

# Modelling the dynamics of decision making

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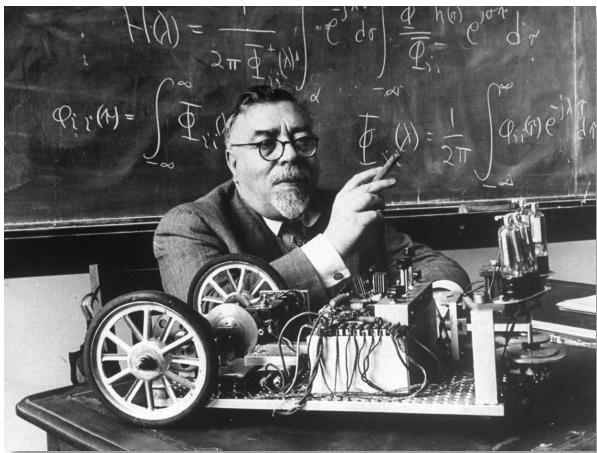
## **Content:**

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

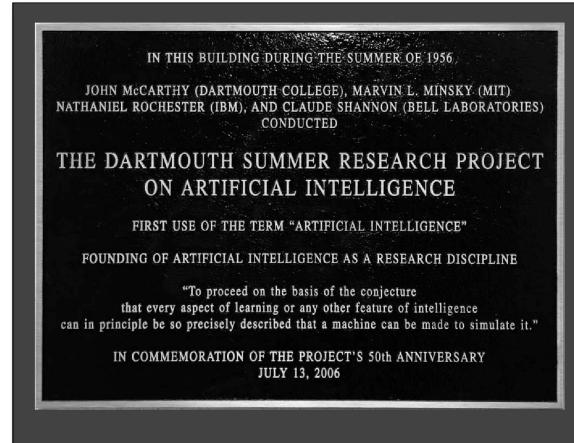
# Computational view of cognition

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

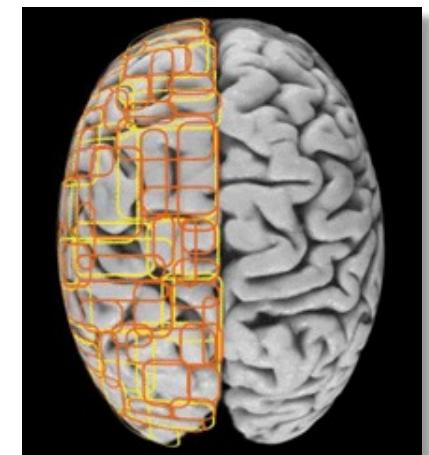
Computational Neuroscience (1980's)



Mathematician Norbert Wiener  
(with his cybernetic moth-bedbug)



Artificial neural networks  
& learning algorithms



Biologically based  
computational &  
mathematical models

# 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

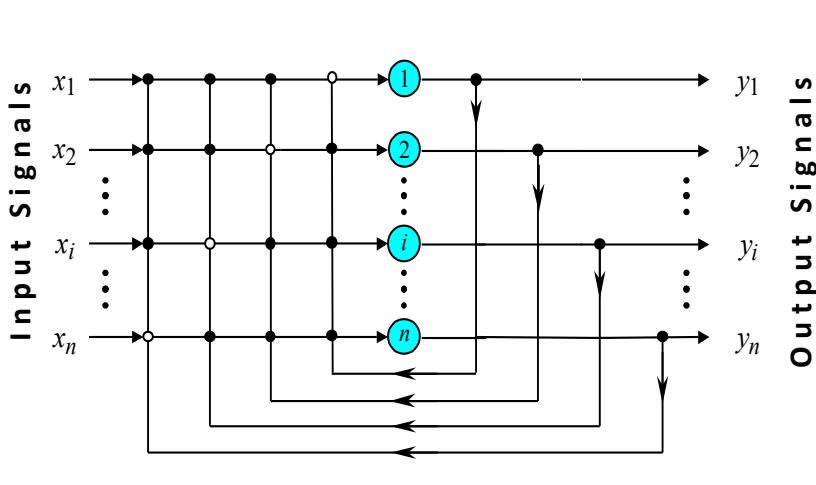
Are there ways to theoretically analyse and conceptually understand neural networks?

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

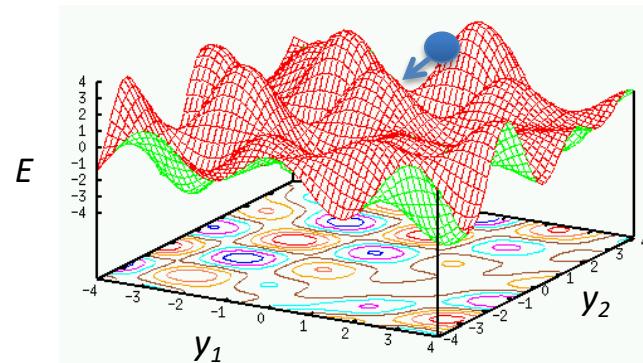
Focus: Network dynamics using the tools in dynamical systems theory (in physics and mathematics), beginning with simple network models

\*Note: There are other theoretical approaches to model cognitive functions

# Recall Hopfield network model (for memory)



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



Discretized updating of states ( $p^{\text{th}}$  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  $y_{p+1} = G(y_p)$

(1<sup>st</sup> 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\*:

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

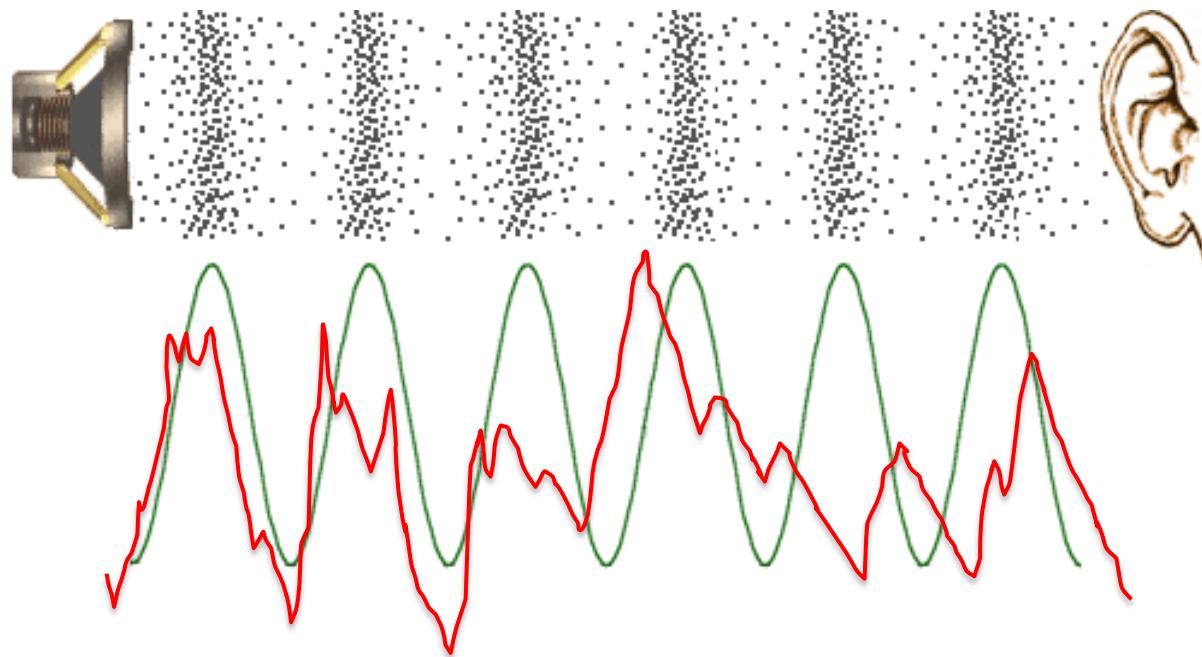
*Differential equations:*  $dx/dt = F(x, \pi, t)$  for continuous dynamics

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.

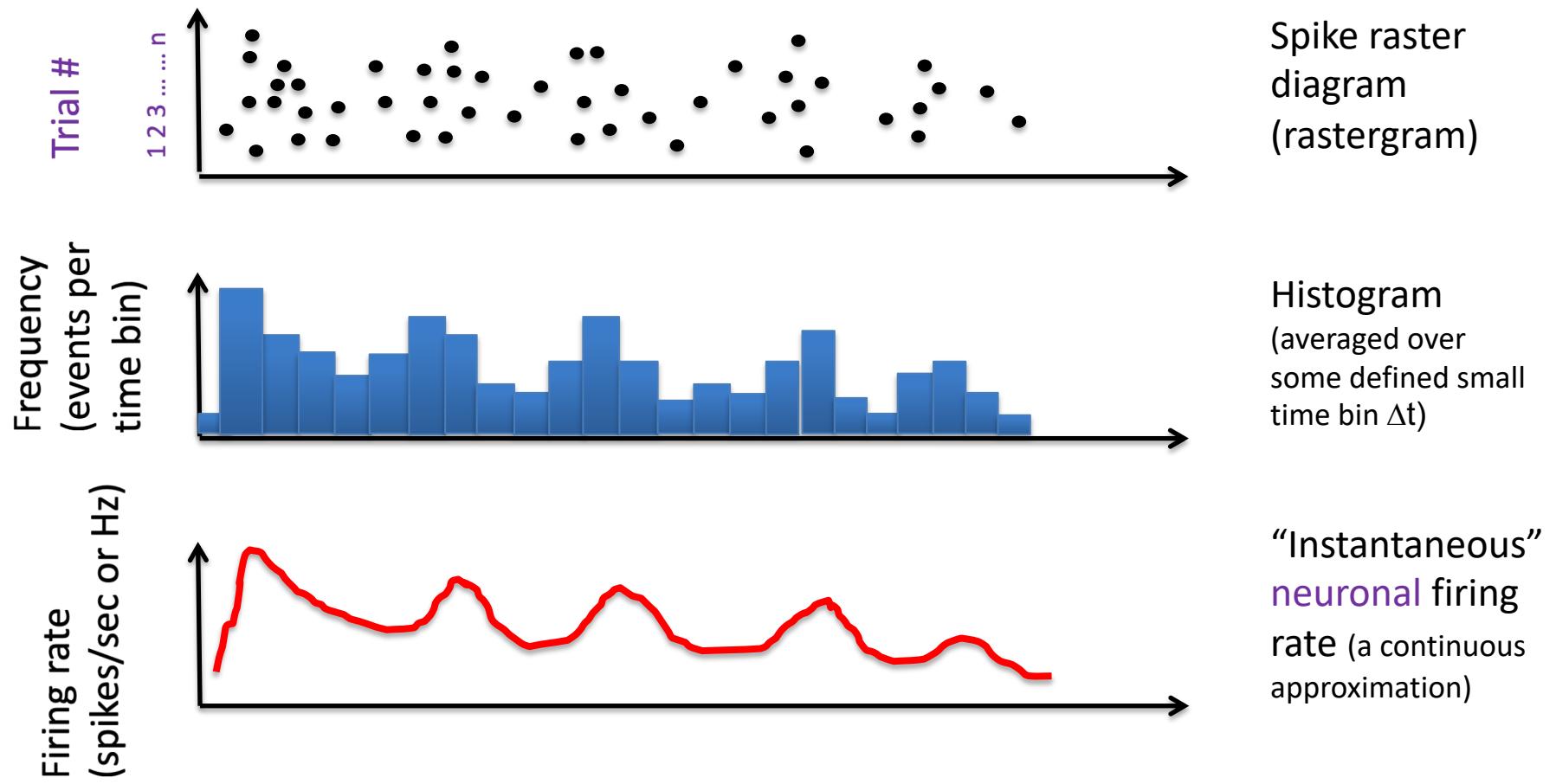
Wait a minute... But we've previously learned that the activity of neurons come in the form of discrete action potentials or spikes. How can we relate that to a continuous stream of activities of a system of neurons, as in the Hopfield model?

