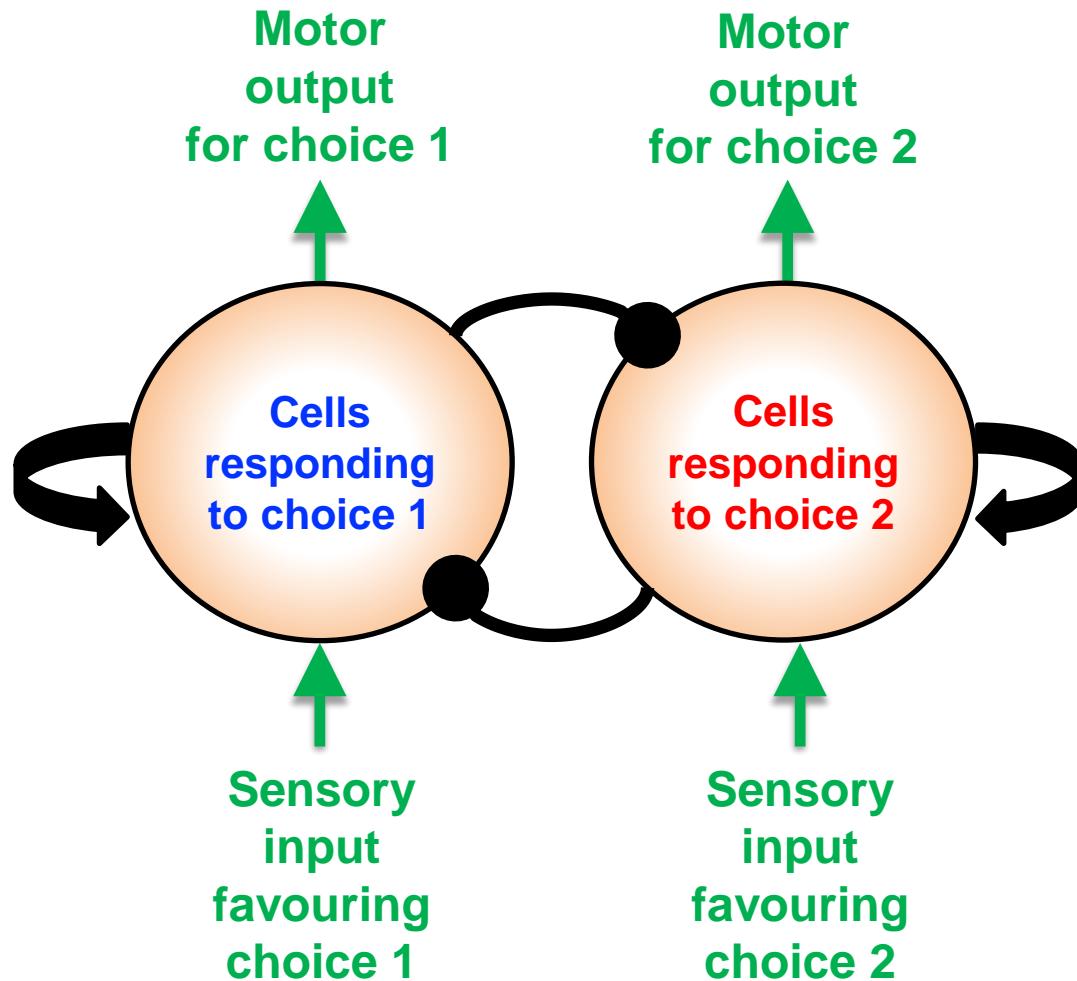


A simpler biologically based neural network model



Wong and Wang, J. Neurosci. (2006)
Roxin and Ledberg, PLoS Comput. Biol. (2008)

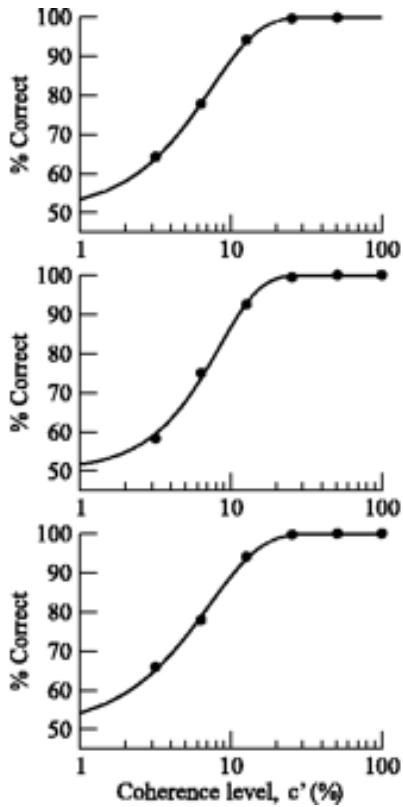
A simpler biologically based neural network model



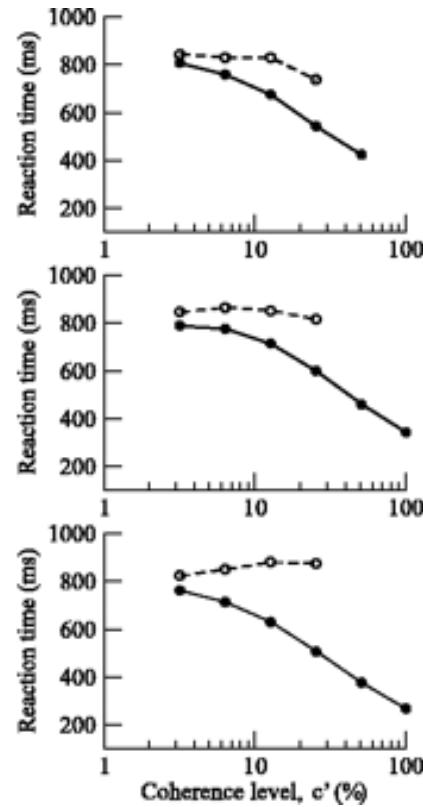
Wong and Wang, *J. Neurosci.* (2006)
Roxin and Ledberg, *PLoS Comput. Biol.* (2008)

A reduced (attractor) neural network model with strong positive feedback

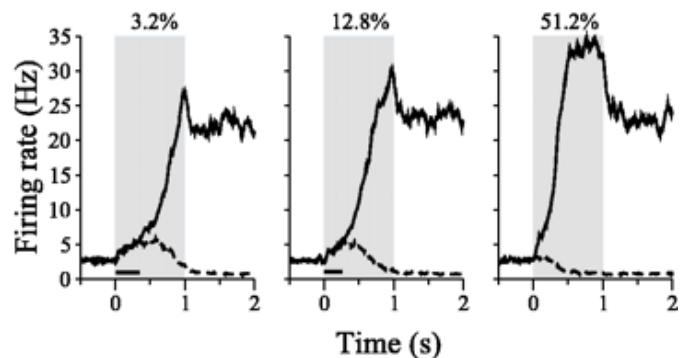
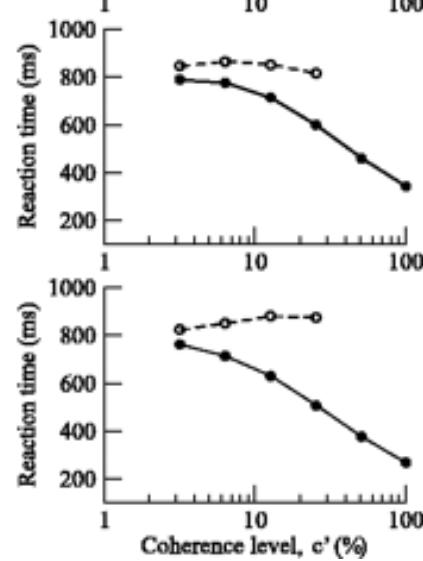
Experimental data



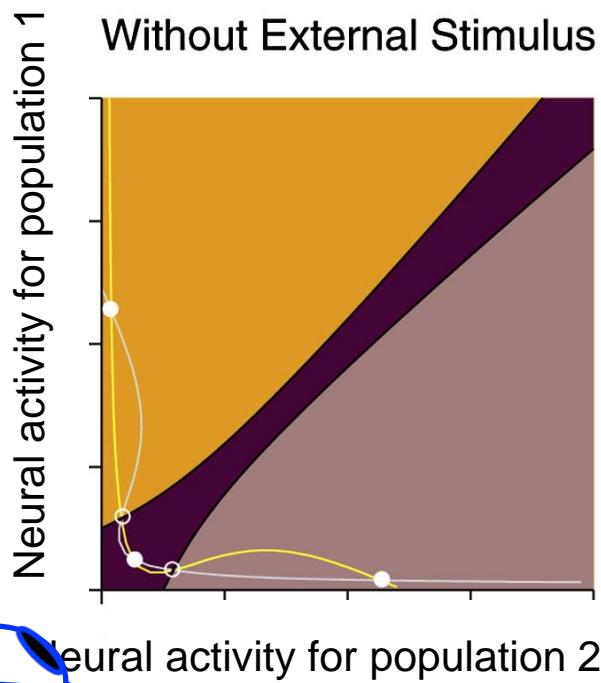
Spiking neuronal network model



Reduced two-variable model

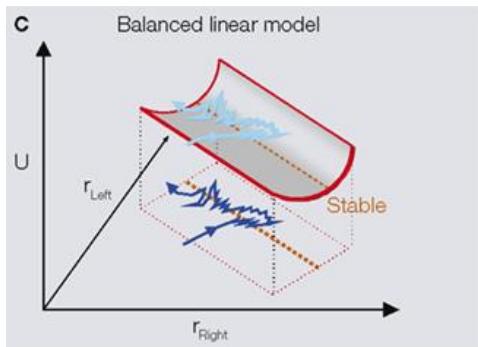
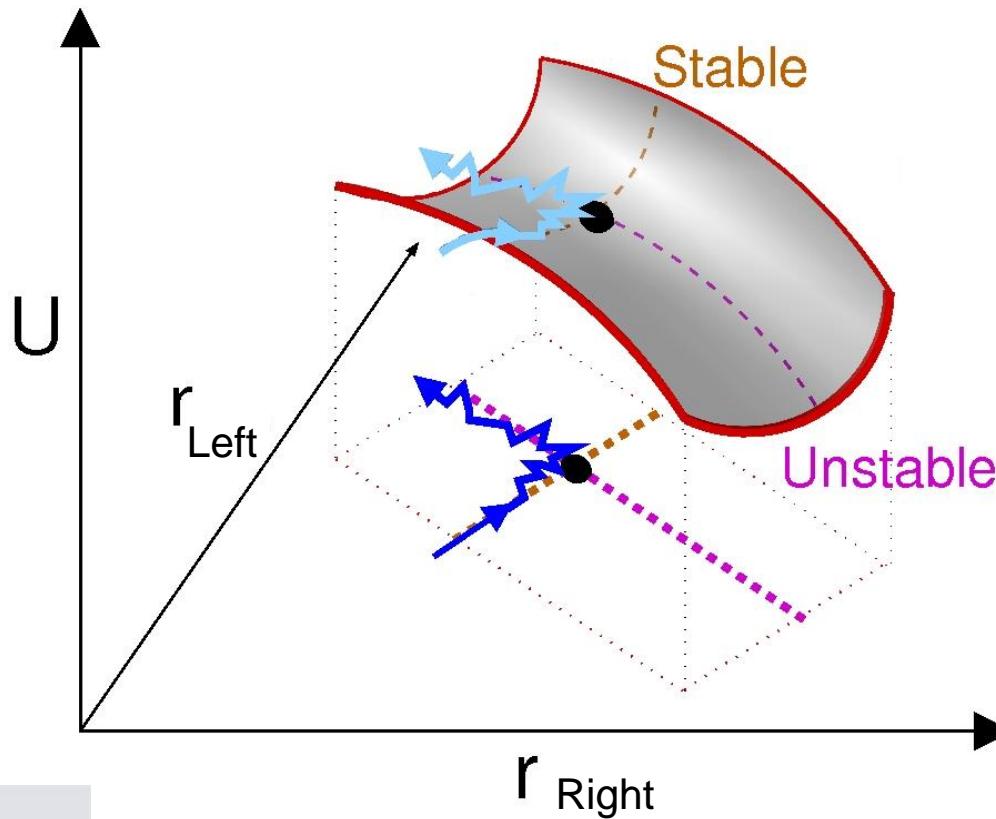


Phase-plane analysis of attractor network model



Wong & Wang, *J. Neurosci.* (2006), adapted

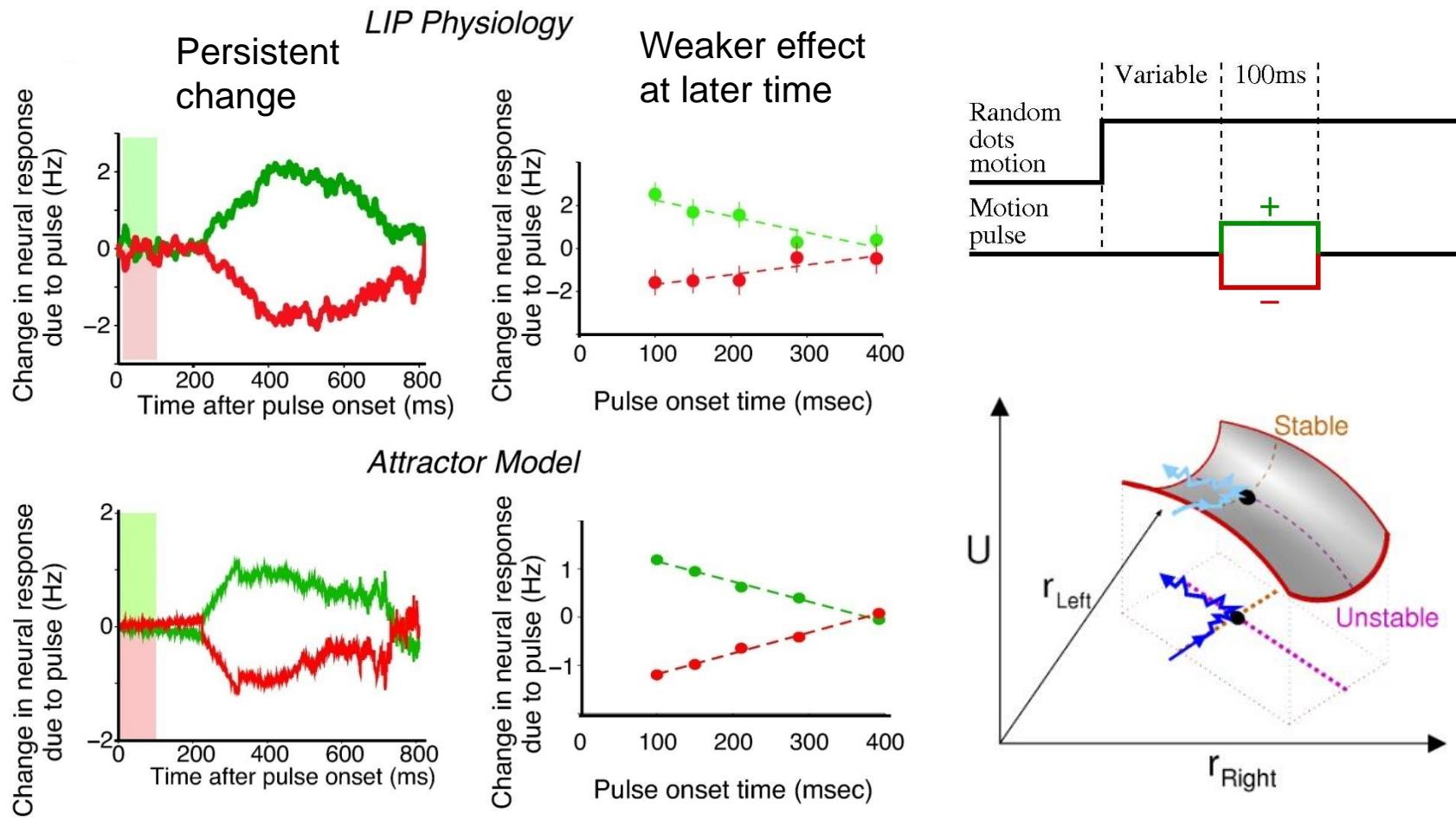
“Potential energy” landscape in phase space



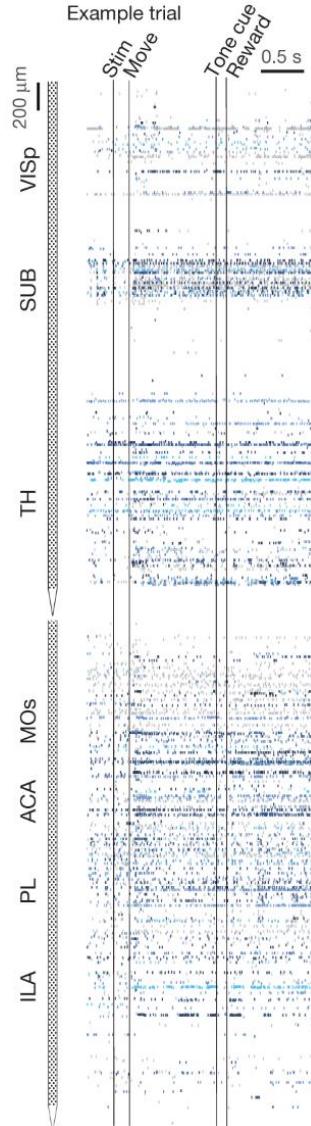
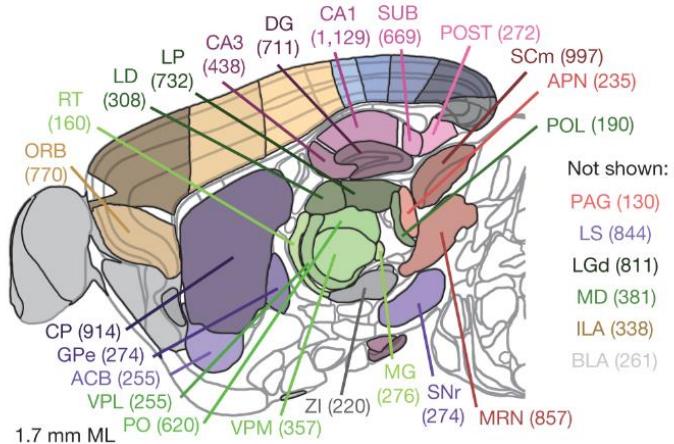
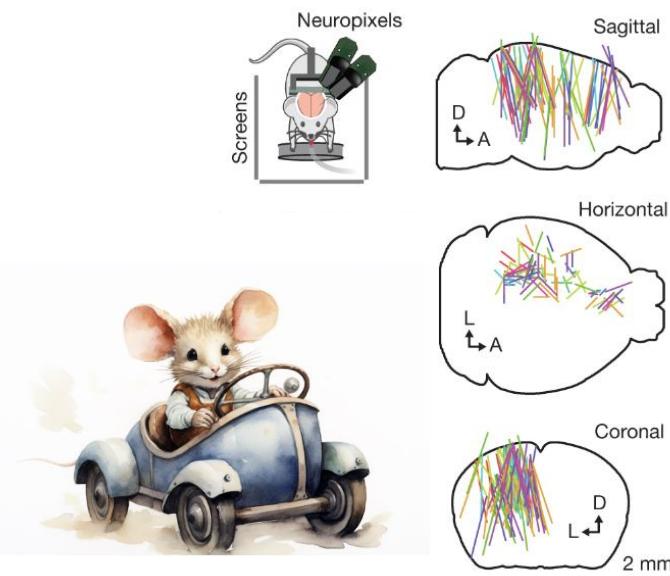
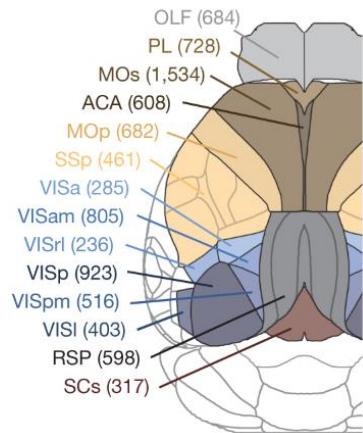
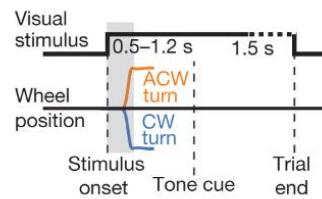
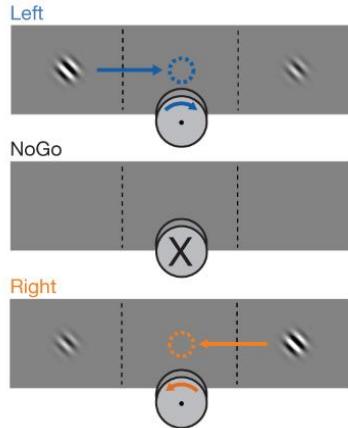
In the vicinity of the unstable “**saddle**” steady state

Wong & Huk, *Front. Neurosci.* (2008)
Bogacz et al., *Psychol. Rev.* (2006)

Model prediction: Attractor network model with “runaway” temporal integration can account for weaker perturbative effects at later times

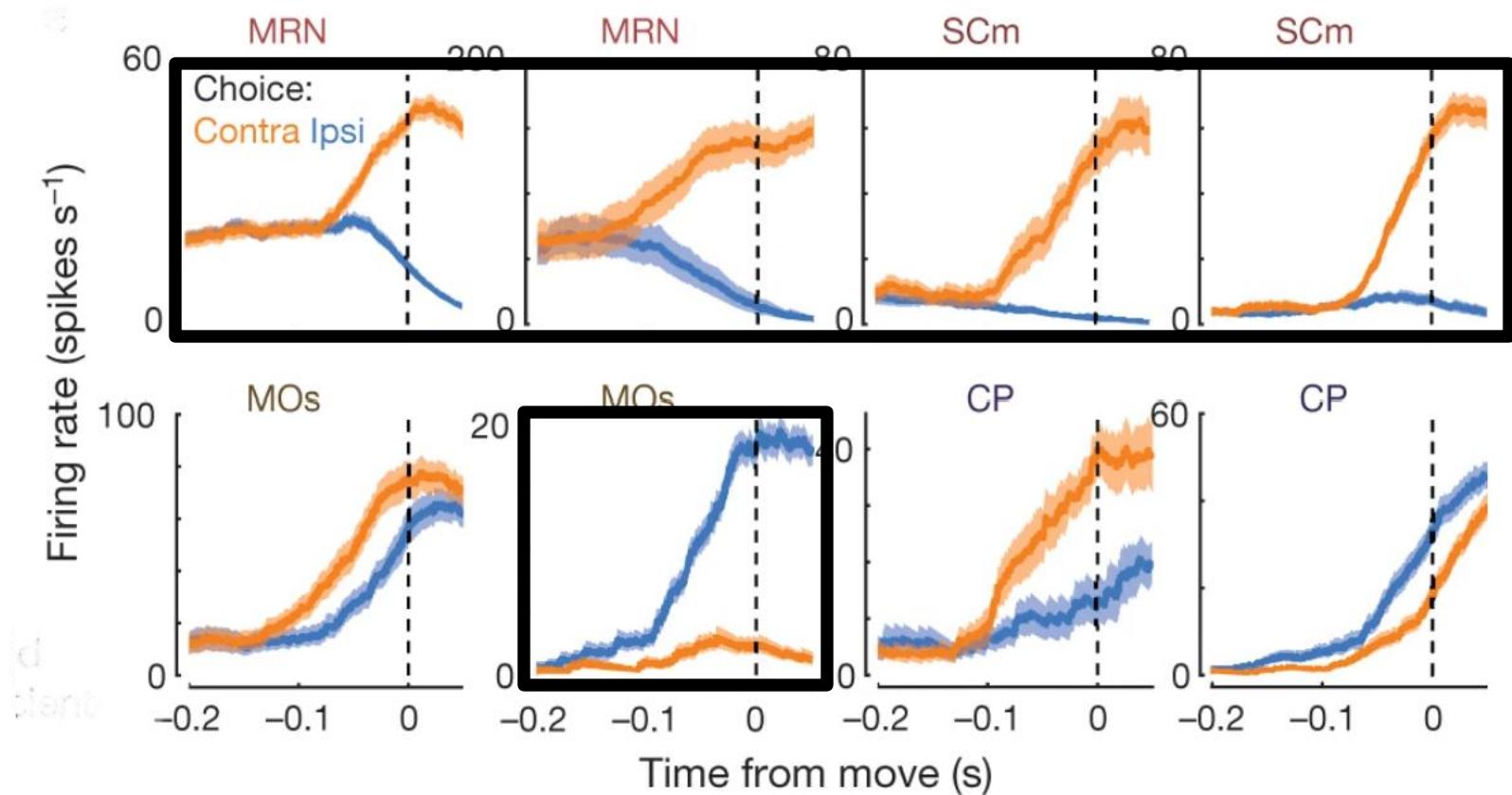


Neural dynamics in higher dimensions from simultaneously recorded neurons



Neural dynamics in higher dimensions from simultaneously recorded neurons

Some sample neuronal activities encoding choice information exhibit winner-take-all behaviour

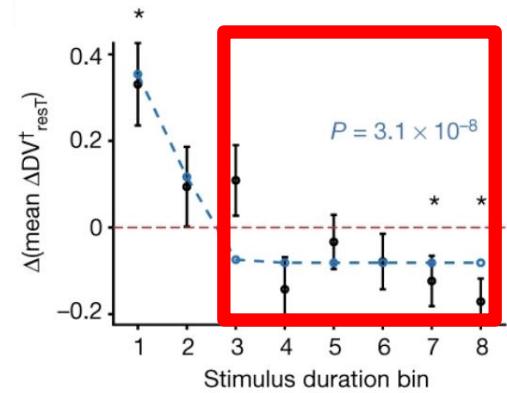
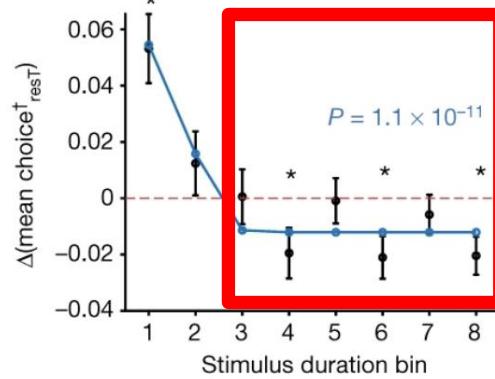
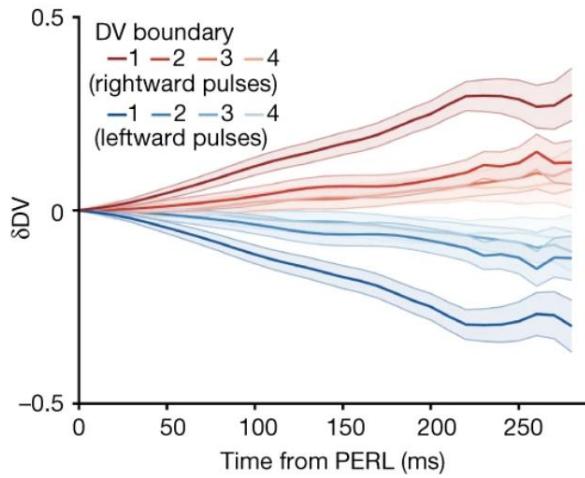
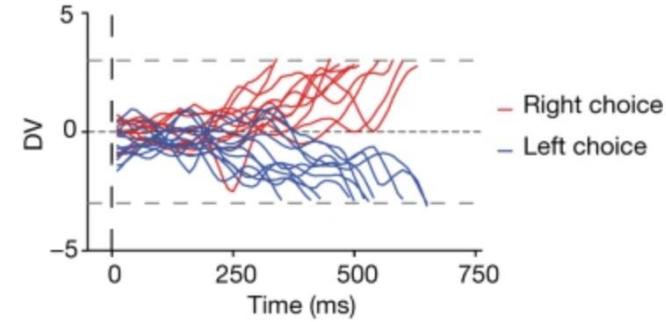
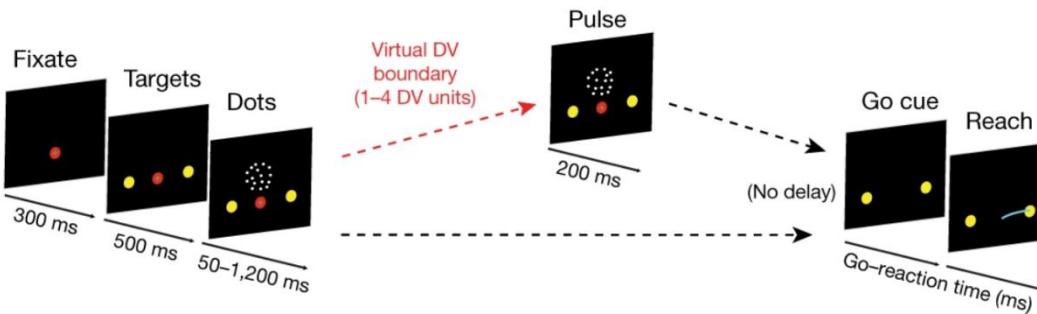


Activities averaged across experimental trials and aligned from movement onset

Steinmetz et al.,
Nature (2019)

Neural dynamics in higher dimensions from simultaneously recorded neurons

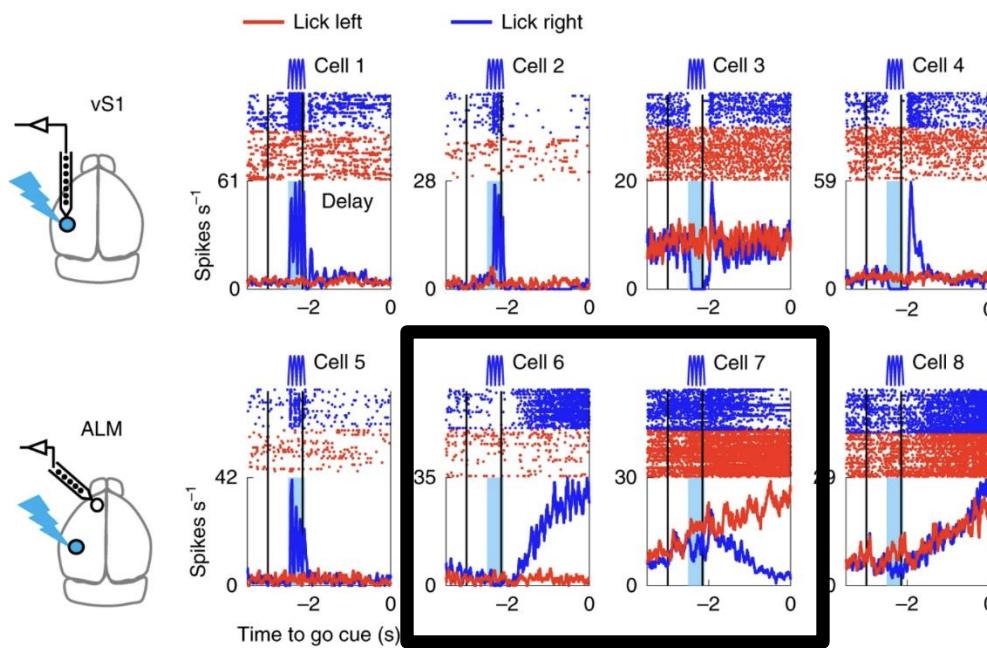
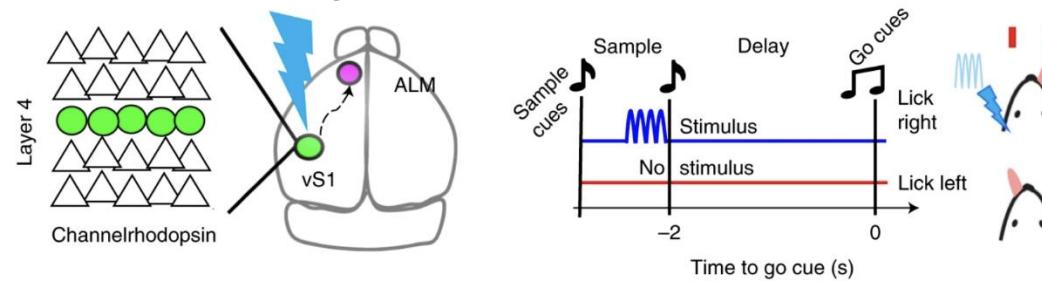
Peixoto et al., *Nat.* (2021)



Neural dynamics in higher dimensions from simultaneously recorded neurons

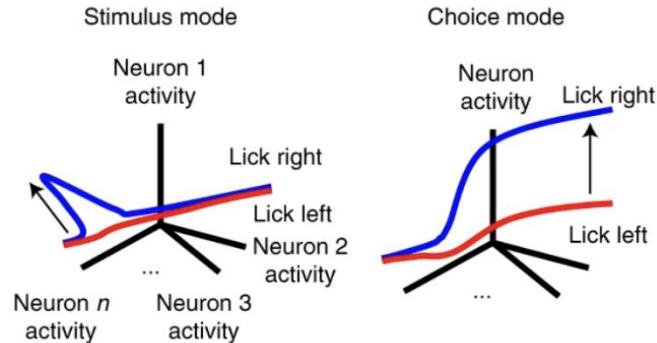
Finkelstein et al., *Nat. Neurosci.* (2021)