# Transforming from discretized to continuous activity

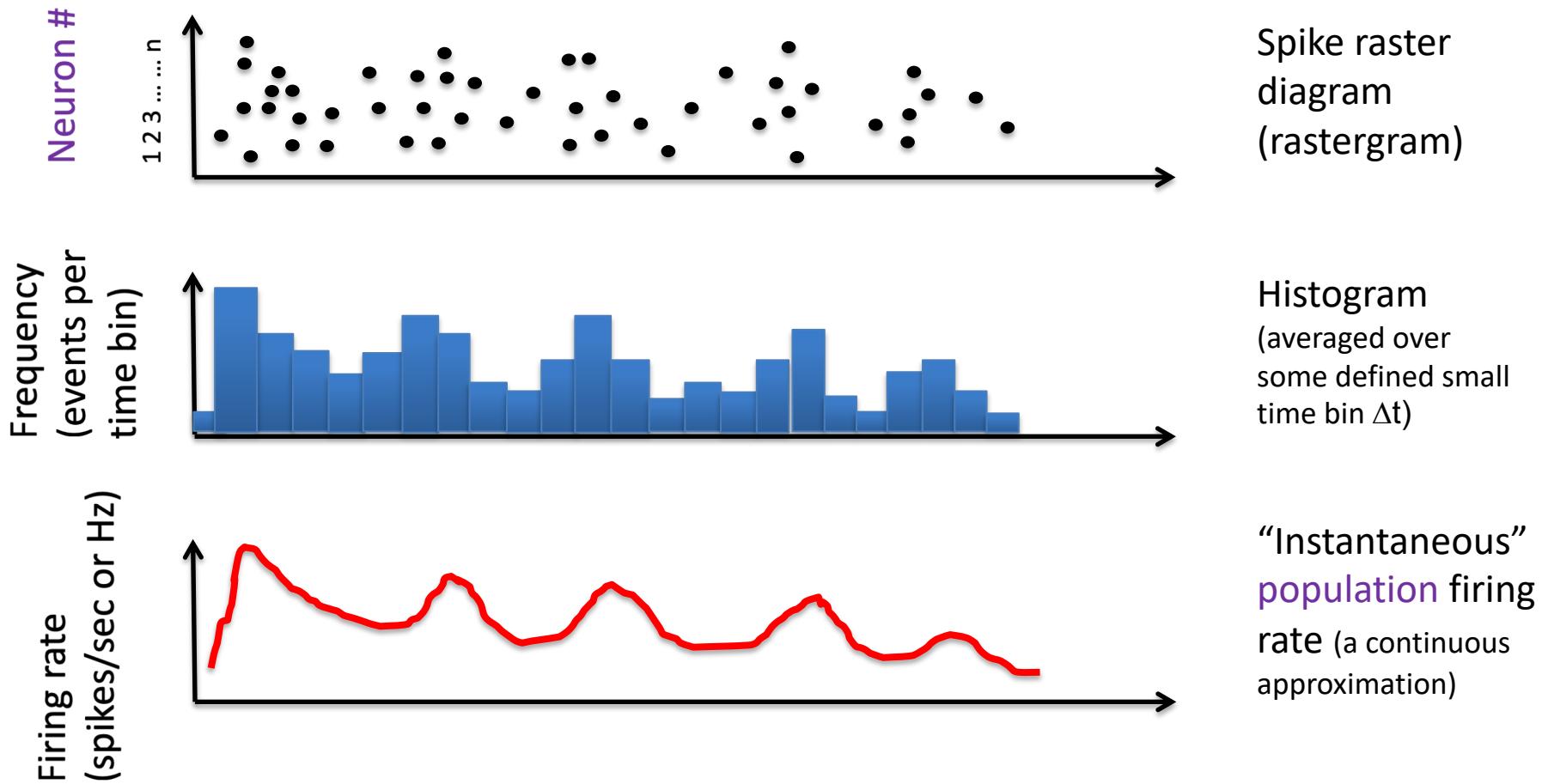


An analogy: from air particle movement to (approximate) continuous sound wave

# 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

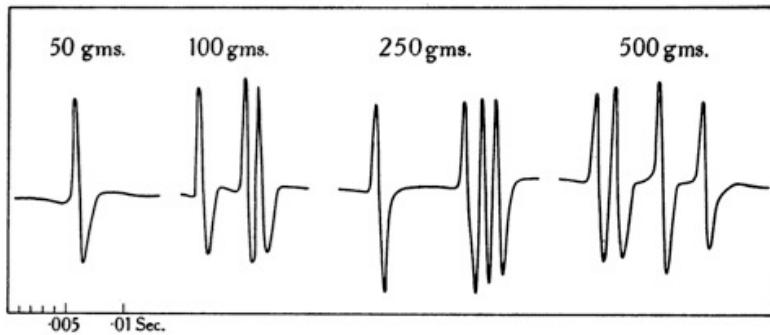


Fig. 5. Analysis of electrometer records, *Exp. 2*, showing that the size of individual impulses does not vary with the stimulus.

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

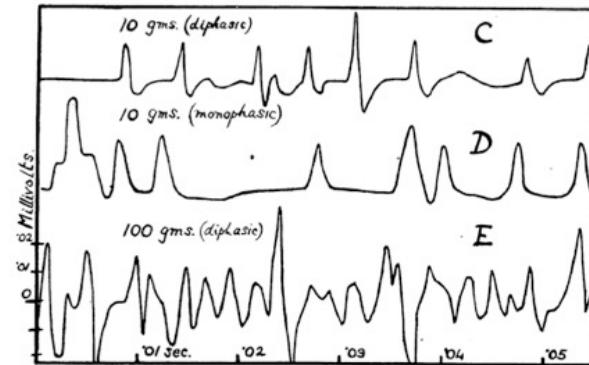


Fig. 4. Analysis of records in Fig. 3 C, D and E.

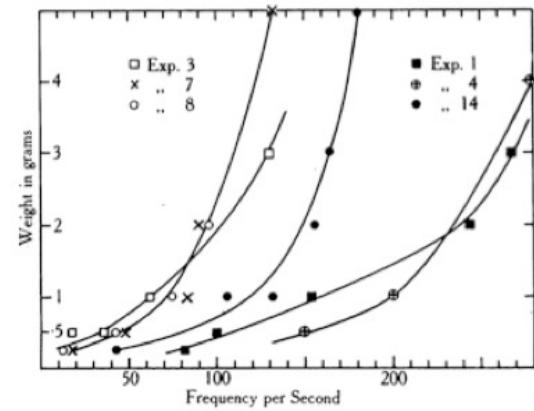


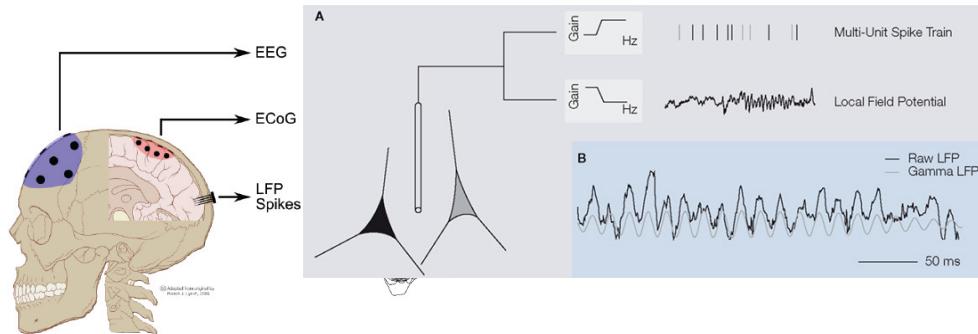
Fig. 9. Relation between frequency and strength of stimulus for various intact muscles.

A.D. Adrian (1926)  
*J. Physiol. (Lond.)*, 61: 49-72.

# Neural recordings

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

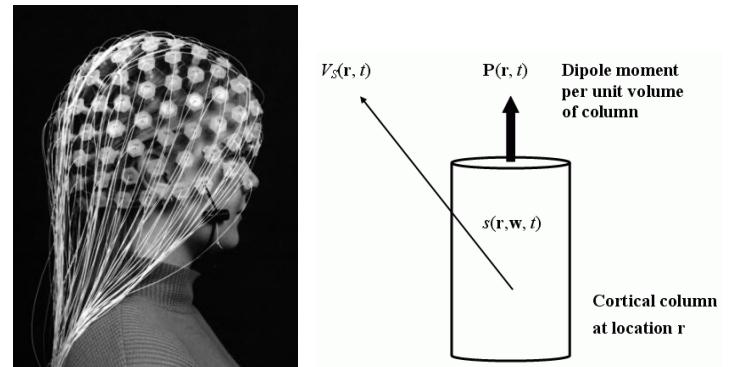
[http://www.scholarpedia.org/article/Local\\_field\\_potential](http://www.scholarpedia.org/article/Local_field_potential)



- Electrical signals from electroencephalogram (EEG)

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

(Or magnetic signals with MEG)

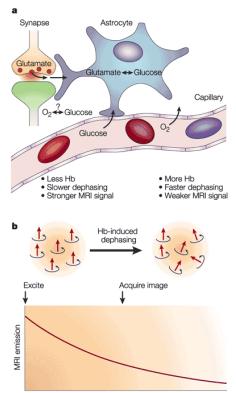
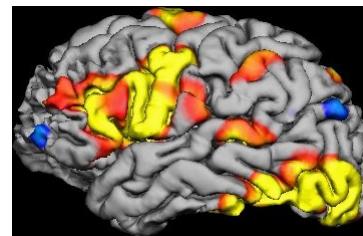


- Functional MRI (fMRI) BOLD signals

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

BOLD: Blood oxygen level dependent

[http://en.wikipedia.org/wiki/Blood-oxygen-level\\_dependent](http://en.wikipedia.org/wiki/Blood-oxygen-level_dependent)



- Computationally, firing-rate models are more efficient – do not have to simulate every single neuronal spiking. Just treat activity as continuous function and averaged over population of neurons.
- Firing-rate network models are more analytically tractable, and hence more conducive for analytical understanding of network behaviour, shedding deeper insights on cognitive processes.
- Firing-rate type models are used in most artificial neural networks including deep learning.