Direct cortical photostimulation in tactile decision-making

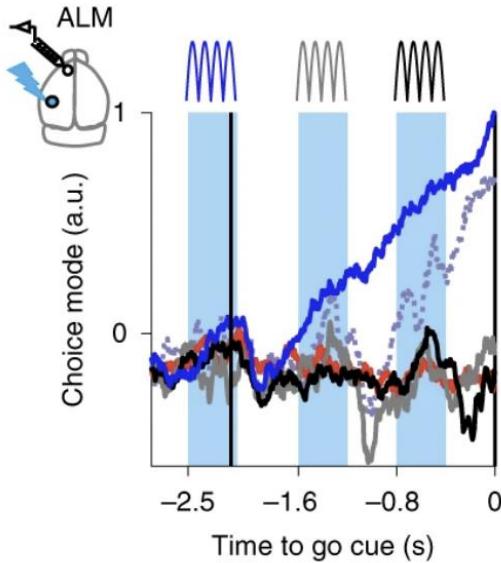


Neural dynamics in higher dimensions from simultaneously recorded neurons

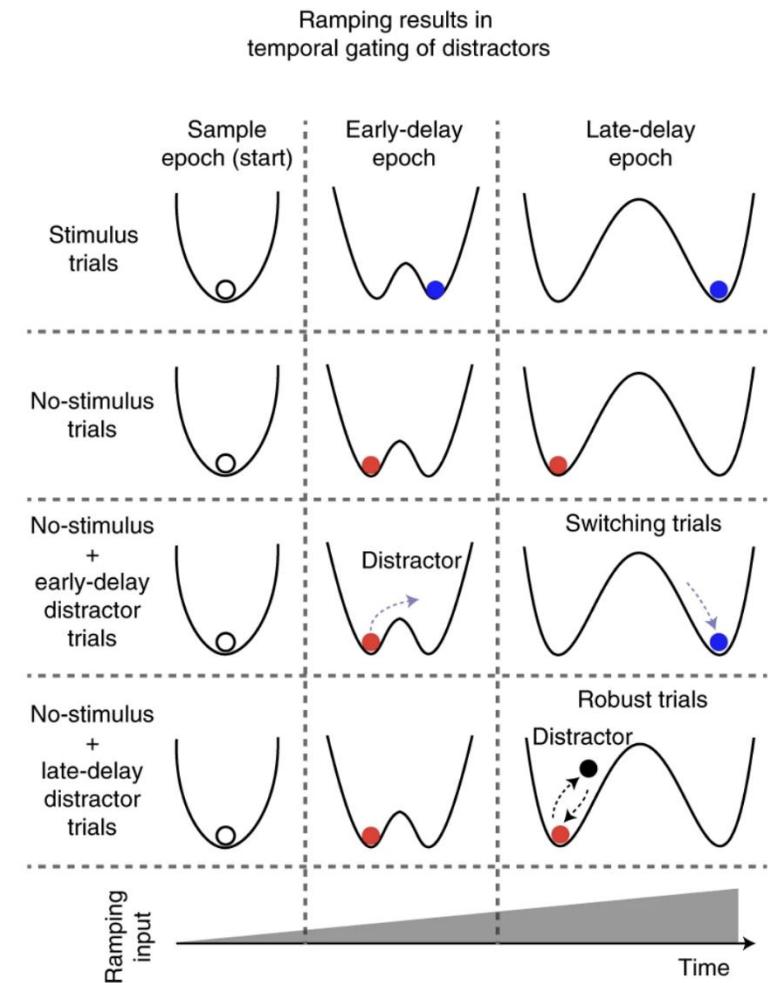
Dimensionality reduction
of population activity in the ALM



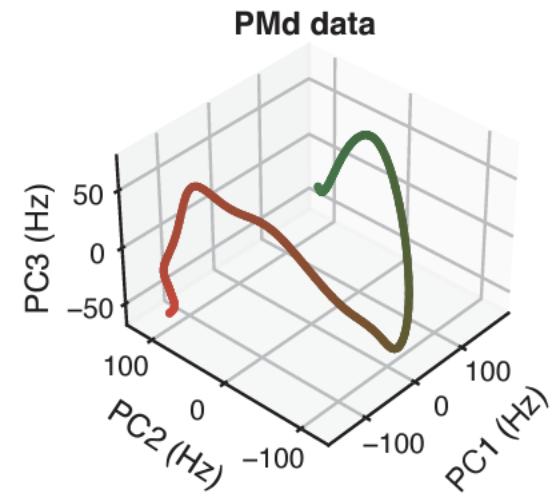
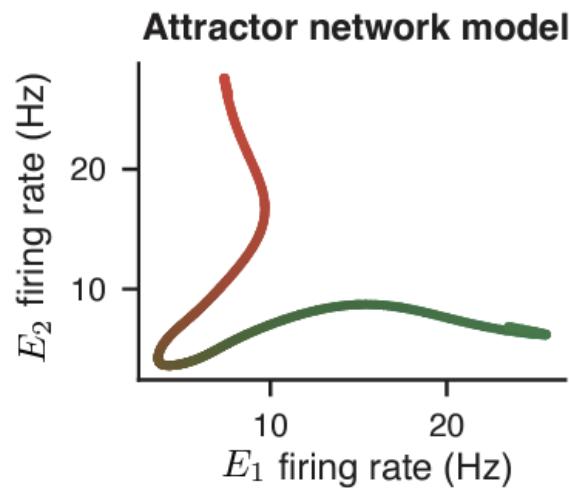
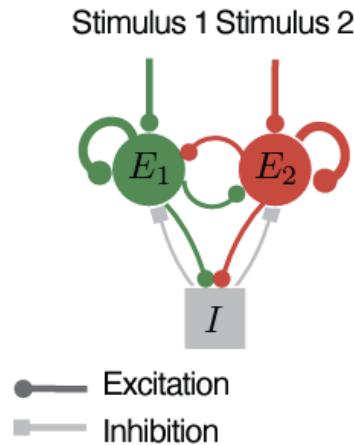
Gating of distractors
in the ALM choice mode



Finkelstein et al., Nat.
Neurosci. (2021)

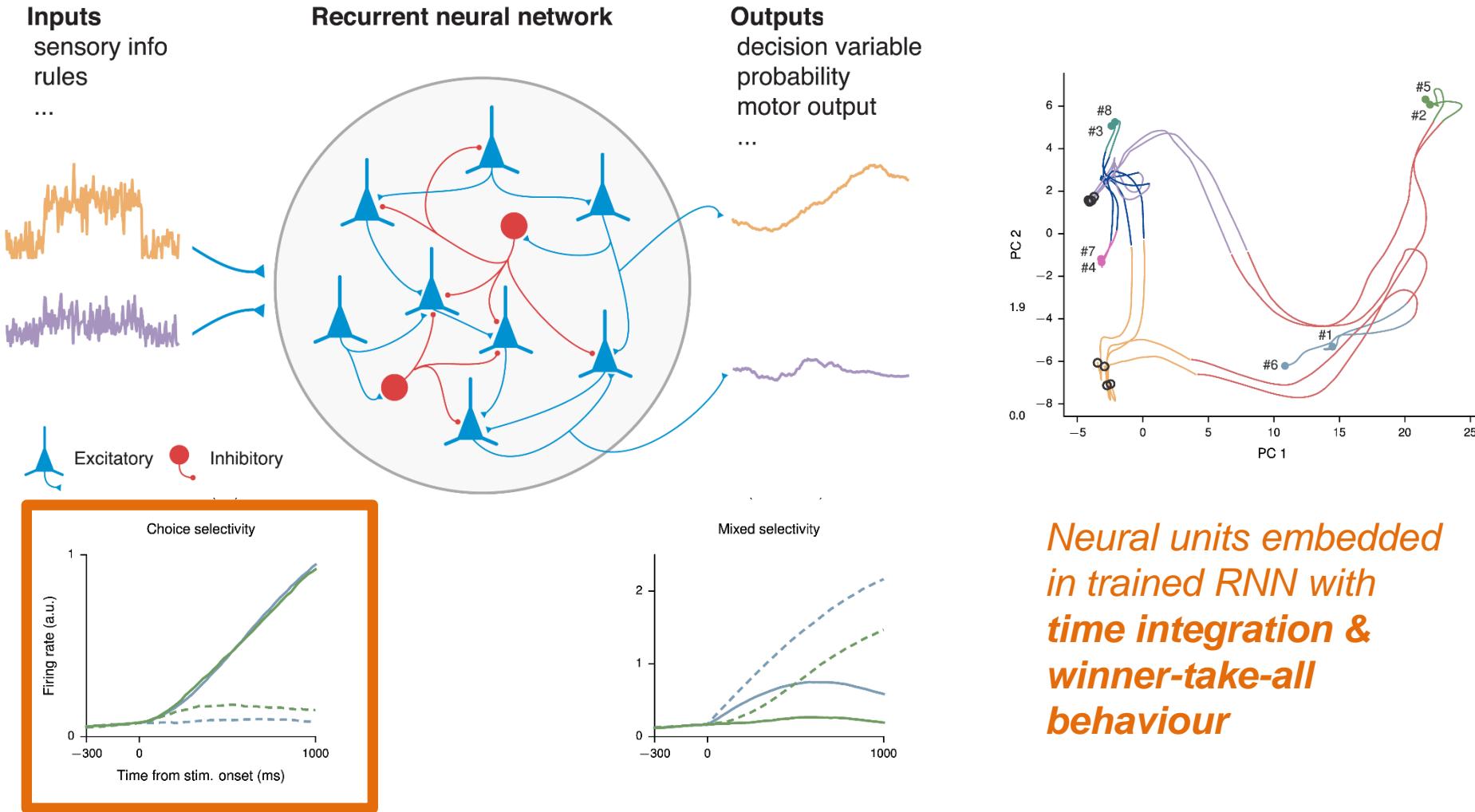


Additional neuron causes neural trajectories to traverse into additional dimension



Genkin, Shenoy,
Chandrasekaran &
Engel, *bioRxiv* (2023)

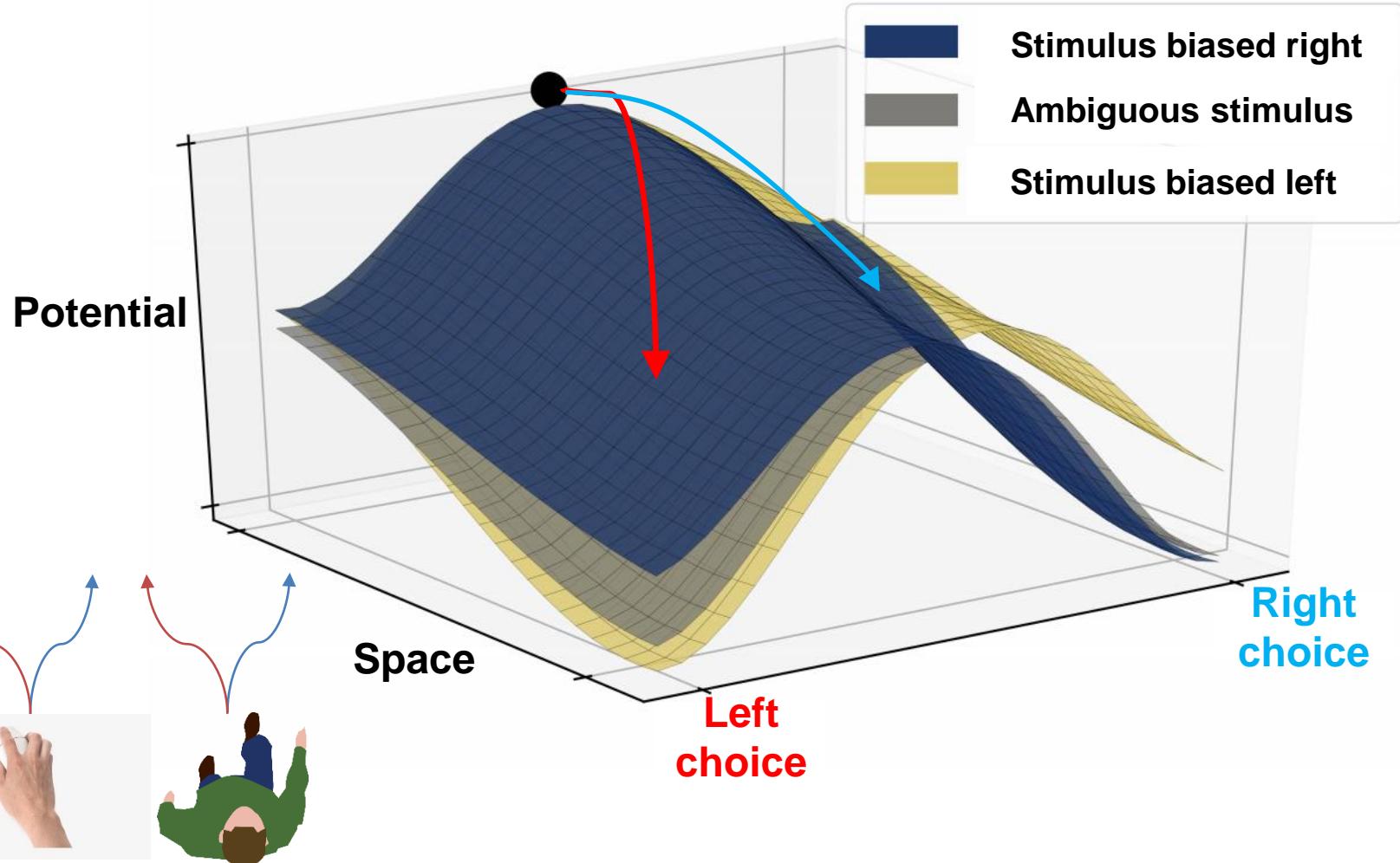
Training excitatory-inhibitory recurrent neural network (RNN) model in decision-making tasks



Neural units embedded in trained RNN with time integration & winner-take-all behaviour

“Potential energy” landscape in space

Reconstructed from walking or computer mouse trajectories

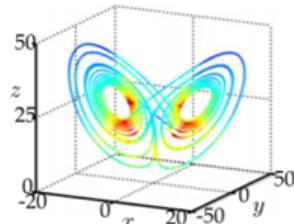


Adapted from Zgonnikov, Atiya, O'Hora, Rano & Wong-Lin (2019) Judgment & Decision Making

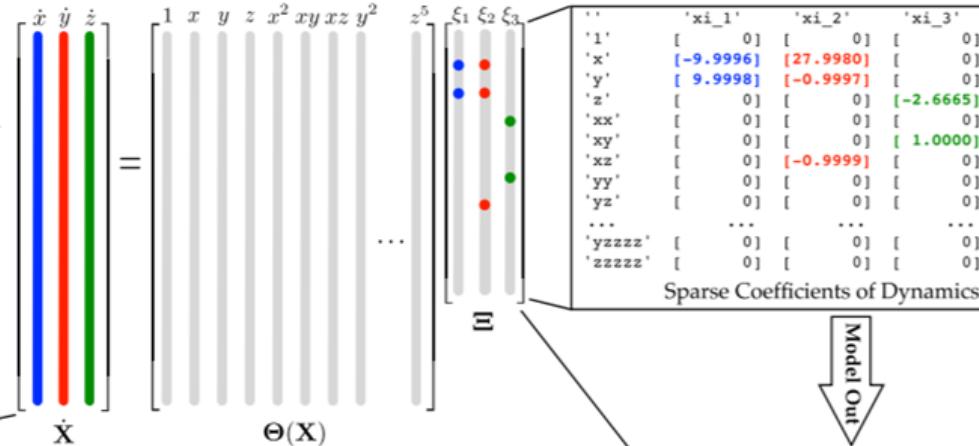
Using machine learning to uncover dynamical equations of low-dimensional state trajectory

I. True Lorenz System

$$\begin{aligned}\dot{x} &= \sigma(y - x) \\ \dot{y} &= x(\rho - z) - y \\ \dot{z} &= xy - \beta z.\end{aligned}$$

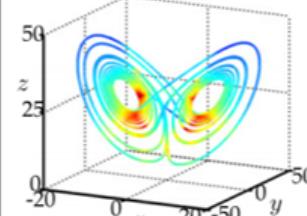


Data In

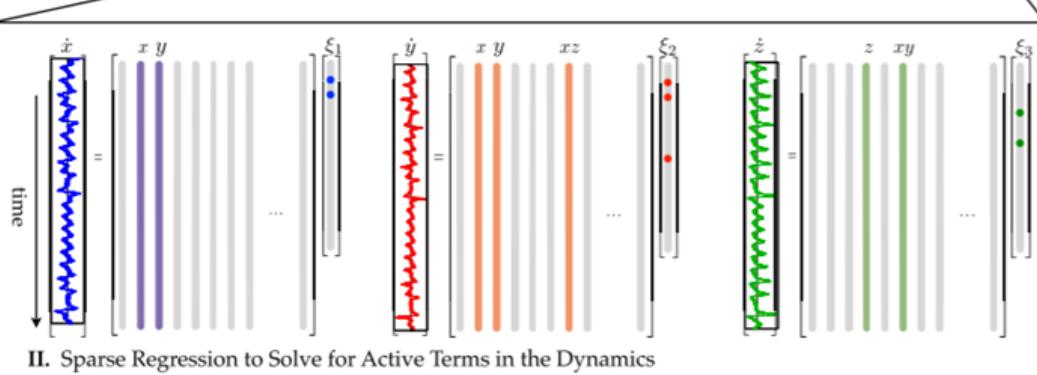


III. Identified System

$$\begin{aligned}\dot{x} &= \Theta(\mathbf{x}^T)\xi_1 \\ \dot{y} &= \Theta(\mathbf{x}^T)\xi_2 \\ \dot{z} &= \Theta(\mathbf{x}^T)\xi_3\end{aligned}$$



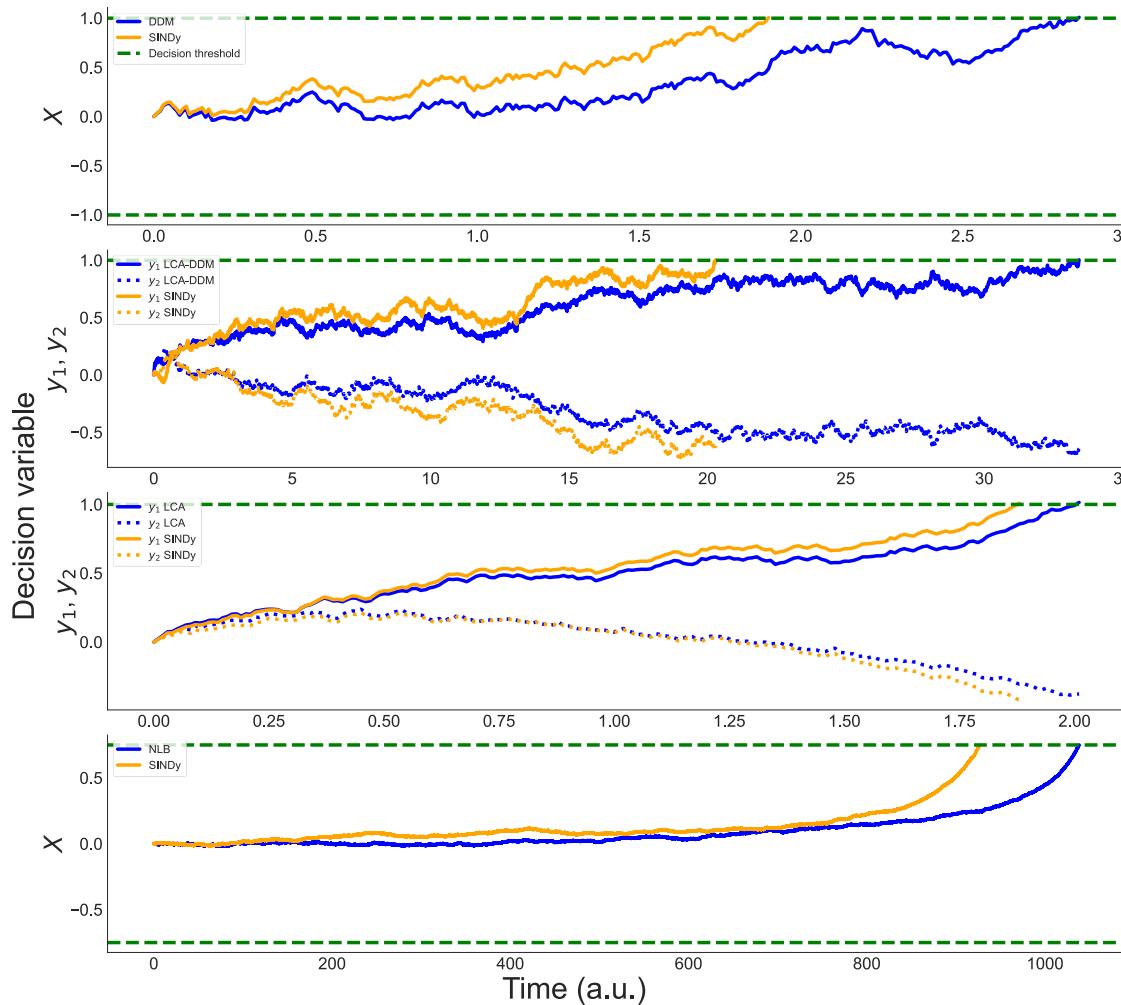
Sparse identification of non-linear dynamics (SINDy) to rediscover governing equations



Brunton, Proctor & Kutz, PNAS (2016)

Using machine learning to uncover dynamical equations of low-dimensional neural trajectory (2-choice tasks)

Decision models



Drift-diffusion model (DDM)

Leaky competing accumulator (LCA) model approx.
DDM with fine-tuning (LCA-DDM)

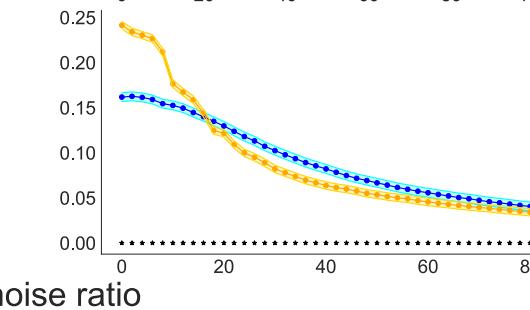
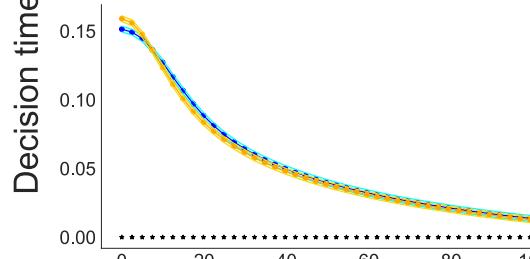
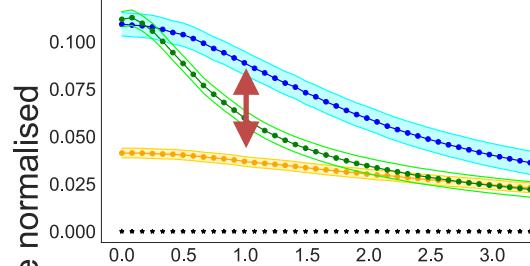
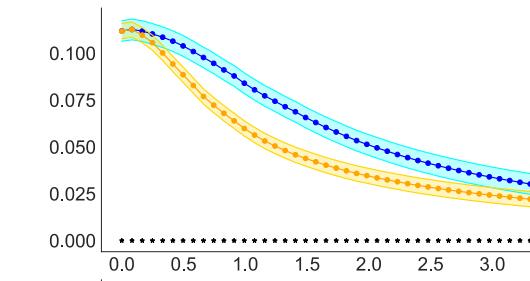
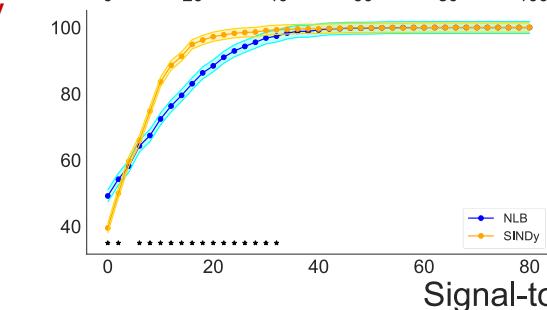
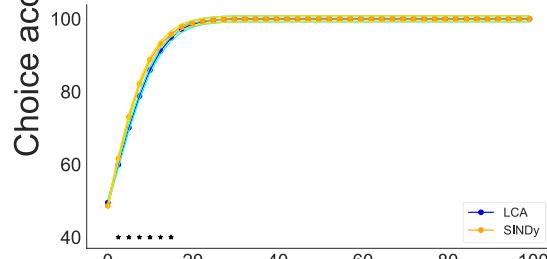
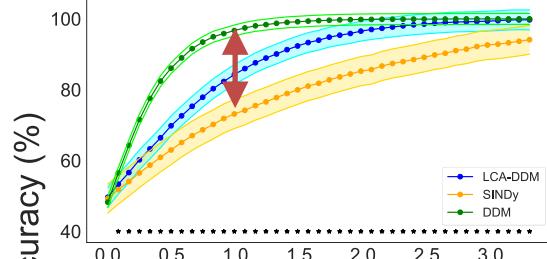
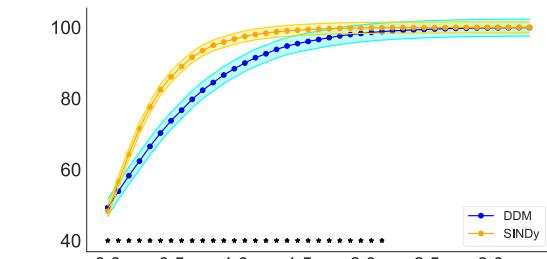
LCA model with saddle fixed point

Nonlinear bistable model (NLB)

Brendan Lenfesty



Using machine learning to uncover dynamical equations of low-dimensional neural trajectory (2-choice tasks)



Decision models

Drift-diffusion model (DDM)

Leaky competing accumulator (LCA) model approx.
DDM with fine-tuning (LCA-DDM)

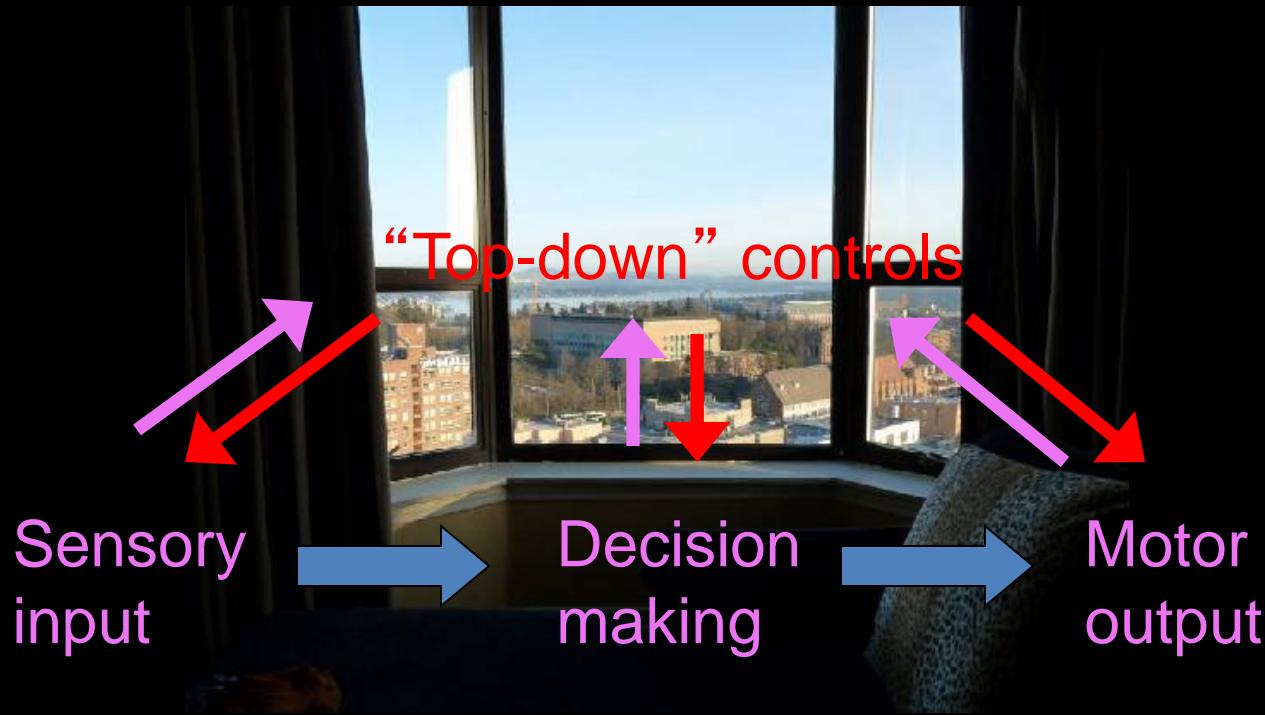
LCA model with saddle fixed point

Nonlinear bistable model (NLB)

Brendan Lenfesty



Perceptual decision making: *Window to higher cognition*



Rule-based decisions and flexible task-switching

Classic Stroop task and task switching: Word reading or colour naming.

BLUE

GREEN

YELLOW

PINK

RED

ORANGE

GREY

BLACK

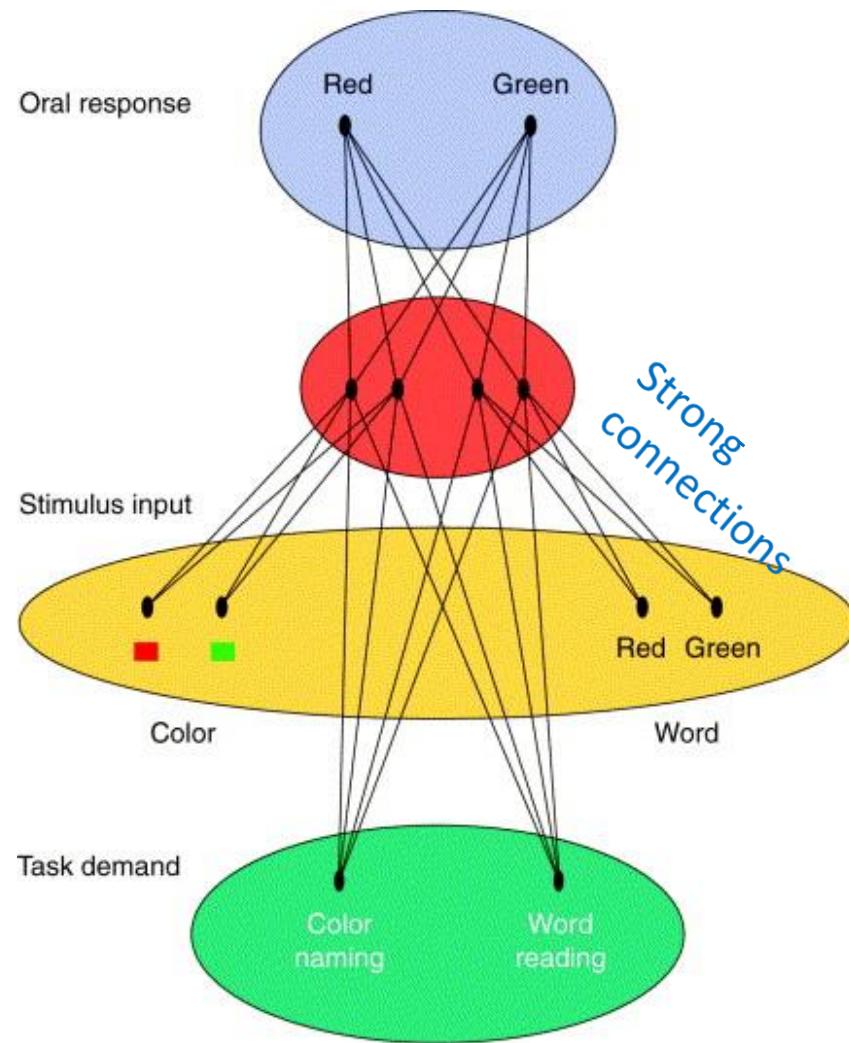
PURPLE

TAN

WHITE

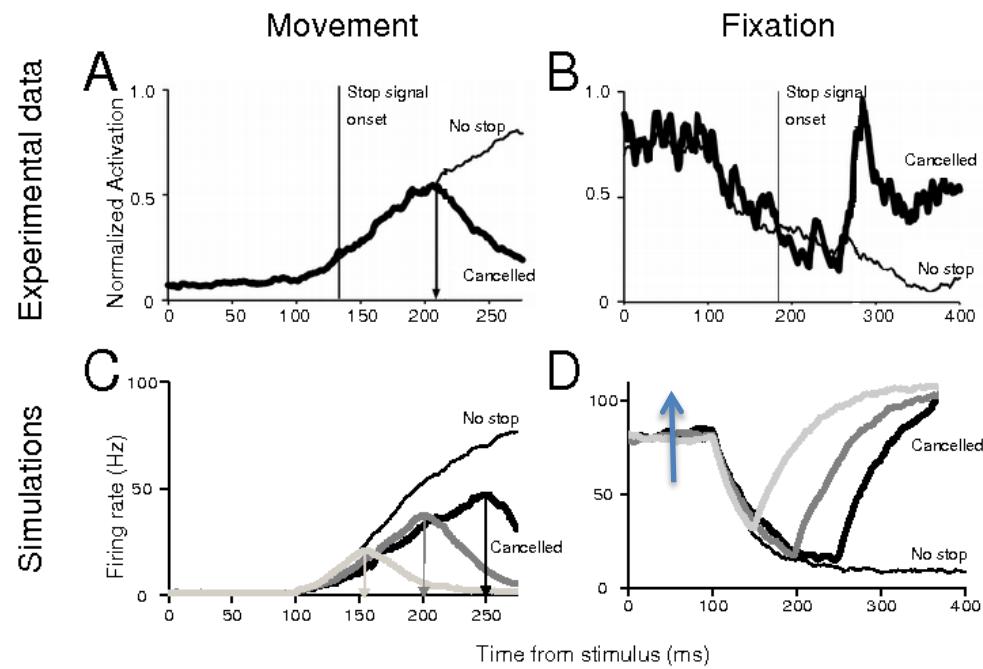
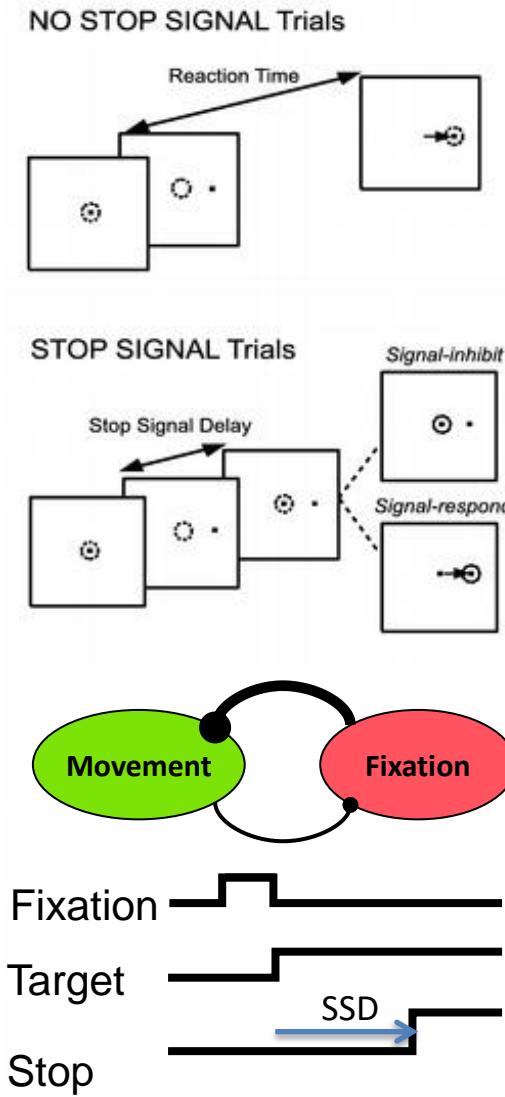
BROWN