# Firing-rate (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*

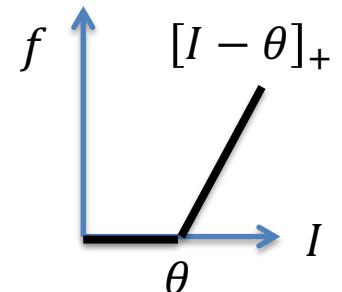
Sometimes, the mean membrane potential  $\langle V_i \rangle$  is used instead of current  $I_i$ .

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,

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



For  $I_i > \theta_i$ ,

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

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.

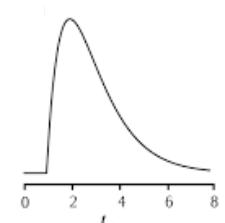
# Heuristic derivations (multiple timescale system)

Suppose a simple (passive) neuronal membrane potential can be described by:

$$\tau_m \frac{dV}{dt} = -V + R_m I(t)$$

and if the afferent current is described by a sum of 2 exponentials,

$$I(t) = \exp(-t/\tau_d) - \exp(-t/\tau_r)$$



Assuming the initial membrane potential is zero, i.e.  $V(0) = 0$ , then the solution is:

$$V(t) = \frac{\tau_d}{\tau_d - \tau_m} (e^{-t/\tau_d} - e^{-t/\tau_m}) - \frac{\tau_r}{\tau_r - \tau_m} (e^{-t/\tau_r} - e^{-t/\tau_m})$$

**Case I:** For  $\tau_m \gg \tau_d \gg \tau_r$

$$V(t) \approx -\frac{1}{\tau_m} e^{-t/\tau_m}$$

**Case II:** For  $\tau_m \ll \tau_d$ ,  
 $\tau_m \& \tau_d \gg \tau_r$

$$V(t) \approx -\frac{1}{\tau_d} e^{-t/\tau_d}$$

# Heuristic derivations (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):*

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

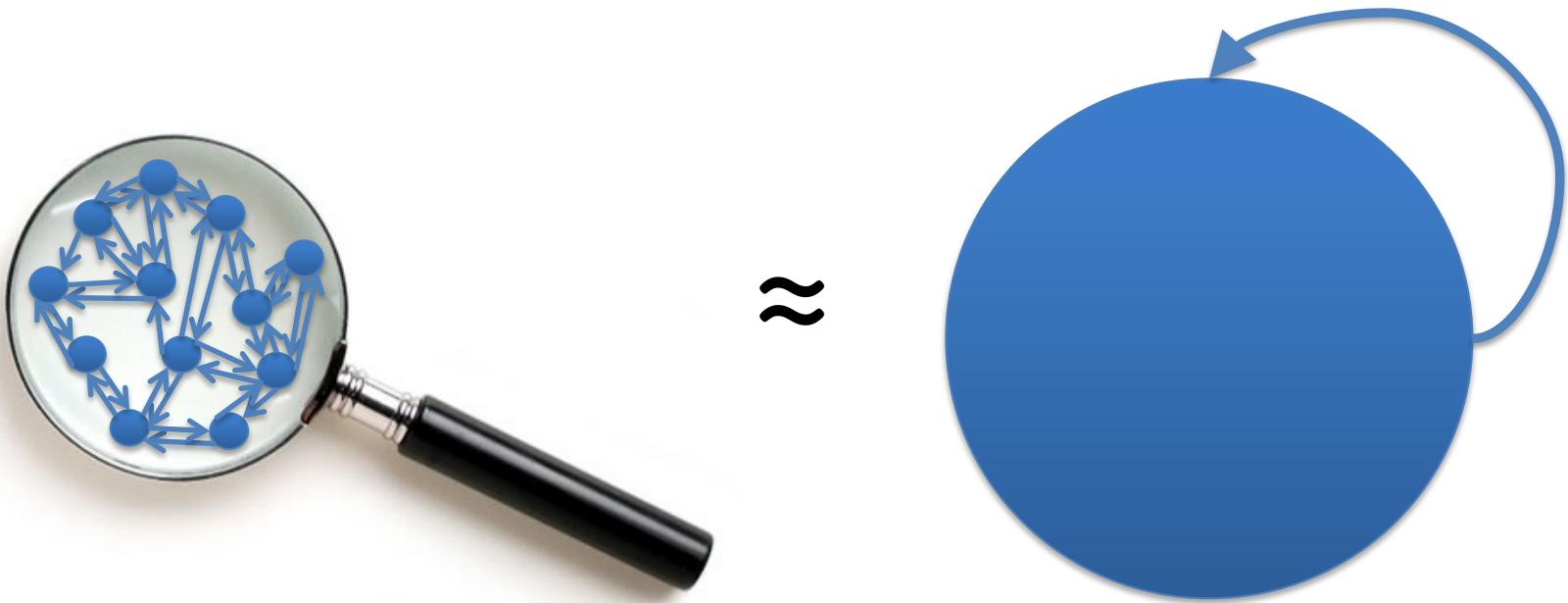
*The qualitative coarser network effects can still be captured.*

*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

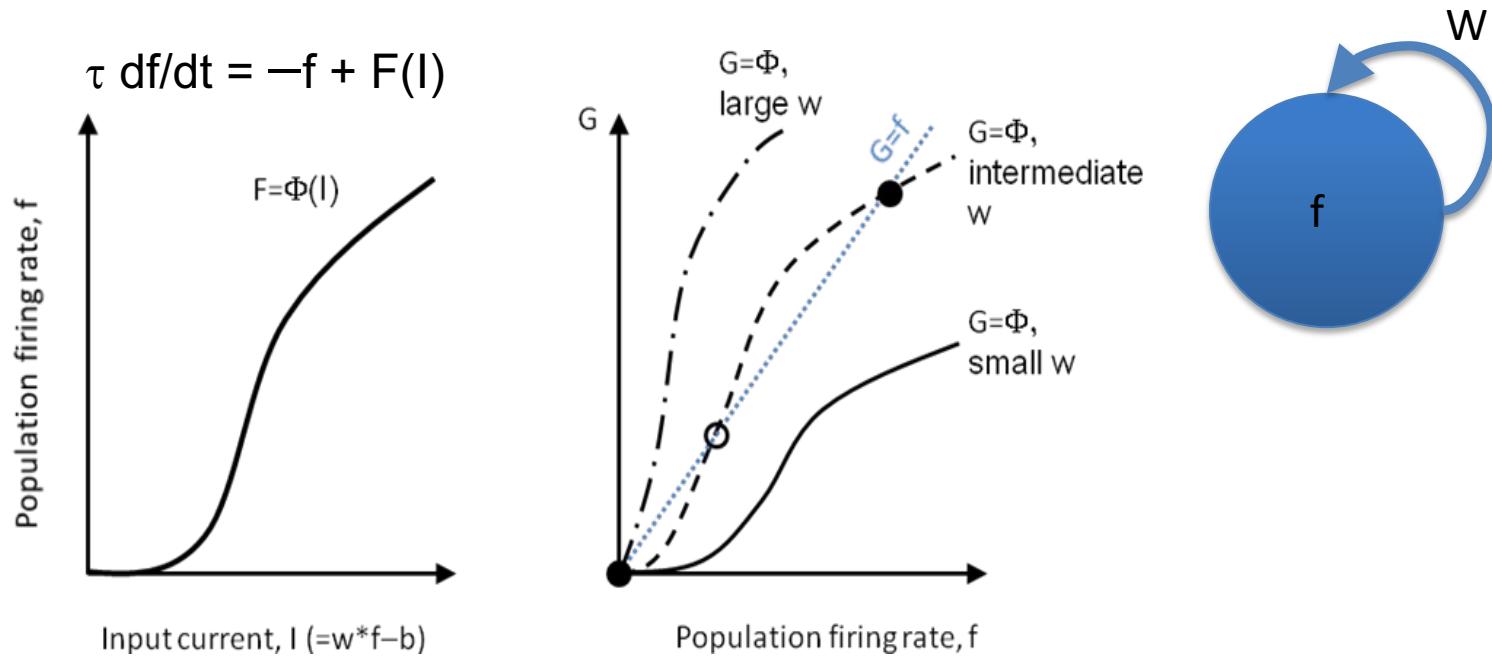
*The simplest recurrent neural network model*



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

# Multi-stability for memory encoding

## Categorical (discretized) memory



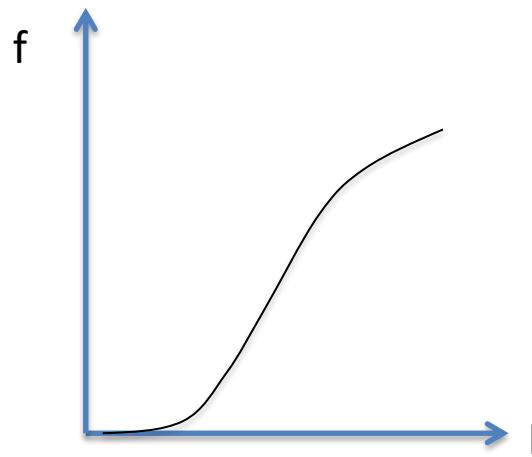
Suppose  $F$  is a nonlinear input-output function  $F$  (e.g. a sigmoidal function) as shown in the left figure. At steady state,  $df/dt = 0$ , which means the firing rate  $f = F(Wf - b)$ . When (function)  $F$  is plotted as a function against (variable)  $f$ , the intersection points between the functions  $G = f$  (i.e. diagonal line) and  $G = F$  will produce the steady states of the system – by definition.

Because of the structure of the nonlinear function, there can be a coexistence of 2 stable steady states plus 1 unstable steady state. This *emergent bi-stable* properties allows the system to store memory at the higher stable (or “up”) steady state. In this simple model, the bi-stable network can only be achieved if the synaptic weight  $W$  is sufficiently large enough, i.e. recurrent excitation has to be strong. A too strong (weak) recurrent strength will result in only a single high (low) stable steady state, thus unable to store any useful memory (right figure). A specific example of such system: a homogeneous population of neurons in a Hopfield network model encoding a specific memory state.