Guided activation theory: Network model with cognitive control for Stroop task



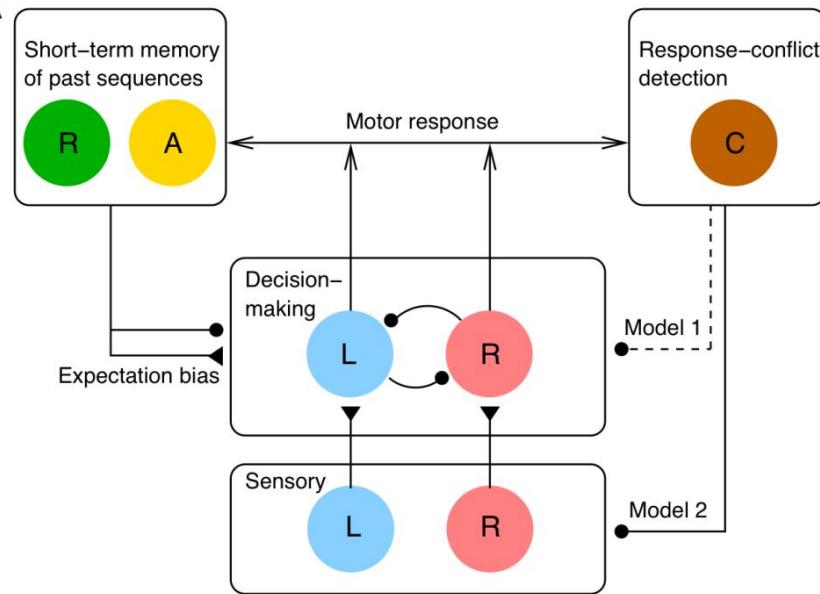
Cohen & Huston (1994)
Colin & MacDonald (2000)
Ito et al. (2022)

Proactive inhibition of an impending decision

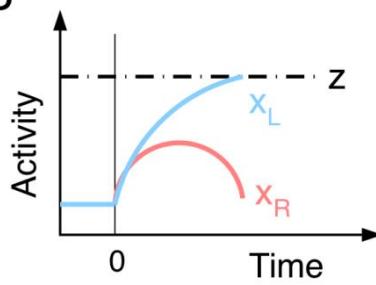


Sequential effects in simple decisions

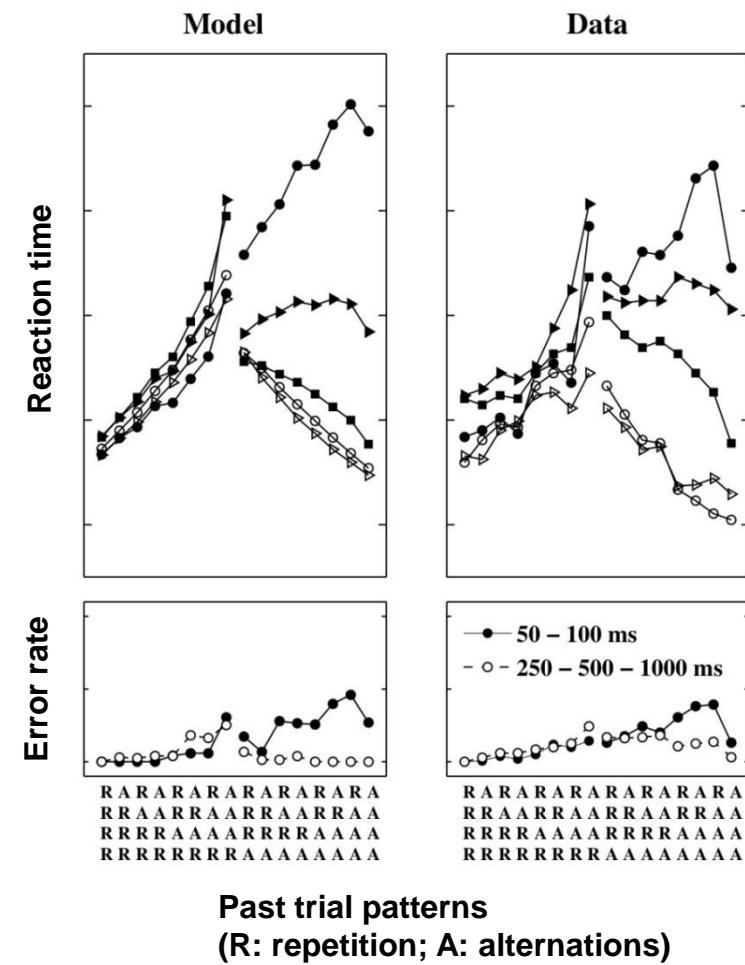
A

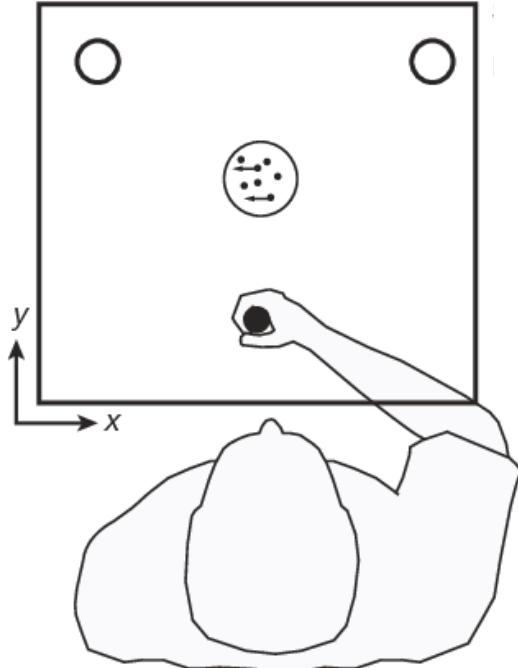


B



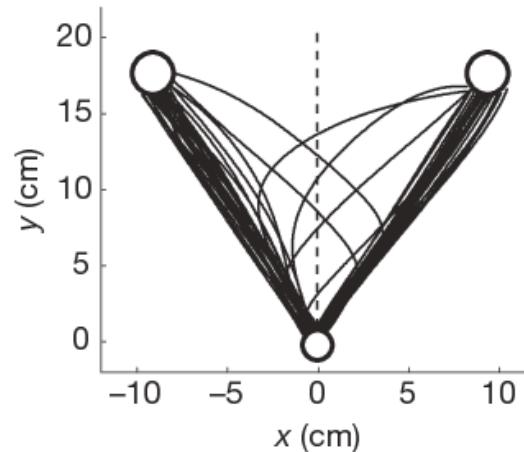
Modified LCA model
(2 biases in drift rate +
post-decision decay)



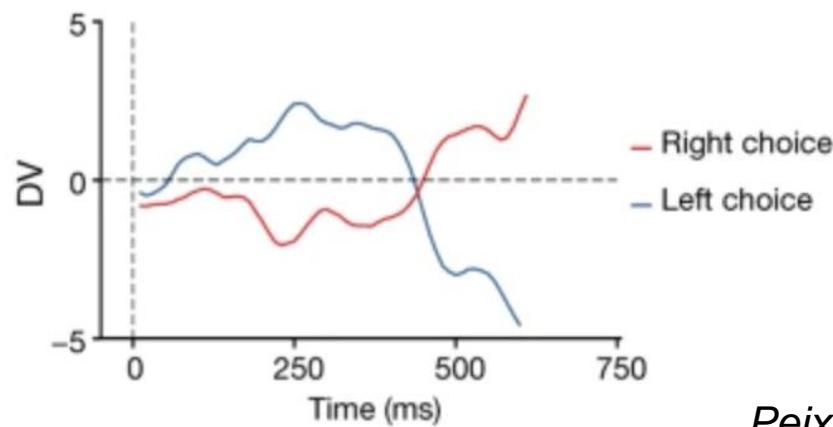


Change-of-mind in experiments

In addition to subjective confidence rating or reaction time

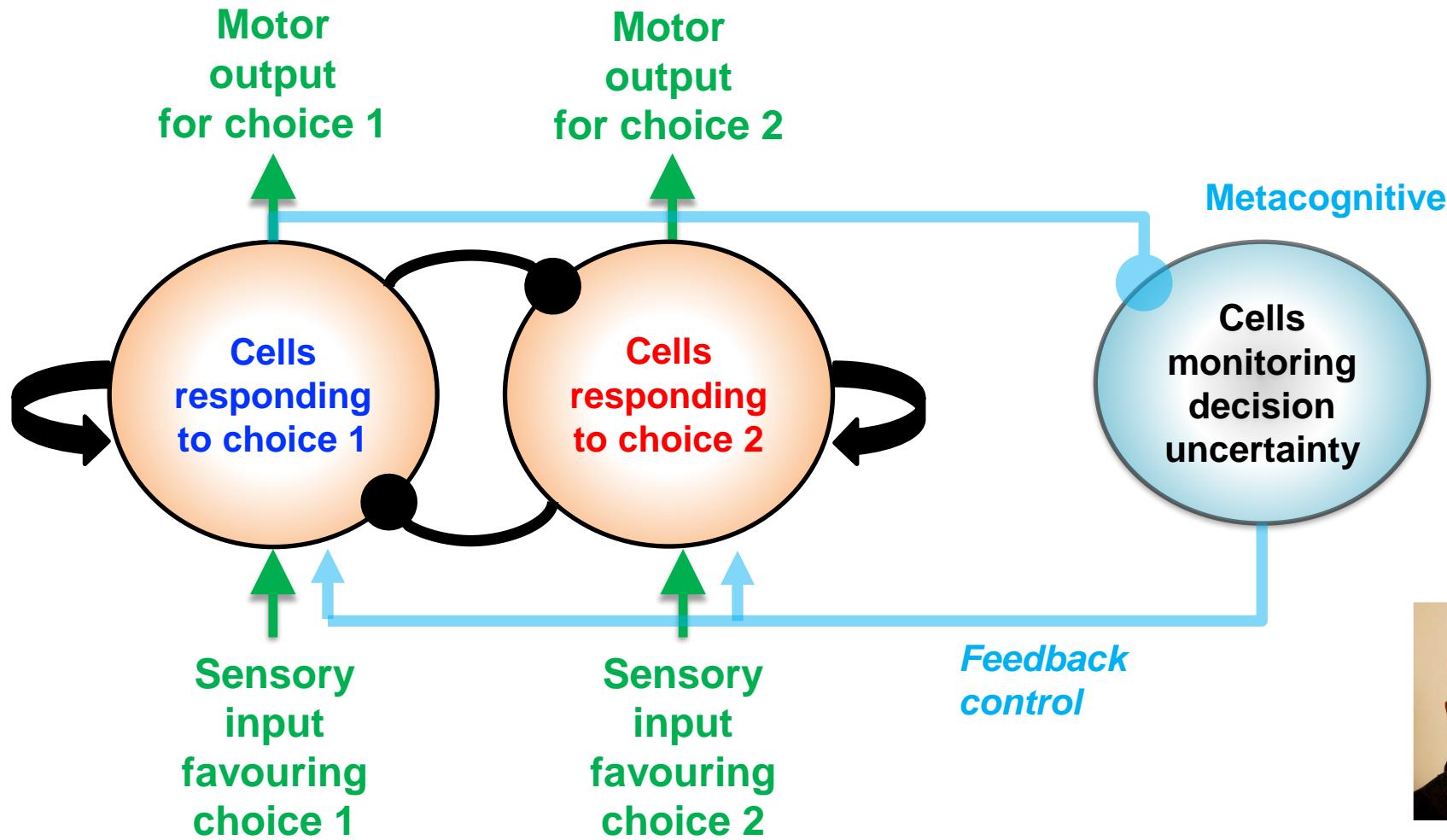


Resulaj, Kiani, Wolpert & Shadlen, Nat. (2009)



Peixoto et al., Nat. (2021)

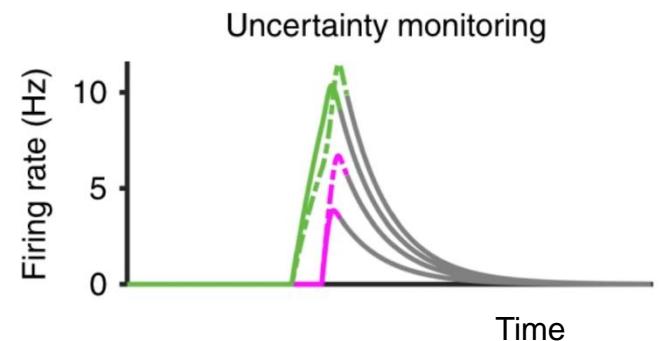
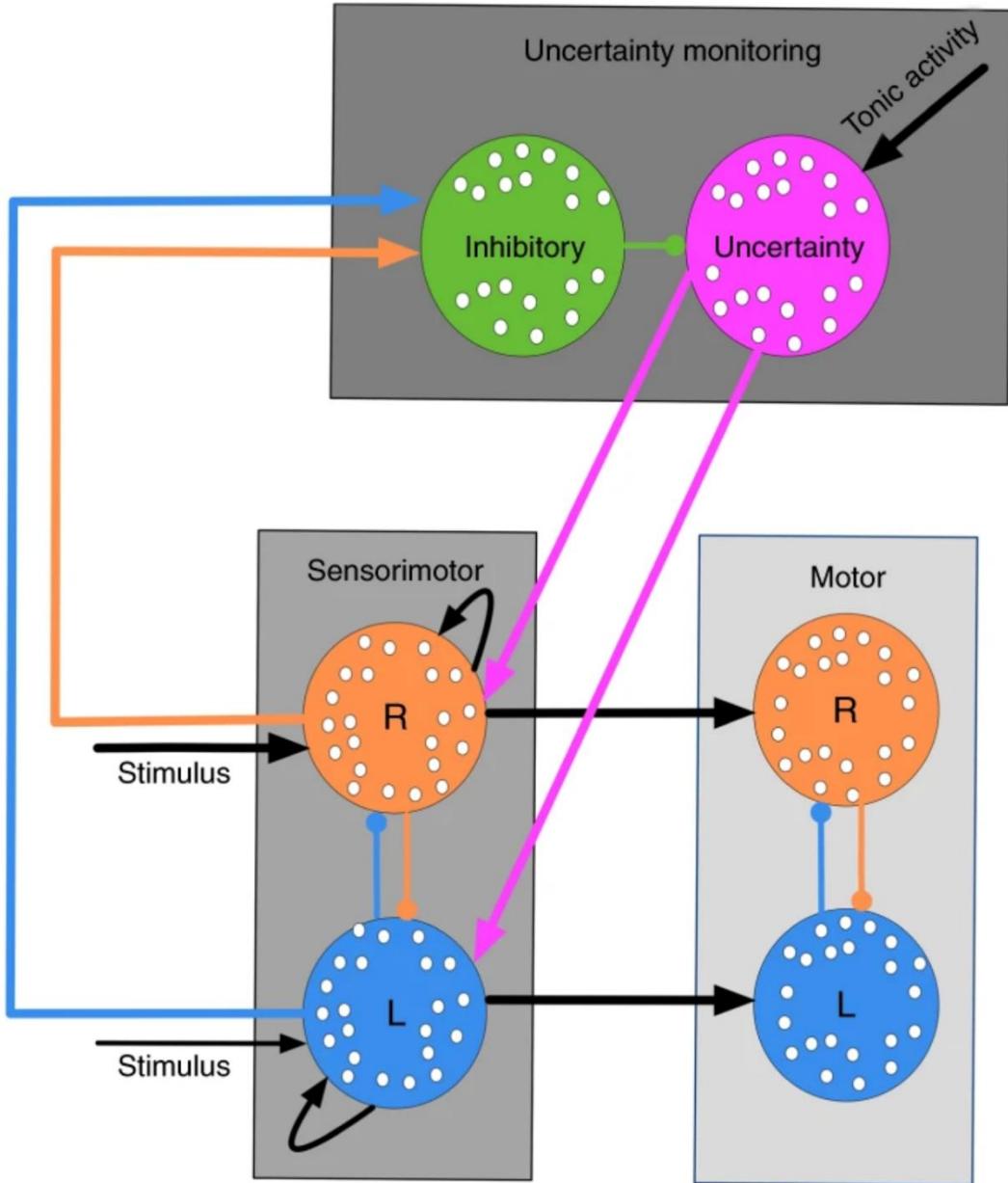
Real-time monitoring of decision uncertainty (“awareness”) and change-of-mind



Nadim Atiya

Atiya, Rano, Prasad & Wong-Lin, *Nat. Commun.* (2019)

Atiya, Zgonnikov, O'Hora, Schoemann, Scherbaum & Wong-Lin, *PLoS Comput. Biol.* (2020)

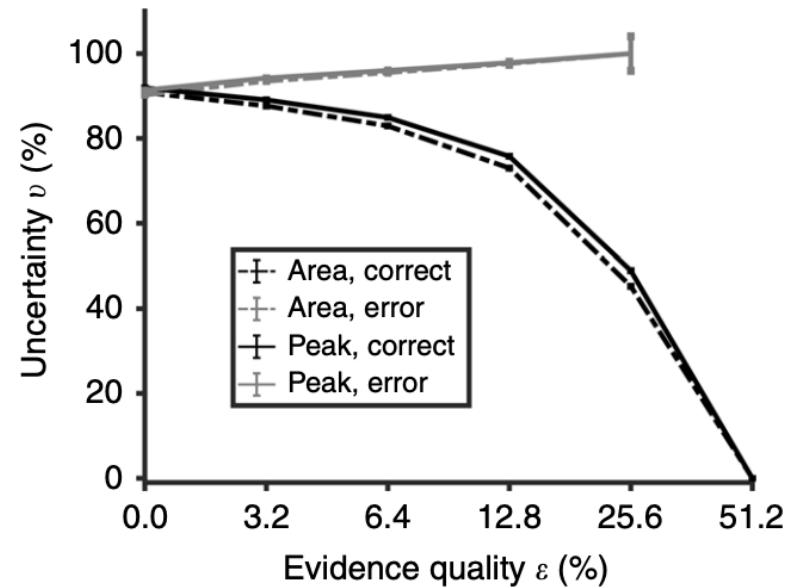
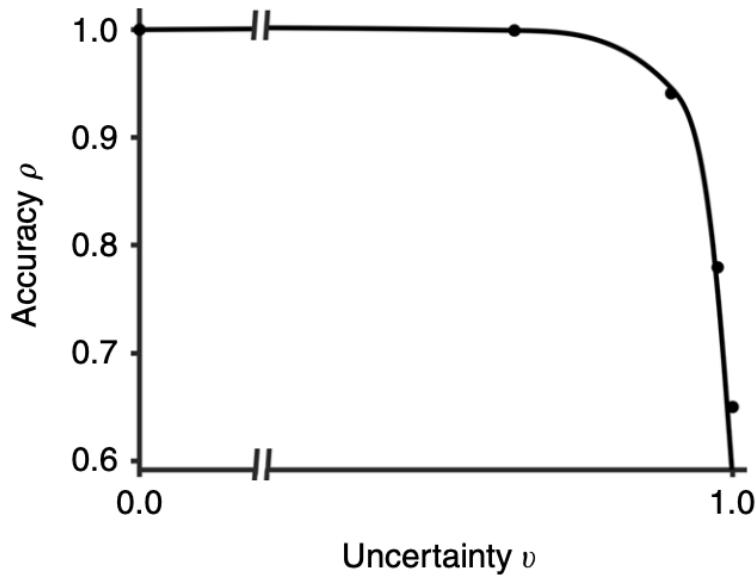


*Dashed: Lower signal
Bold: Higher signal*

Atiya, Rano, Prasad & Wong-Lin,
Nat. Commun. (2019)

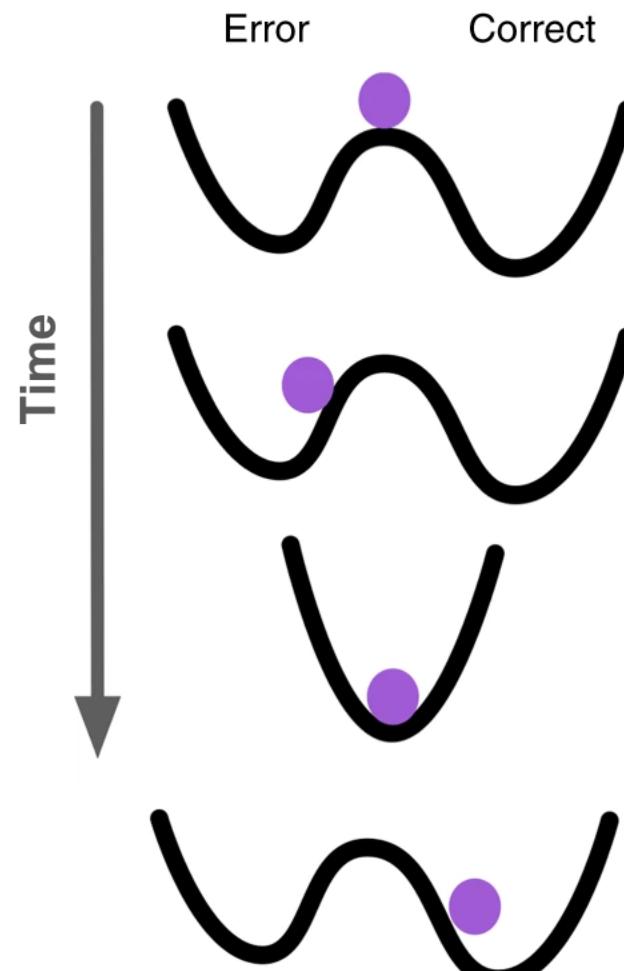
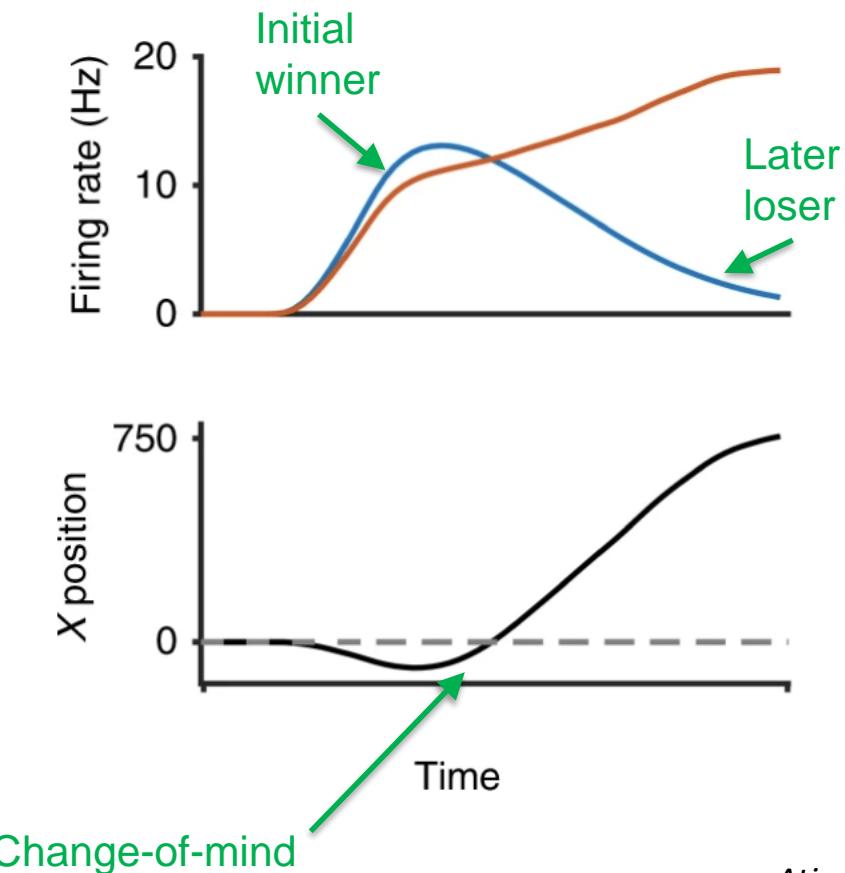
Model captures key characteristics of decision confidence/uncertainty

“<” or “X-shaped”

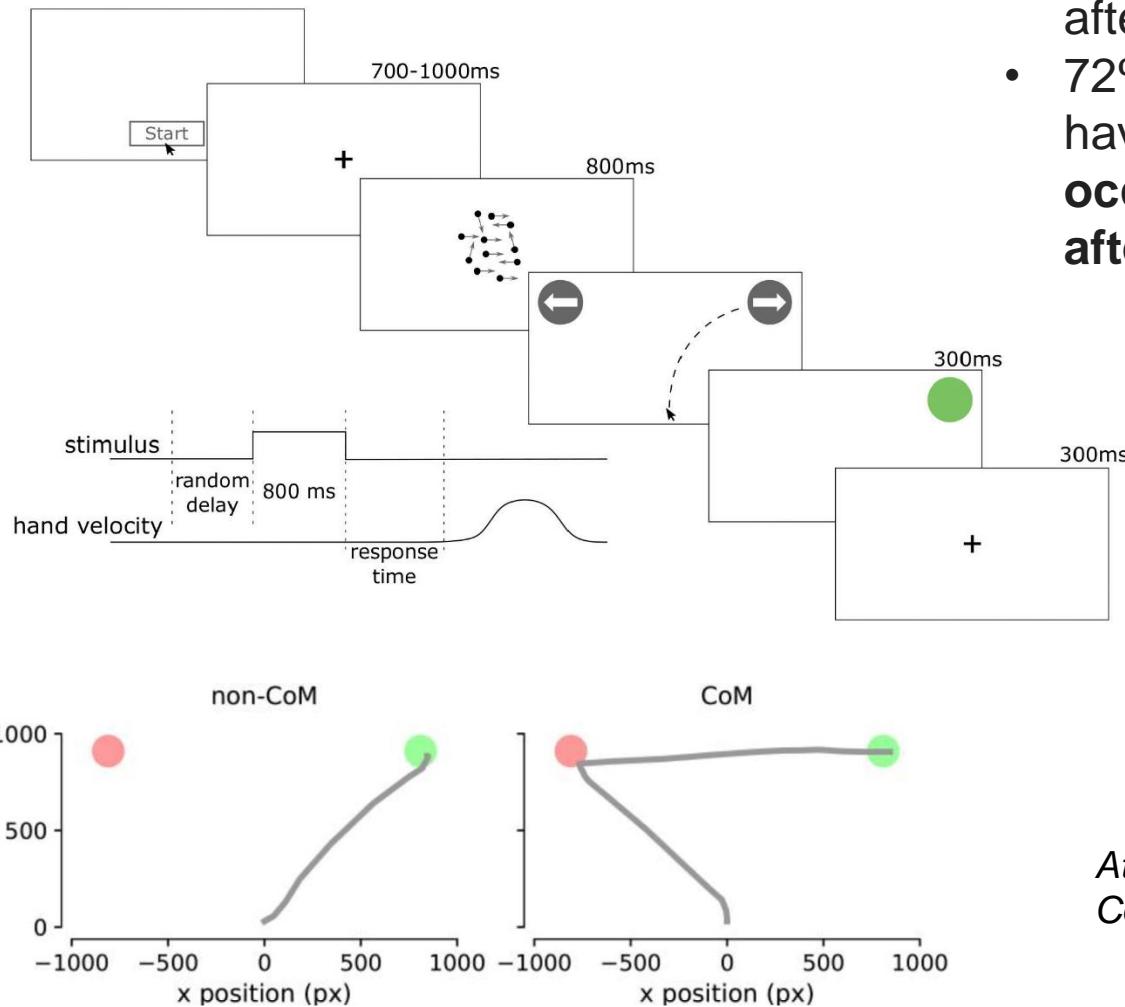


Atiya, Rano, Prasad & Wong-Lin, *Nat. Commun.* (2019)

Model provides an explanation for change-of-mind



Model prediction: Changes-of-mind can occur in the absence of additional evidence after initial decision



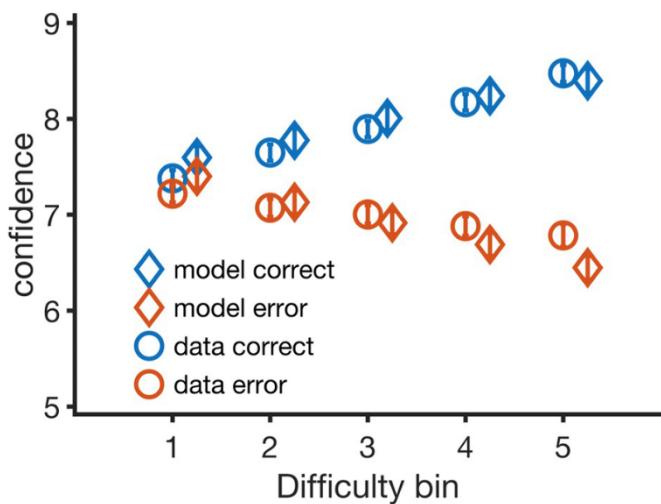
- Participants respond only after stimulus offset
- 72% change-of-mind trials have **decision reversal occurring later than 450ms after stimulus offset**

Atiya, Zgonnikov et al., PLoS
Comput. Biol. (2020)

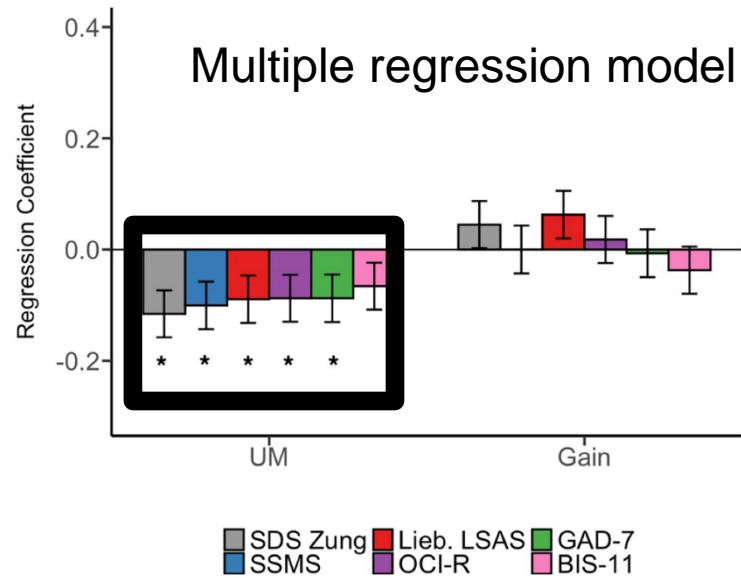
Model accounts for data in separate study:

Weaker model uncertainty monitoring connectivity associated with self-reported mental health symptoms

A



B



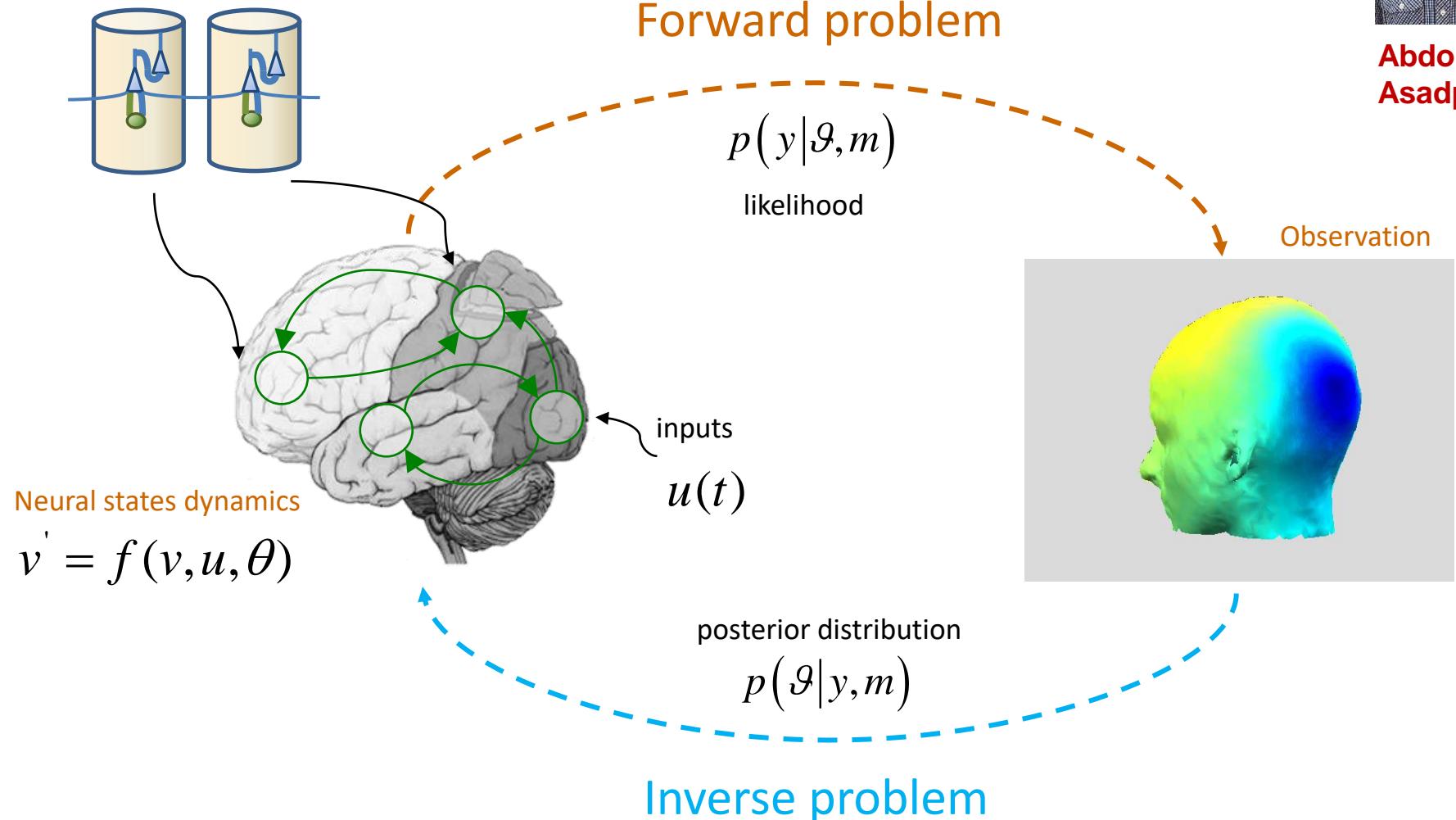
Atiya, Huys, Dolan & Fleming, PLoS Comput. Biol. (2021)

Self-report measures of depression, schizotopy, social anxiety, obsessive & compulsive symptoms & generalised anxiety associated with weaker uncertainty modulation but not impulsivity. No association with stimulus gain parameter.