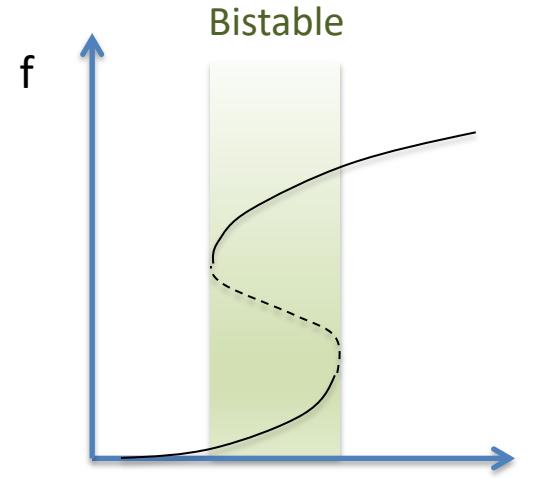
# “Working” memory: remembering a brief stimulus

Effective input-output function:

Weak recurrent self-excitation

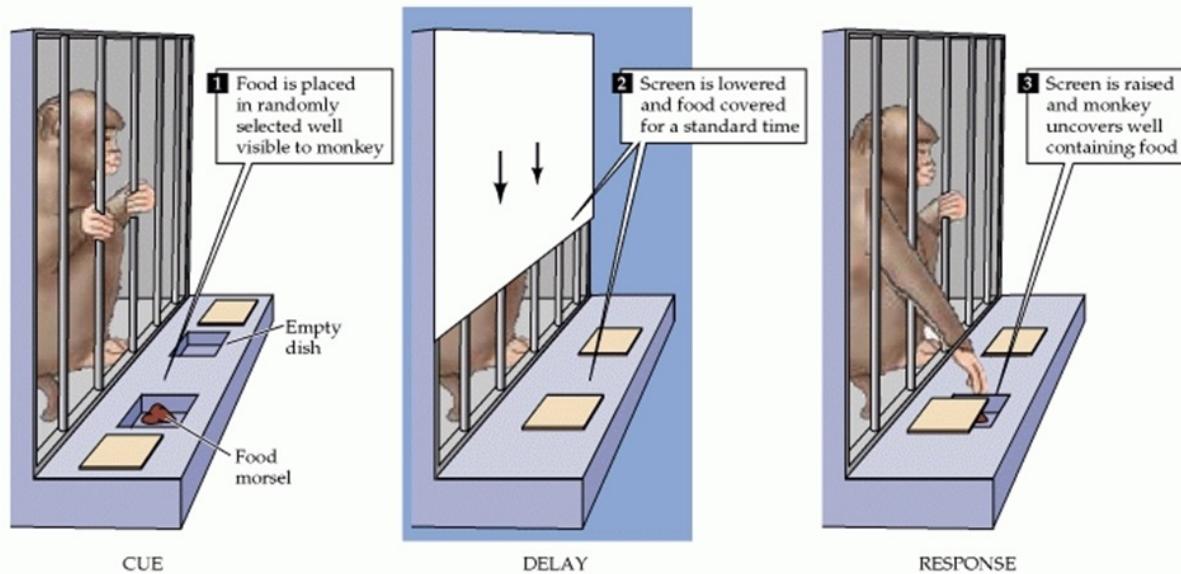


Sufficiently strong recurrent self-excitation → “kinks”

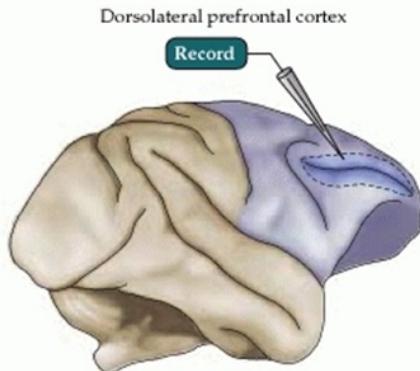


# Persistent activity during delay period

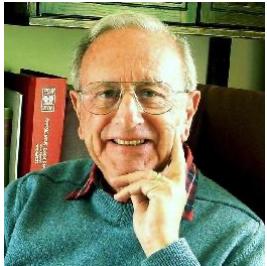
(A)



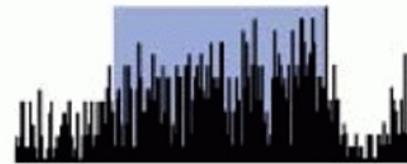
(B)



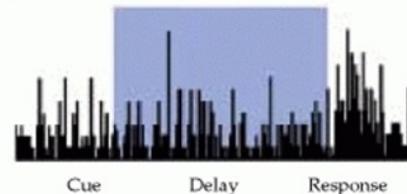
Joaquin Fuster



(C) Stimulus (food morsel) presented



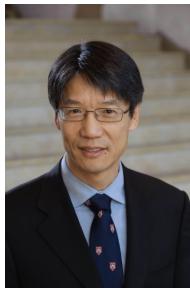
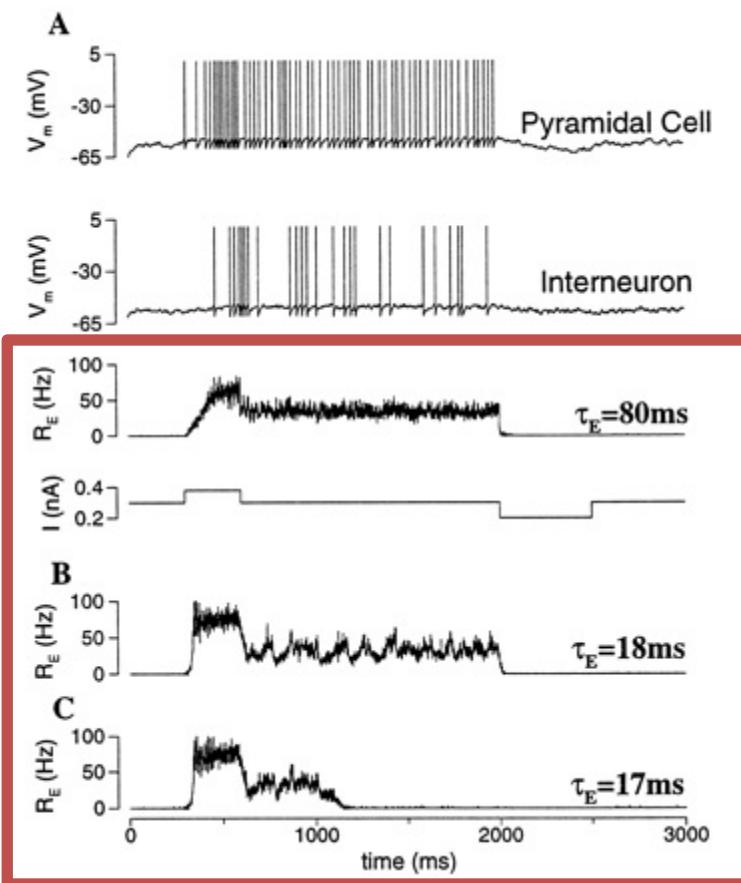
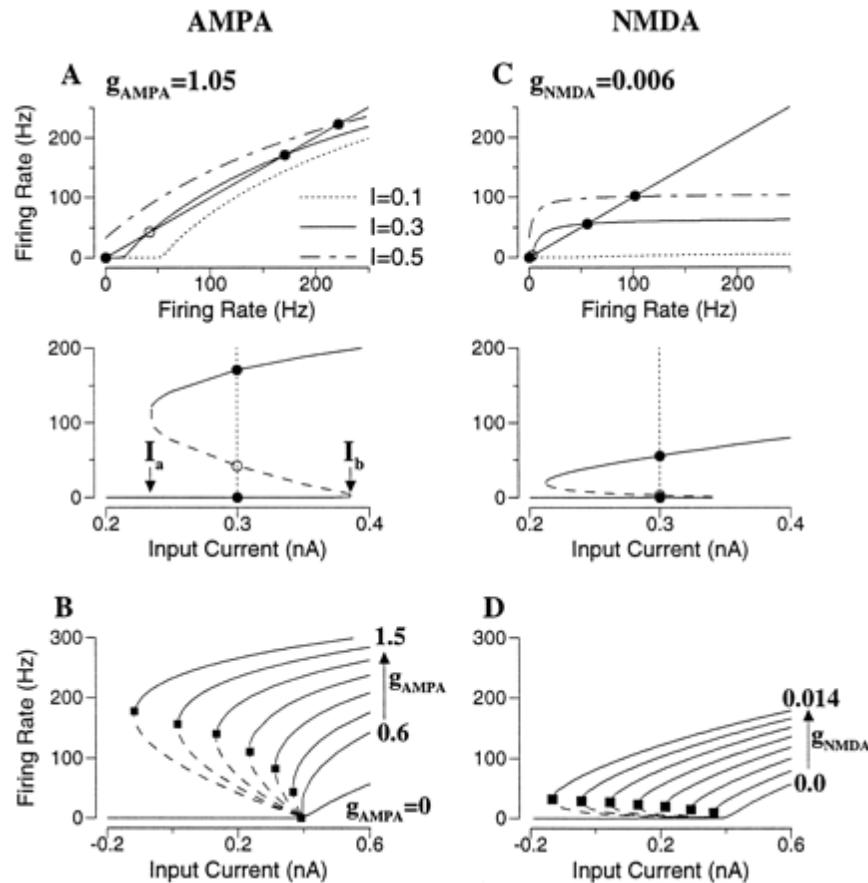
(D) No stimulus presented