Dynamic causal modelling (DCM) to understand effective connectivity in human decision confidence



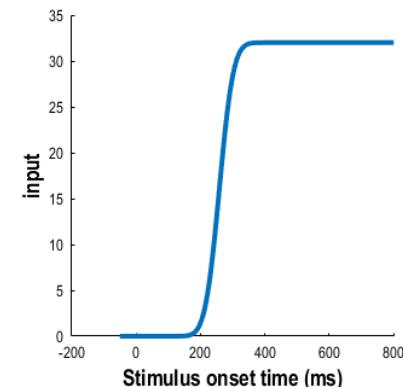
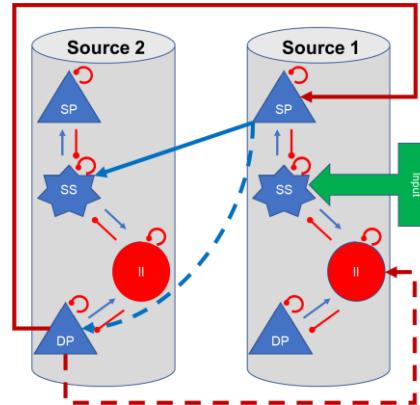
Abdoreza
Asadpour



Friston group

fMRI informed EEG-DCM reveals different active networks at source level

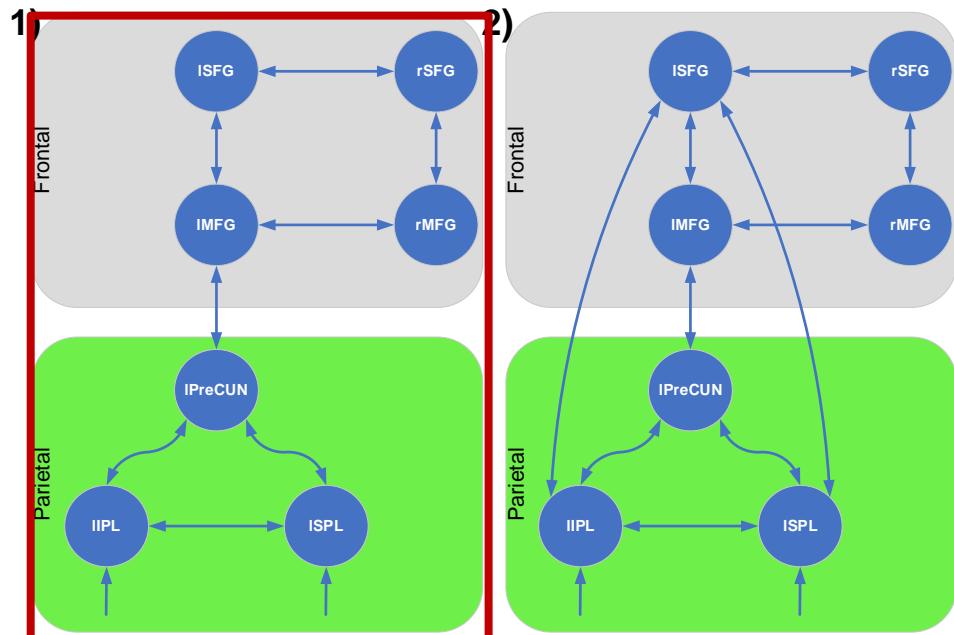
Common regions: left Middle Frontal Gyrus & left Precuneus



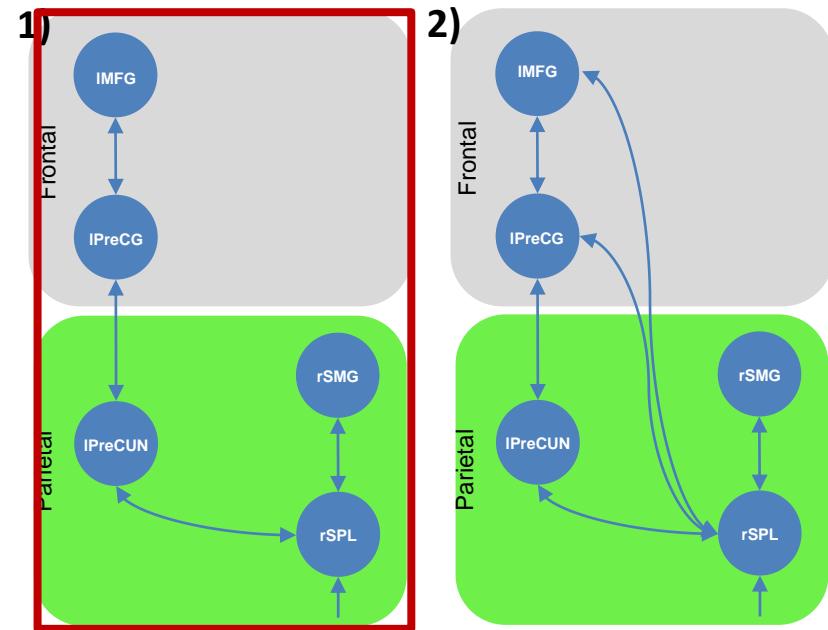
Canonical model

Model input

Low vs high confidence rating

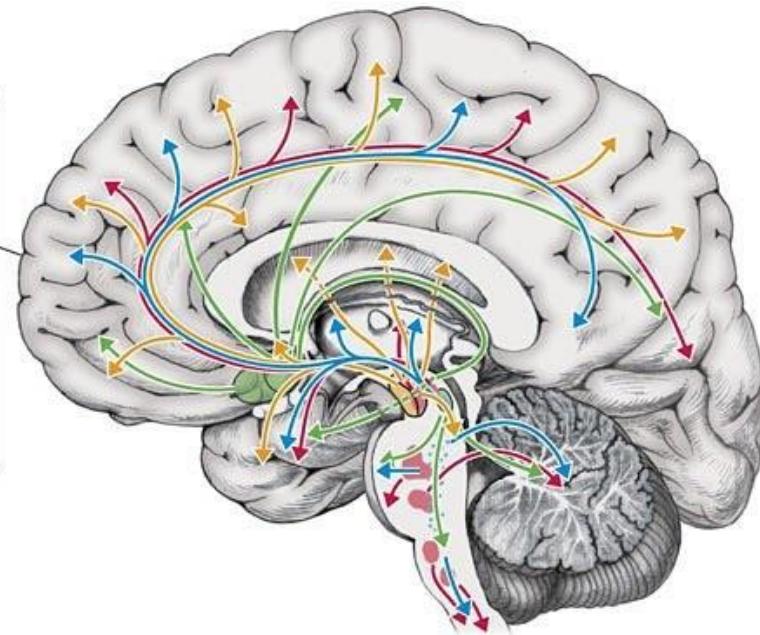


Slow vs fast response

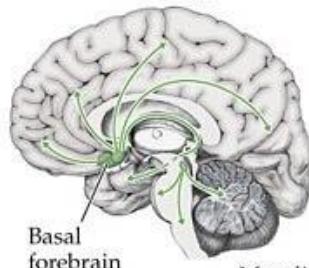


Chemical neuromodulation

In this midline view, the brain nuclei containing cell bodies of neurons that release four of the major transmitters are shown in different colors, as are the projections of their axons. Although the projections may overlap, each neurotransmitter projects to a distinct set of brain targets.

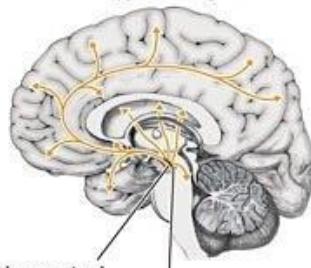


Cholinergic



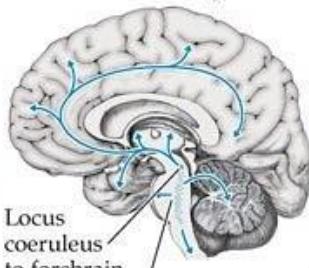
Basal forebrain

Dopaminergic



Mesolimbocortical pathway: ventral tegmental area (VTA) to nucleus accumbens and cortex

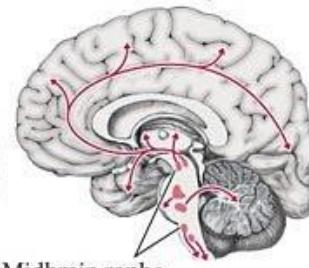
Noradrenergic



Locus coeruleus to forebrain

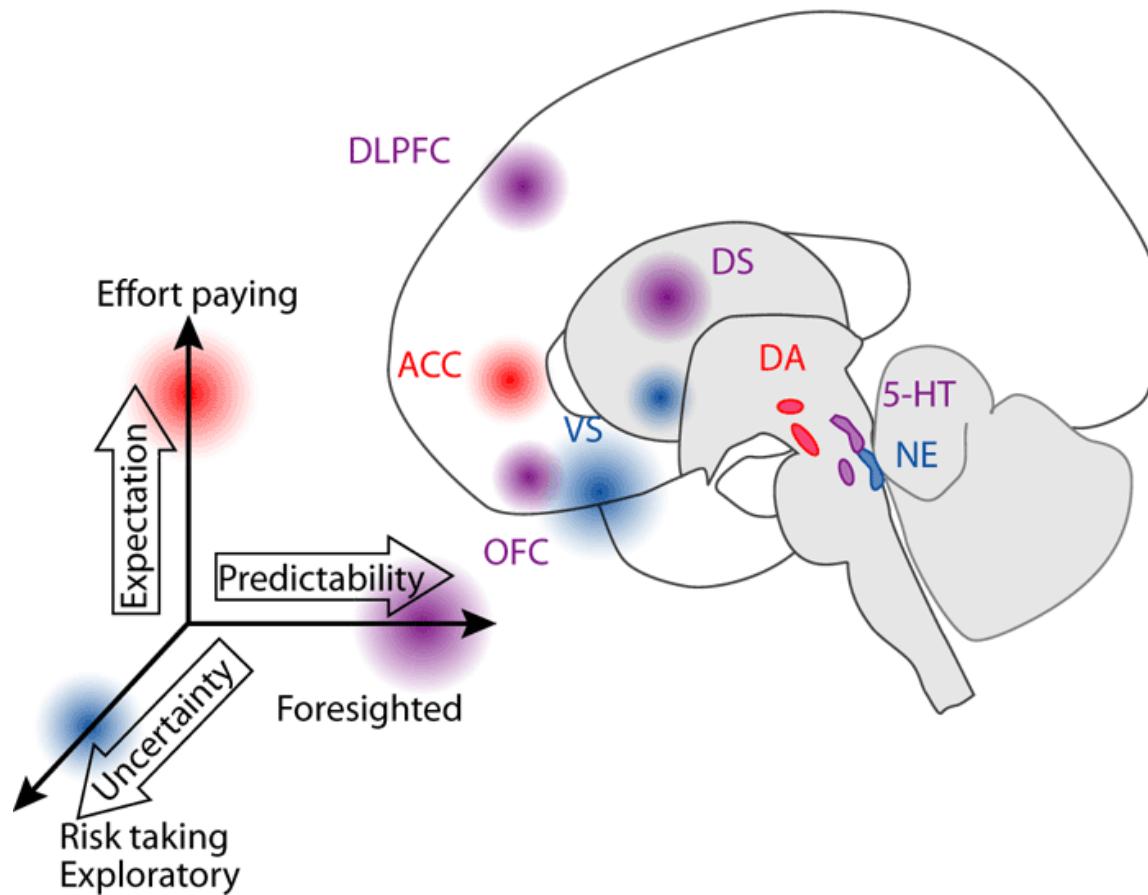
Lateral tegmental area to brainstem and spinal cord

Serotonergic



Midbrain raphe nuclei to forebrain; brainstem raphe nuclei to spinal cord.

Theories of chemical neuromodulation on decision-making

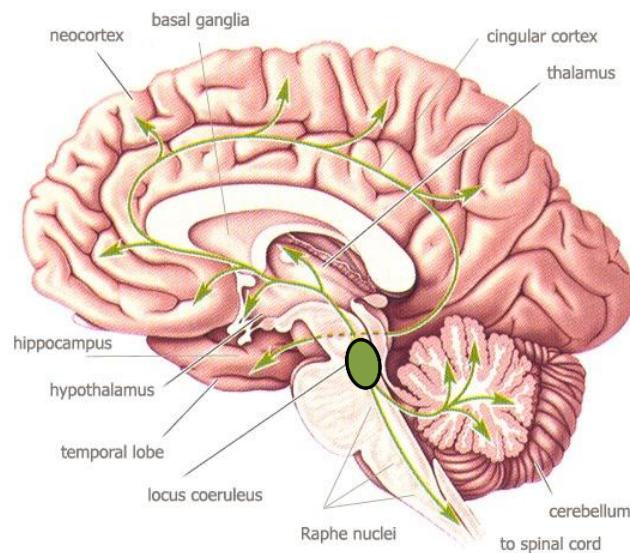


Kenji Doya, Modulators of decision making, Nat. Neurosci. (2008)

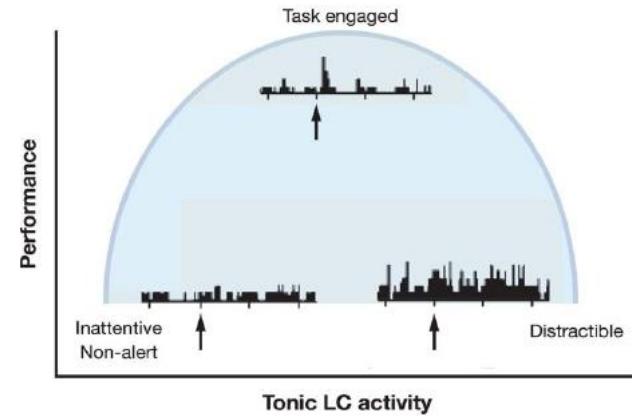
Norepinephrine / noradrenaline (NE / NA)

Involves in arousal, stress, “fight-or-flight” response, attention, etc

The locus coeruleus (LC) releases NE throughout the brain, modulating neural network.



Different LC/NE levels are correlated with different behaviours

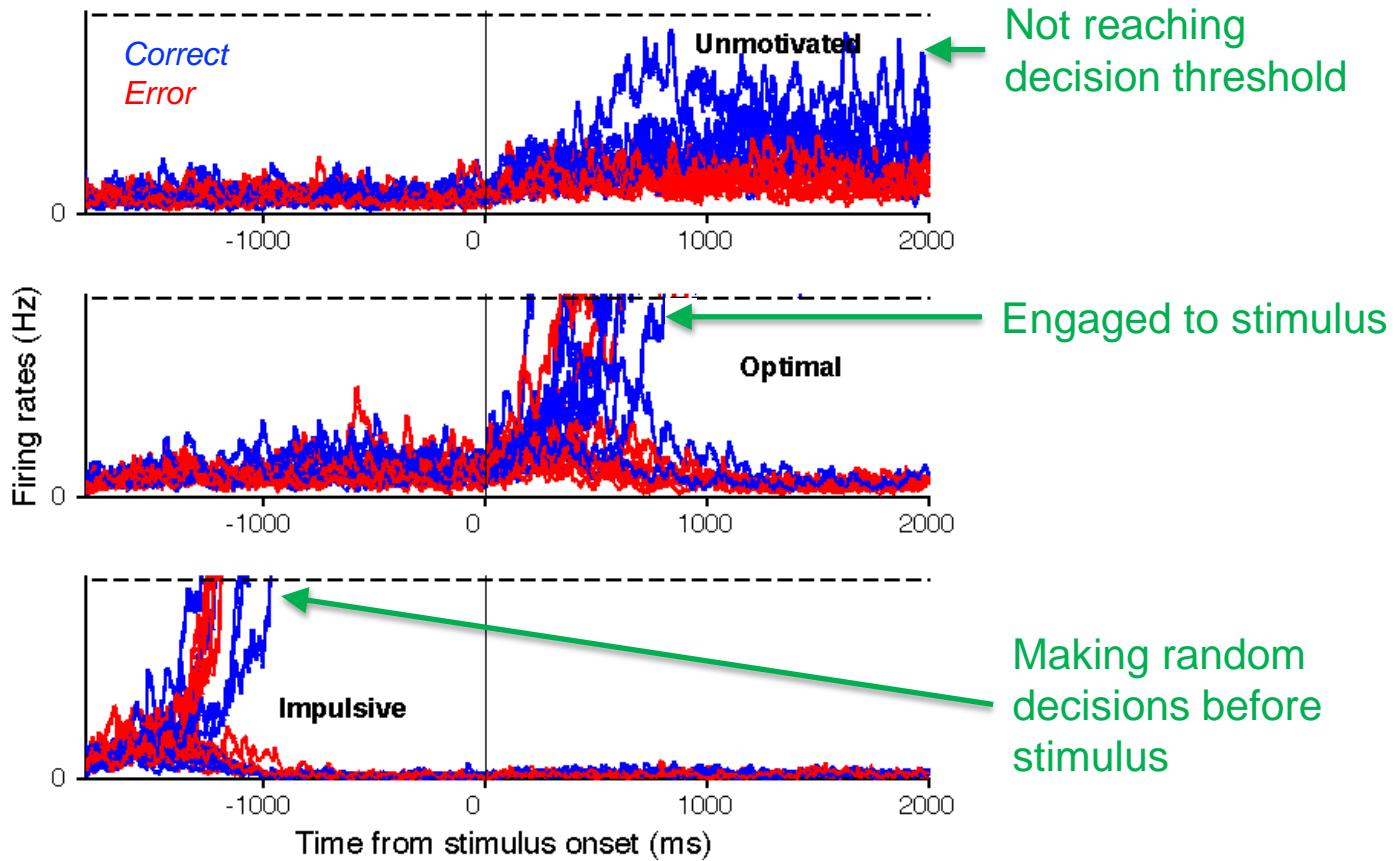


Aston-Jones et. al (1999); Aston-Jones and Cohen (2005)

Change in model decision dynamics under “chemical” modulation (of internal state)

10 sample trials with the same external stimulus but increasing neuronal excitability and synaptic efficacy.