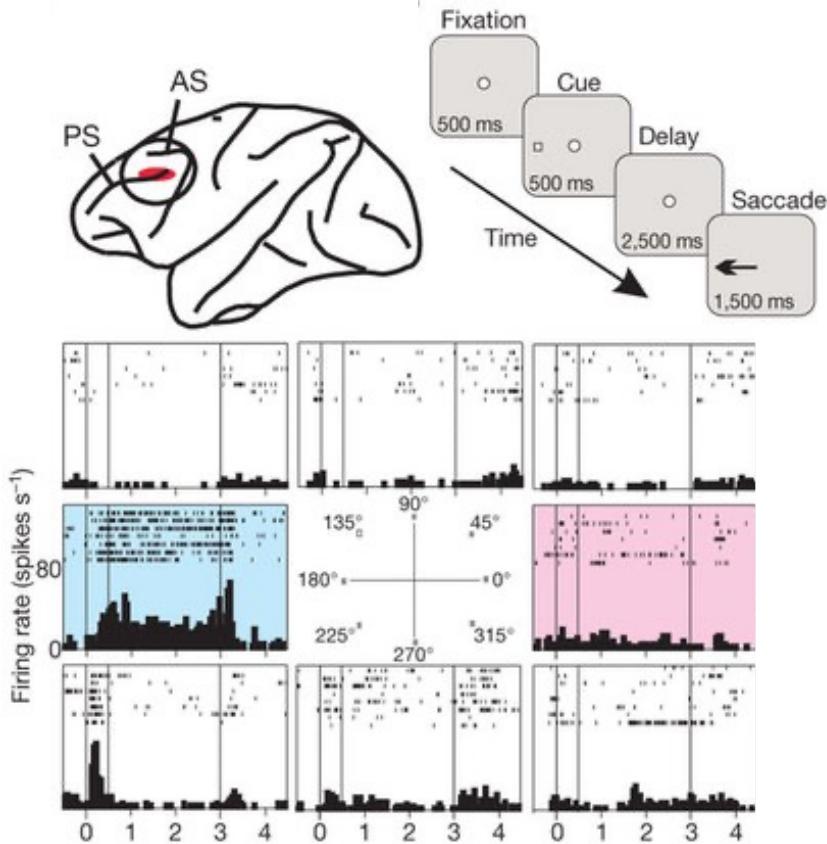
Patricia Goldman-Rakic



# Importance of slow (NMDA-mediated) synapses for reliable persistent activity



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

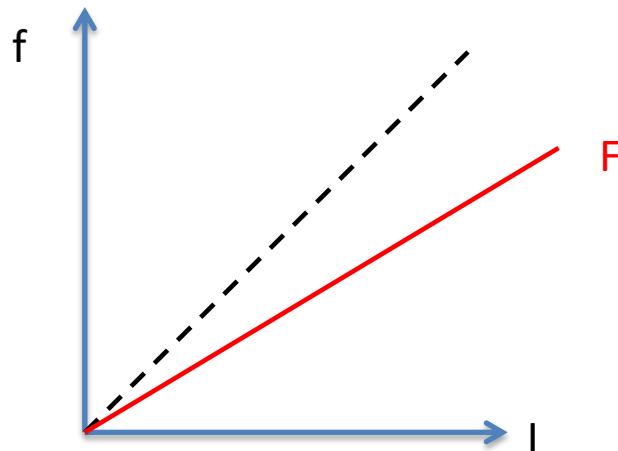


## *Spatial working memory*

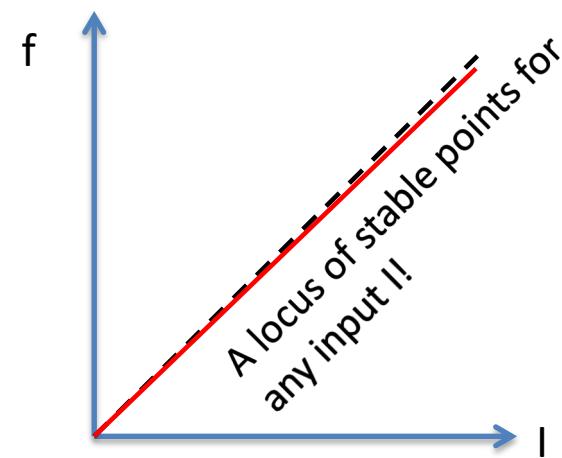
# What if the input-output function $F$ is linear?

Parametric (continuous) memory

Weak recurrent excitation

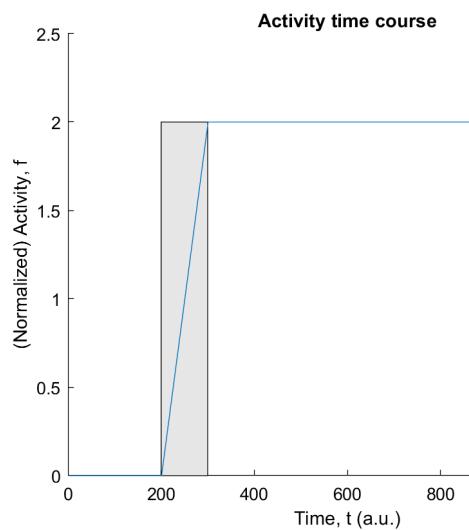


Sufficiently strong recurrent excitation, i.e. memorise continuous values perfectly

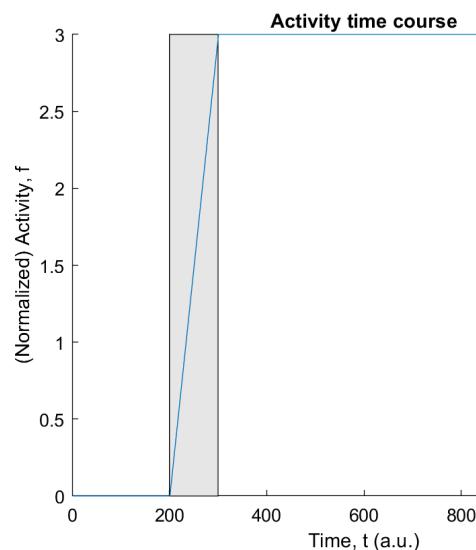


# What if the input-output function $F$ is linear?

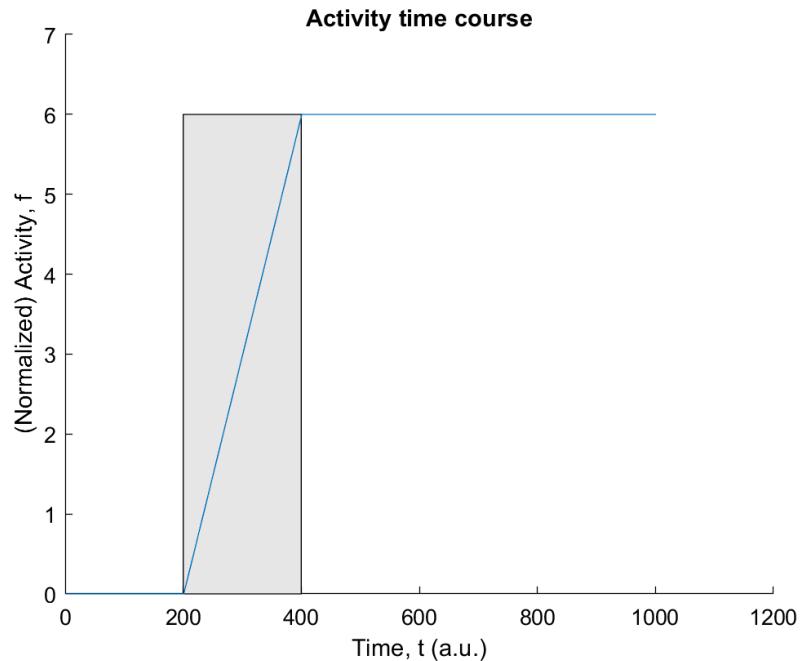
Parametric (continuous) memory



*Input: 0.2*  
*Duration: 100*



*Input: 0.3*  
*Duration: 100*



*Input: 0.3*  
*Duration: 200*

# Multi-stability for memory encoding

## Parametric (continuous) memory Derivation

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

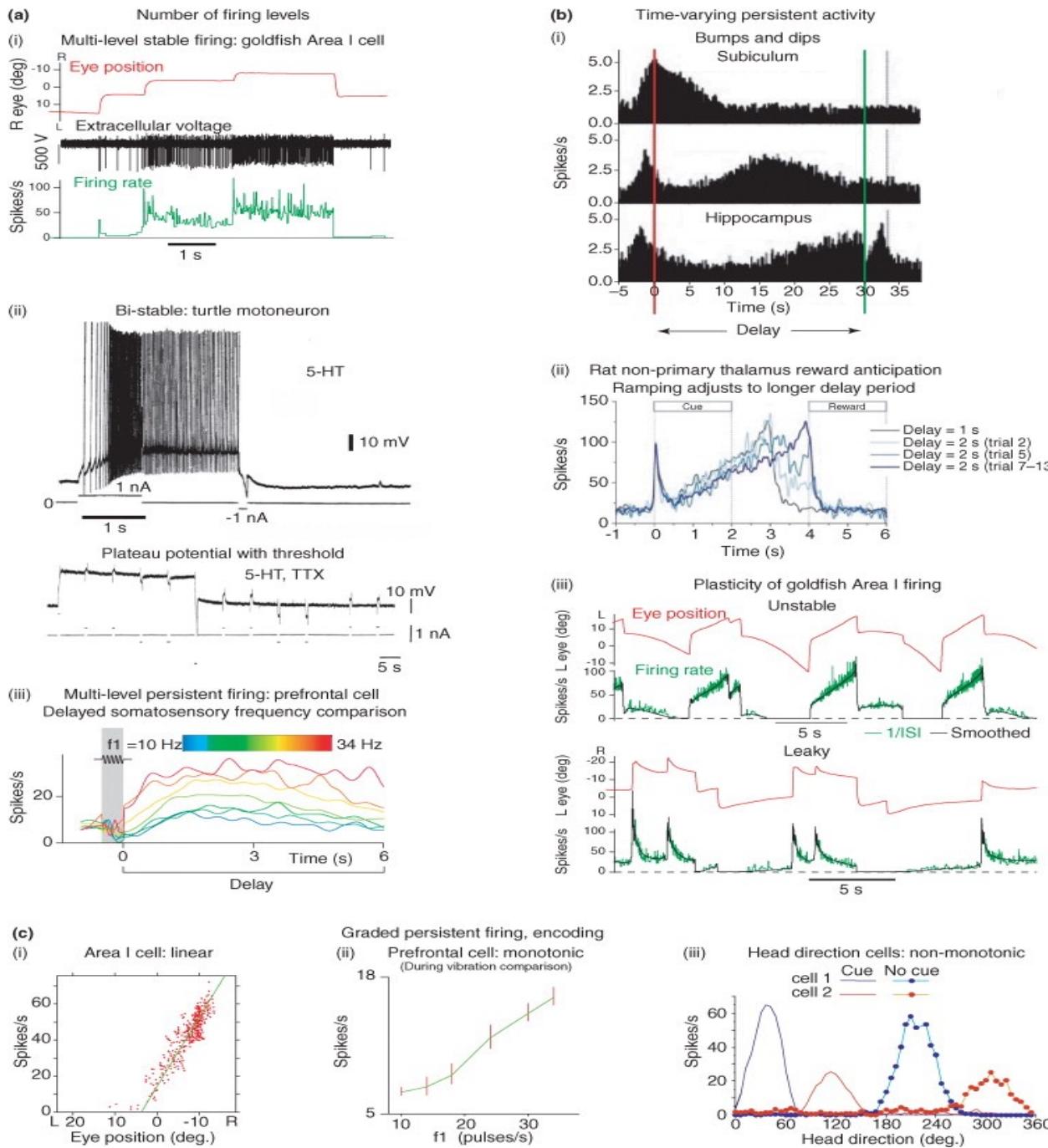
$$\tau_{\text{eff}} = \tau/(1 - W),$$

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*):

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

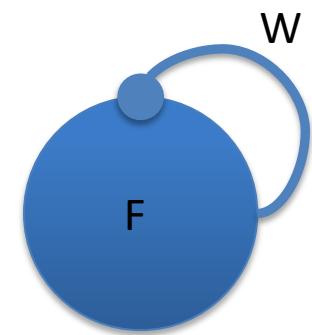
# Characteristics of different kinds of persistent neural activity.