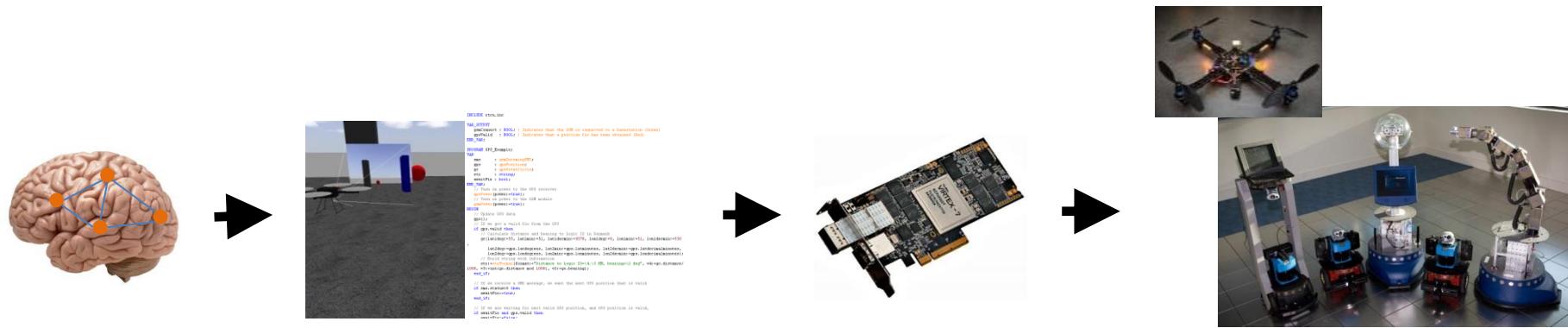
Increasing
LC / NE



Eckhoff, Wong-Lin & Holmes, J. Neurosci. (2009)

Eckhoff, Wong-Lin & Holmes, SIADS (2011)

Applications to intelligent technologies

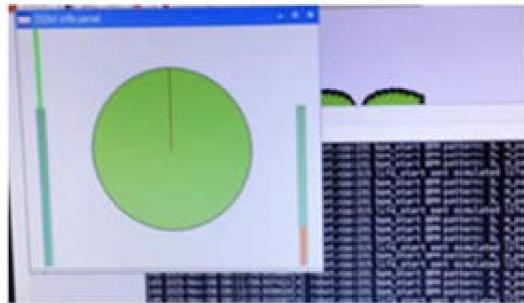


Computational cognitive neuroscience

Computational models, novel algorithms, & simulations

(Neuromorphic) Implementations in hardware for real-time applications

Sensor data fusion using drift-diffusion model implemented in a single computing chip



(A)



(B)



(C)



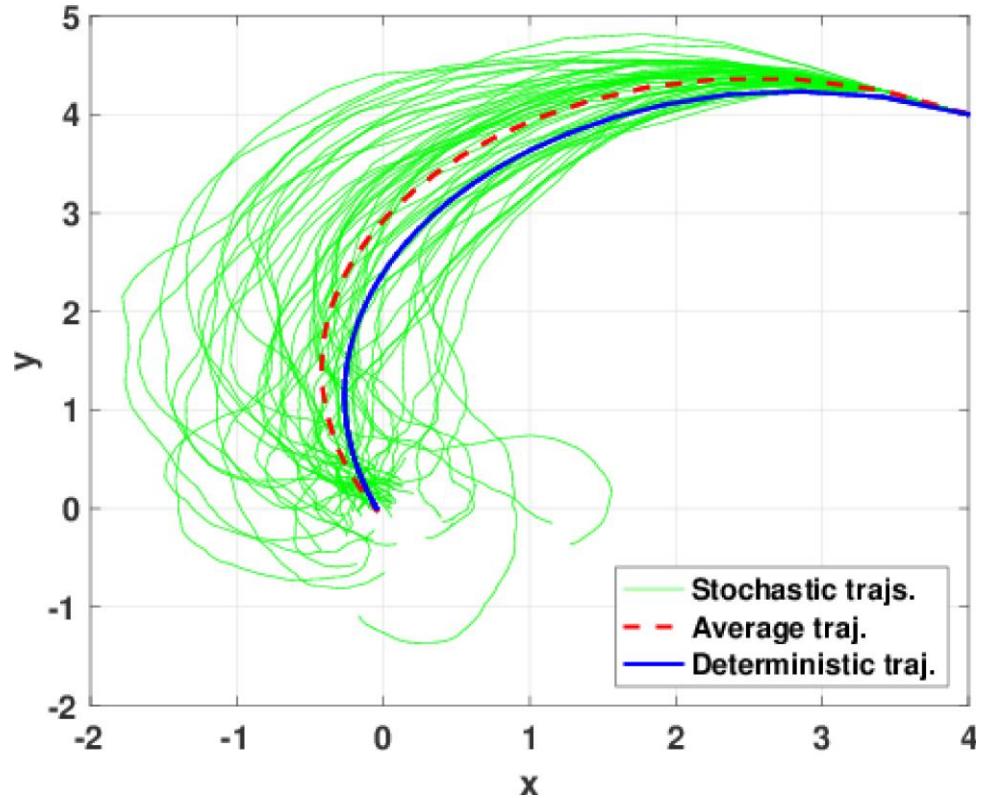
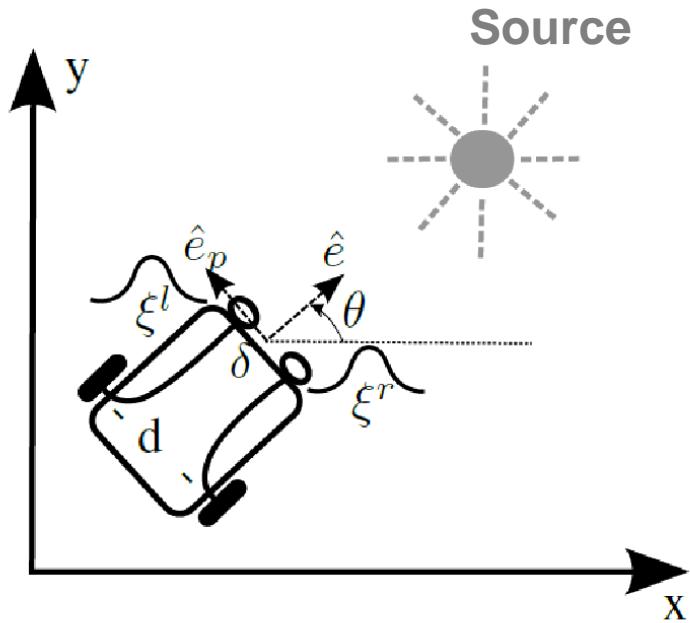
(D)



(F)

Yang, Wong-Lin, Raño & Lindsay (2017) IntelliSys.

First source-seeking mobile robotic model with noisy sensory information: as a drift-diffusion model process

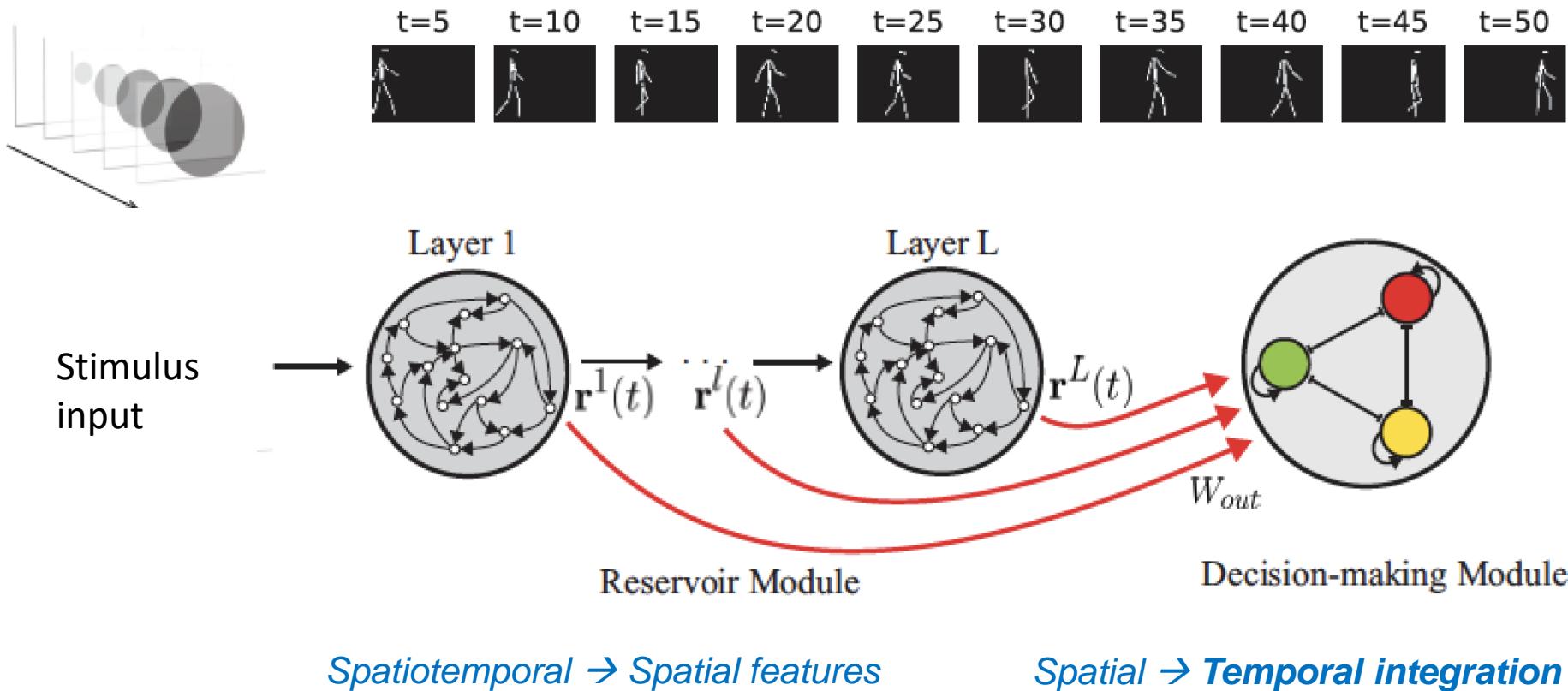


Rañó, Mehdi & Wong-Lin (2017) A drift-diffusion model of biological source seeking for mobile robots. ICRA.

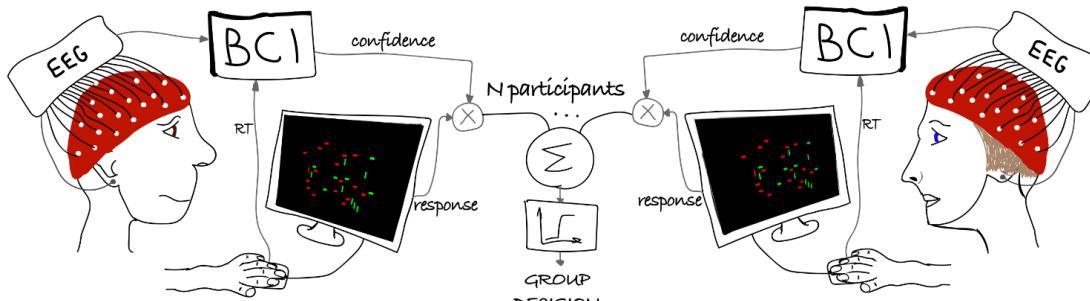
Information processing over space & time

Looming pattern detection

Individual's gait identification

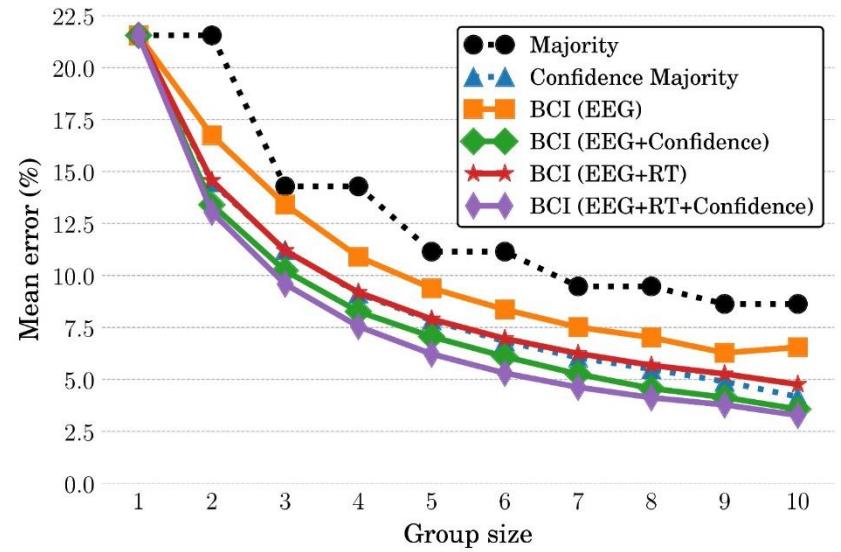
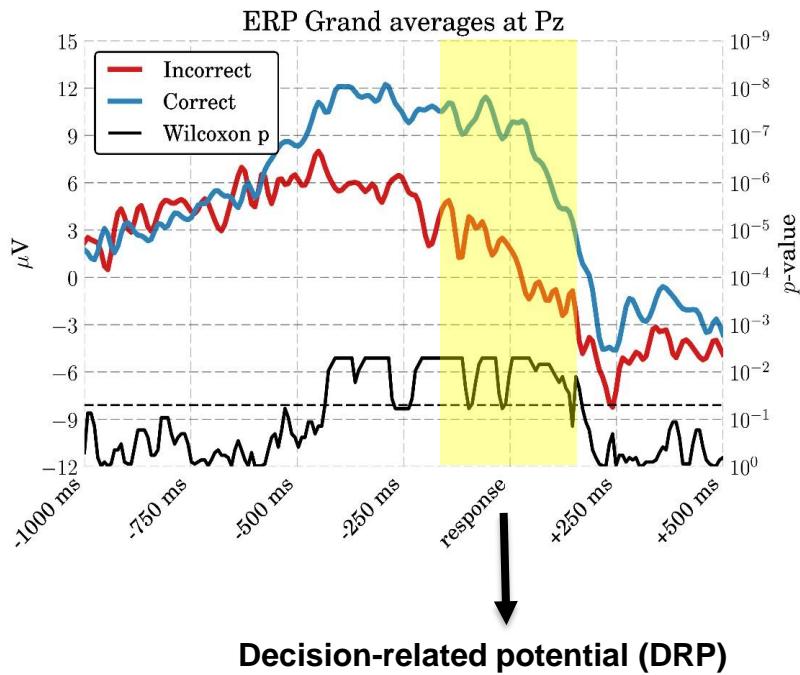


Neurotech: Collaborative BCI (cBCI) using decision confidence to augment group decision-making



cBCI Framework

Bhattacharyya et al. (2019; 2021)



Decision-related potential (DRP)

Summary

- Network dynamics as representation and tools for understanding brain functions
- Low-dimensional decision models can account for (and explain) key dynamics in neural data and choice behaviour
- More complex choice behaviour and dynamics can be built on simpler models, e.g. as cognitive control
- Artificial Intelligence (machine learning) largely based on making decisions (classification, regression and reinforcement learning) → opportunities for neuro-inspired decisions

... More general message on neural modelling

- Mathematical theory and computational modelling/simulation are important in understanding cognition & decision making, and even metacognition.
- A good theory/model:
 - (i) can account for empirical data;
 - (ii) can be sufficiently simple (concepts);
 - (iii) is generalisable to novel (testable) predictions.
- Understanding brain mechanisms can lead to or inspire novel computational algorithms and intelligent technologies.

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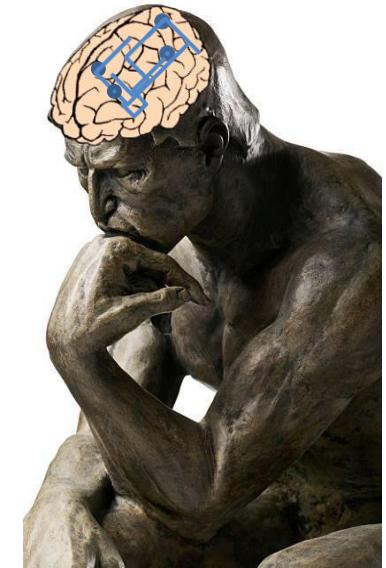
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