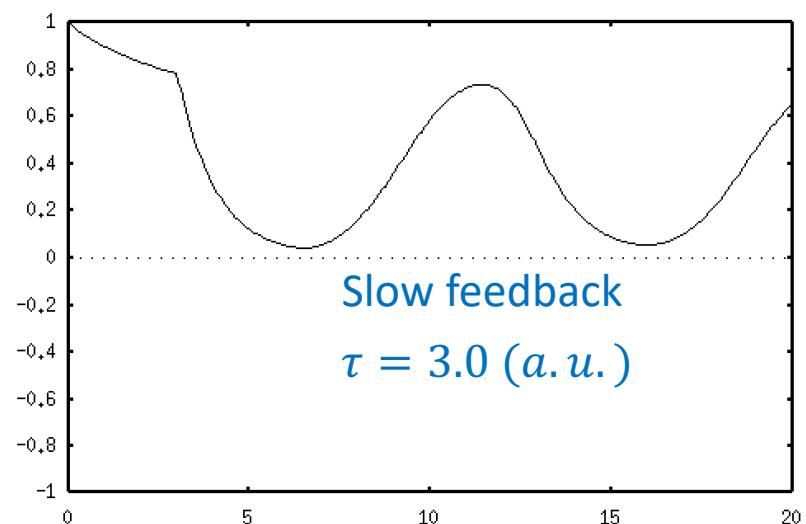
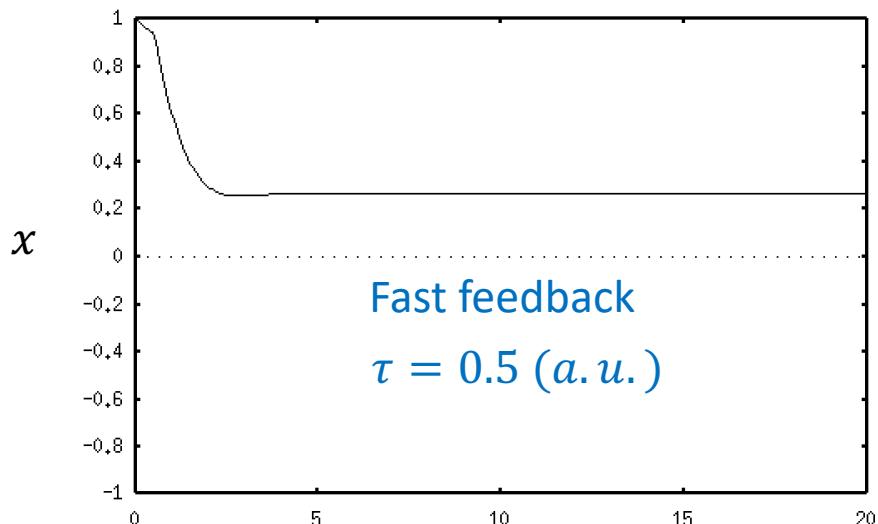
## Example: A simple self-inhibitory feedback population of neurons with time delay

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

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



For some inhibitory feedback delay of time  $\tau$



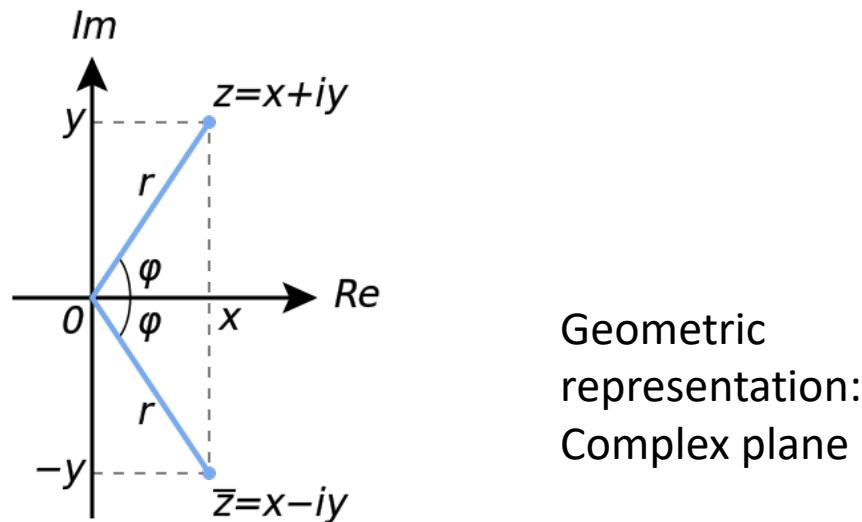
**What if we have 2 populations of  
neural populations/units  
interacting?**

# Refresher: Complex numbers

$$i^2 = -1 \text{ or } i = \sqrt{-1}$$

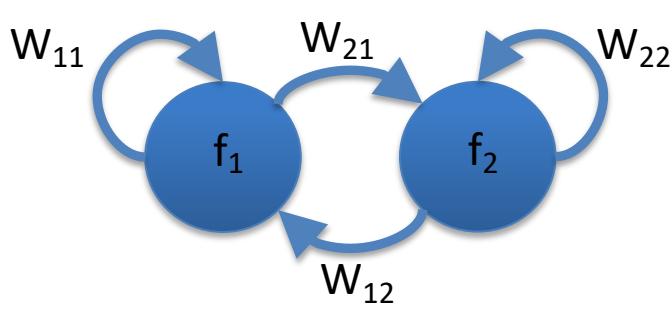
In general:  $x + iy$  where  $x$  is real (Re) while  $iy$  is imaginary (Im)

Re      Im



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



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

$$\text{Jacobian matrix, } J = \begin{bmatrix} \frac{\partial F_1}{\partial f_1} & \frac{\partial F_1}{\partial f_2} \\ \frac{\partial F_2}{\partial f_1} & \frac{\partial F_2}{\partial f_2} \end{bmatrix}$$

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

For linear coupled equations in matrix form

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

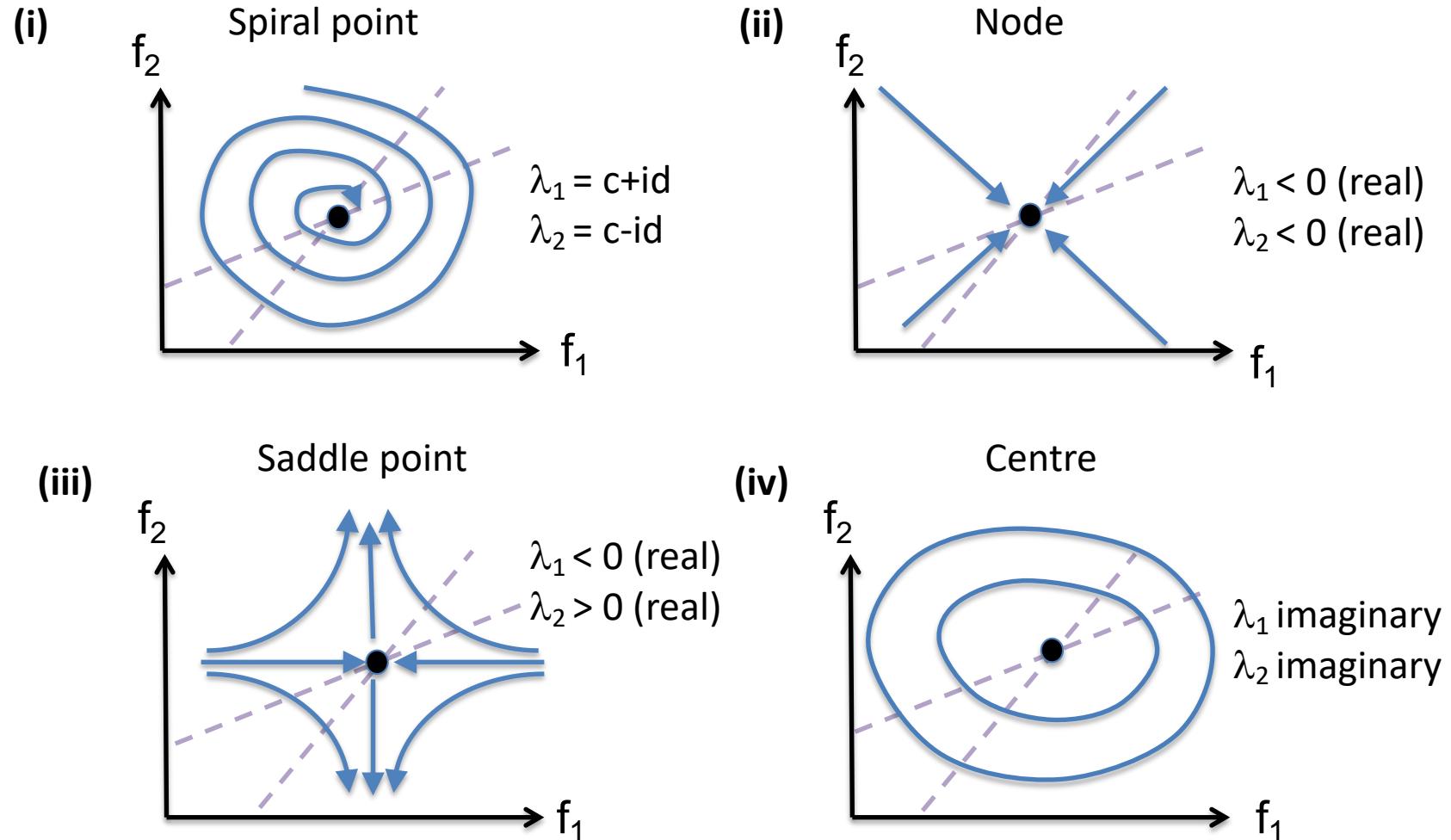
$$J = \begin{bmatrix} \frac{\partial(W_{11}f_1 + W_{12}f_2)}{\partial f_1} & \frac{\partial(W_{11}f_1 + W_{12}f_2)}{\partial f_2} \\ \frac{\partial(W_{21}f_1 + W_{22}f_2)}{\partial f_1} & \frac{\partial(W_{21}f_1 + W_{22}f_2)}{\partial f_2} \end{bmatrix}$$

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  $\frac{df}{dt} = \mathbf{W} \cdot \mathbf{f}$ . 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 the steady state.

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

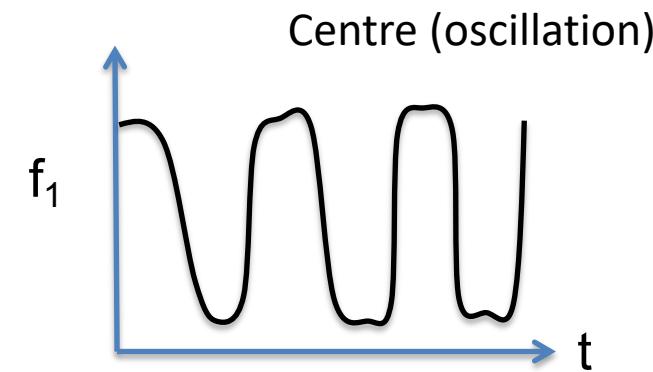
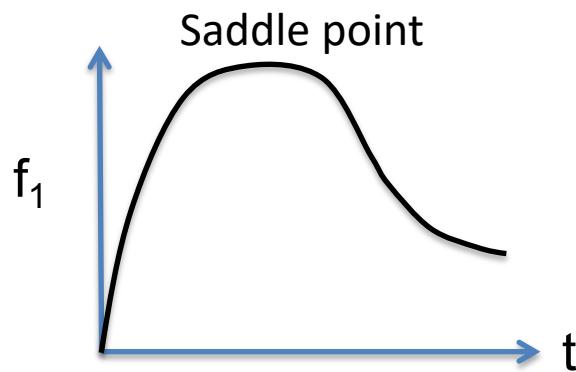
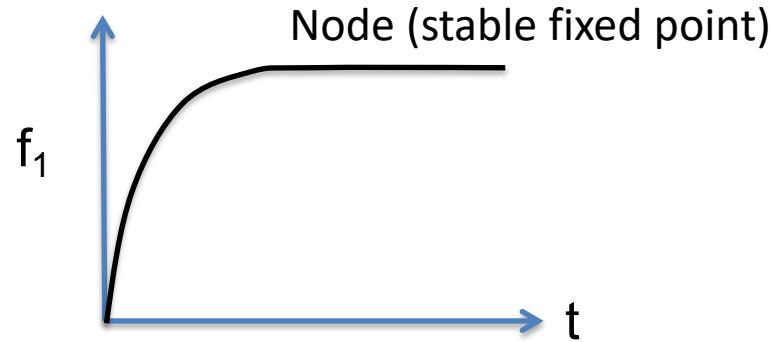
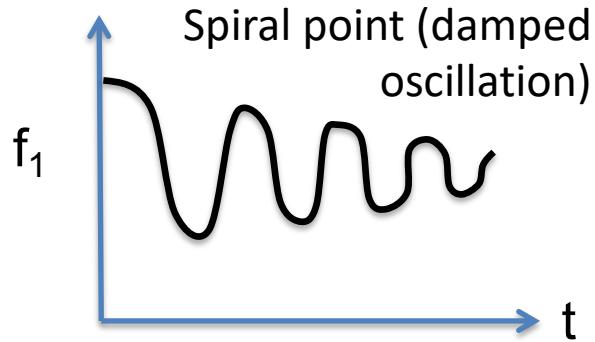
- (i) **Spiral point**, which can result in damped (or amplifying) oscillation of the system. Requires the eigenvalues to be *both real (both negative for damped, and positive for amplifying) and non-zero imaginary parts*;
- (ii) **Node**, which can result in strictly attracting towards (or repelling 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* in 2-dimensional linear systems $\frac{df}{dt} = \mathbf{A} \cdot \mathbf{f} + \mathbf{B}$ , $\mathbf{f} = (f_1, f_2)$



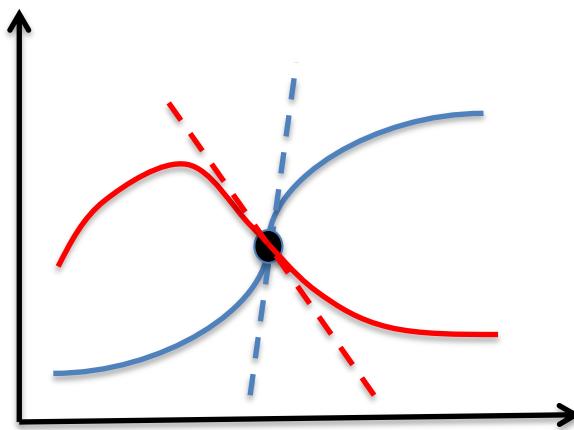
# Possible functions?

- 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; decision dynamics.

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

# What if the system is nonlinear?

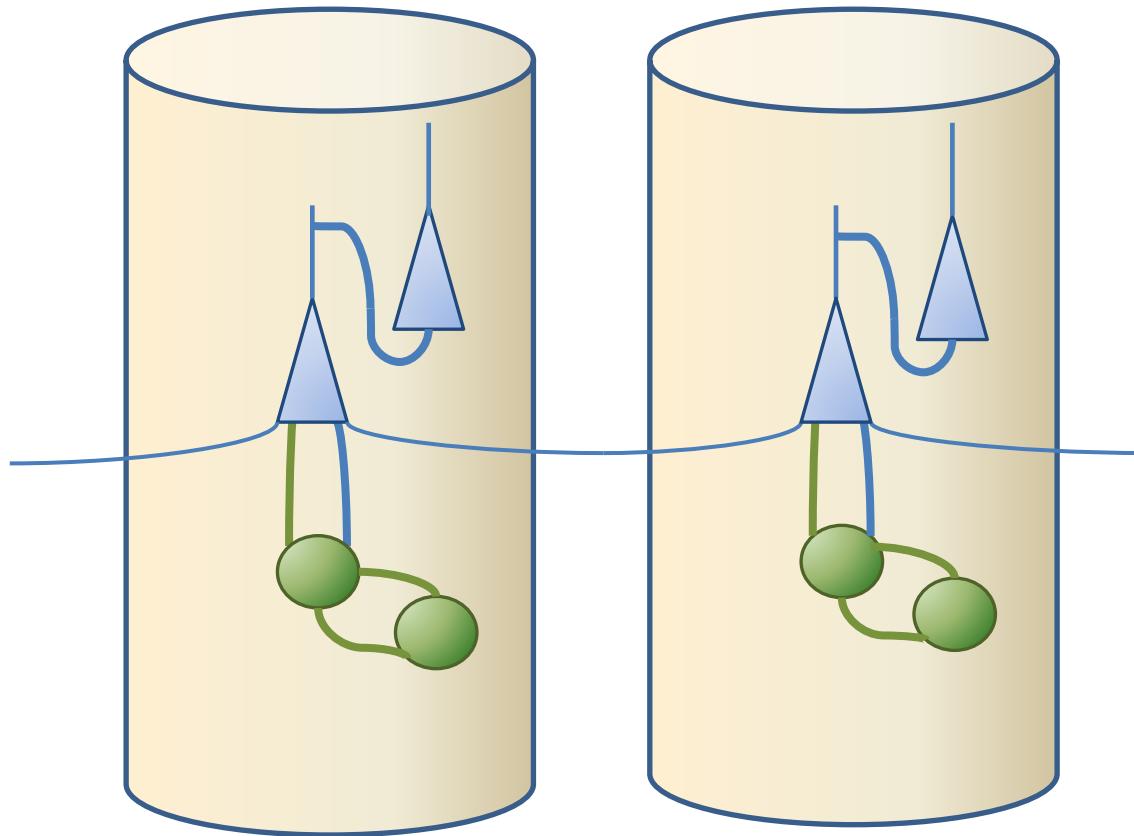
We can still use the same technique (linear stability analysis) as for linear system – It turns out that according to a mathematical theorem, the stability of a nonlinear system's dynamics *sufficiently near a steady state* is the **same** as the linear system near the *same* steady state!



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

# Example: Excitatory-inhibitory networks

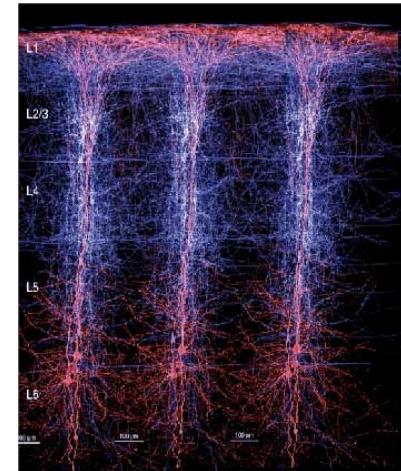
Cartoon rep. of cortical columns



Excitatory  
neuron

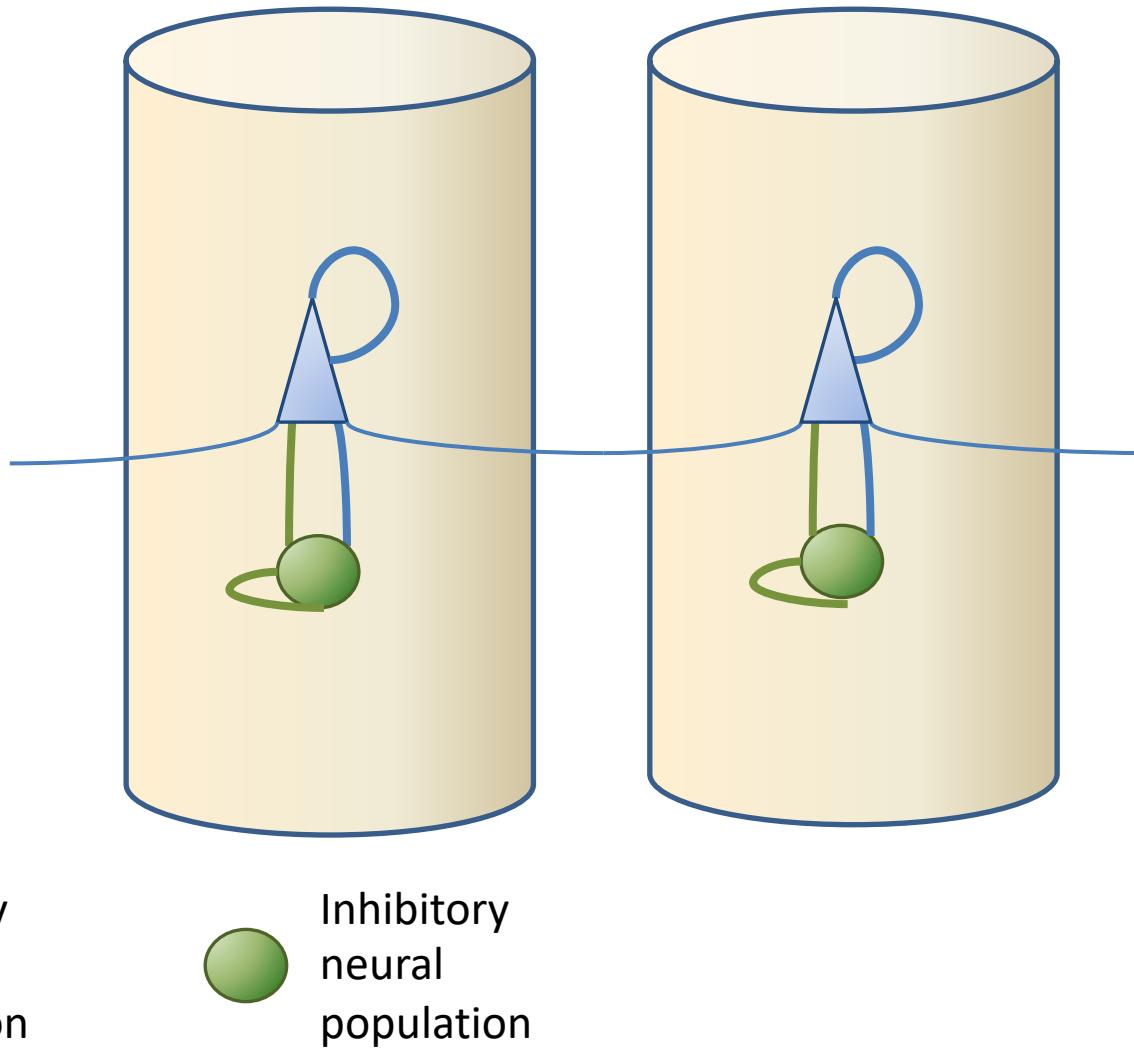


Inhibitory  
neuron

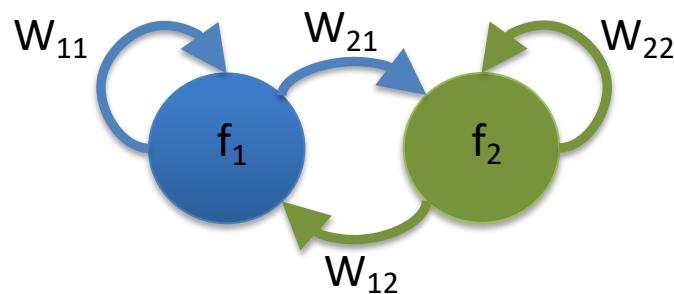


# Example: Excitatory-inhibitory networks

A simplified network architecture (assuming homogenous neurons)



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



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

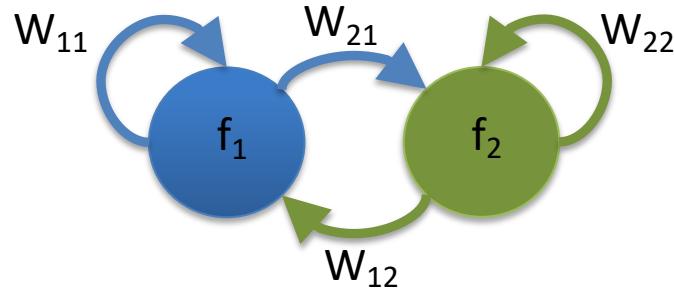
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} w_{11} & w_{12} \\ w_{21} & w_{22} \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} b_1 \\ b_2 \end{bmatrix}$$

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.

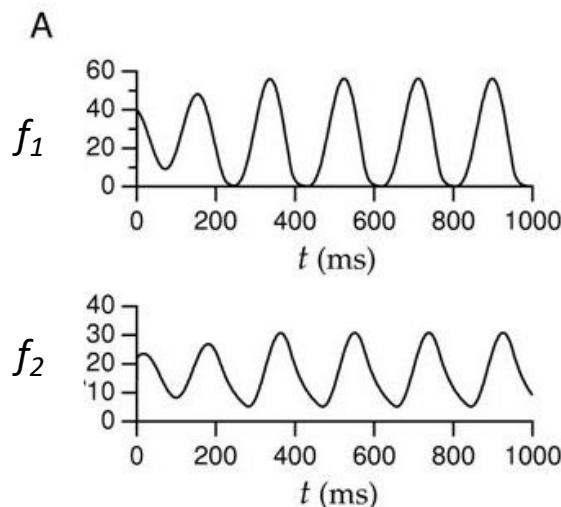
# What kind of dynamics can an excitatory-inhibitory coupled network produce?



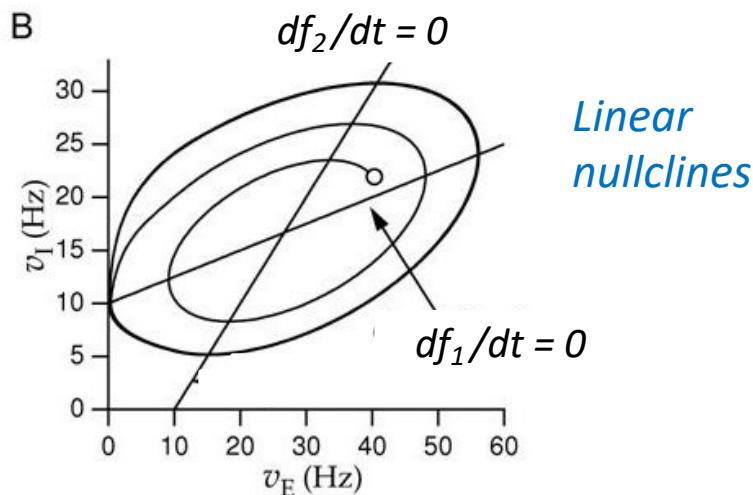
$$\frac{d}{dt} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} = \begin{bmatrix} F(f_1, f_2) \\ G(f_1, f_2) \end{bmatrix}$$

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

Temporal behavior

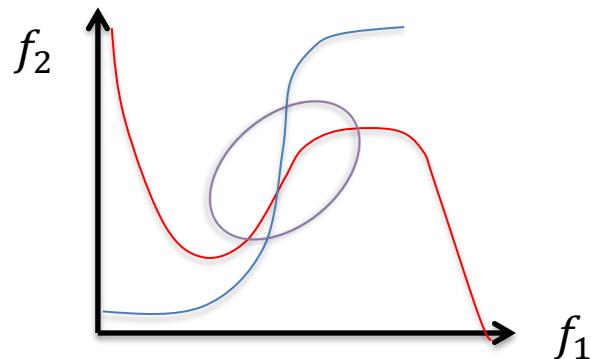


Unstable fixed point – limit cycle



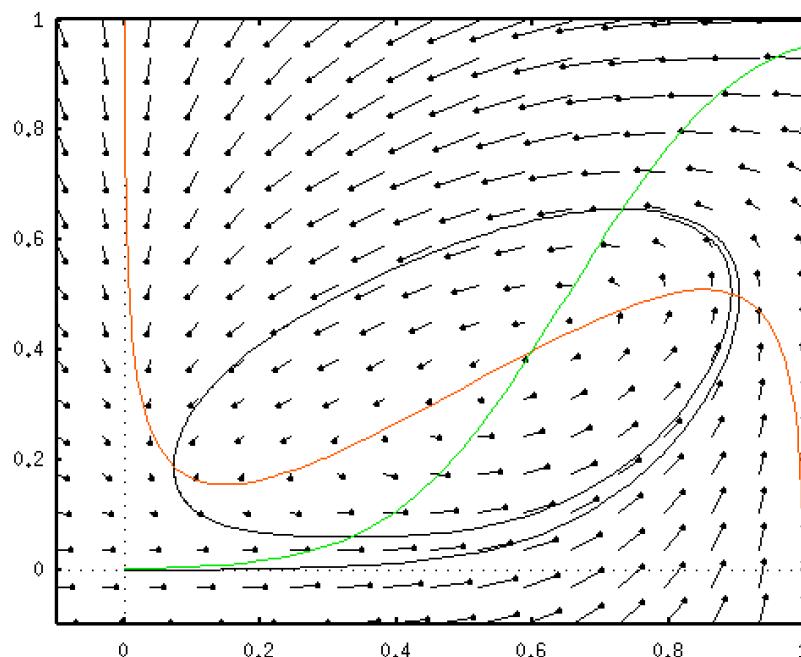
$$W_{21} > 0, W_{12} < 0$$

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



*Nonlinear nullclines  
(blue and red lines):  
Obtained by algebraically  
solving each differential  
equation*

Excitatory-inhibitory network (Wilson-Cowan type)



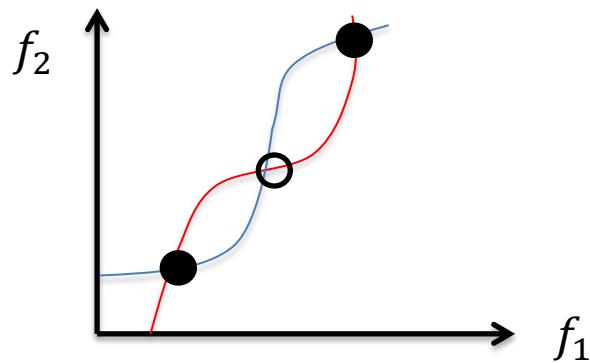
*With vector field  
(used XPPAUT software)*

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

# Mutually Inhibitory neural units

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

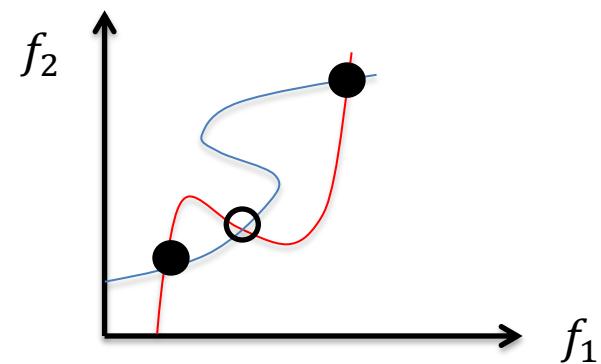
Weak  $W_{11} > 0, W_{22} > 0$



Mutual excitation with weak self-connections

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

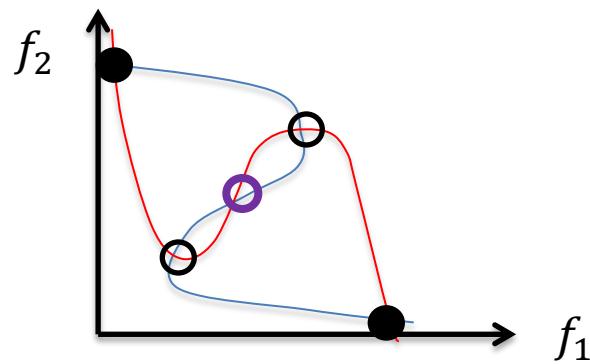
Strong  $W_{11} > 0, W_{22} > 0$



Mutual excitation with strong self-connections

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

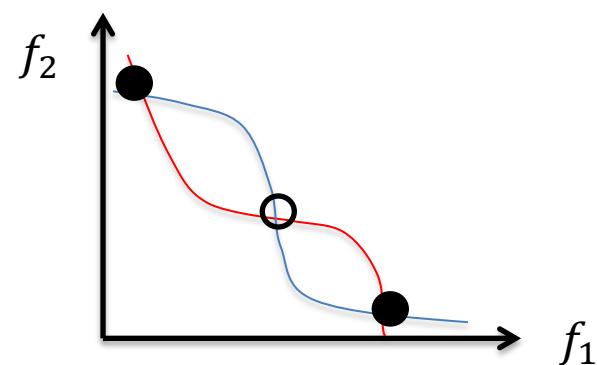
Strong  $W_{11} > 0, W_{22} > 0$



Mutual inhibition with strong self-connections

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

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

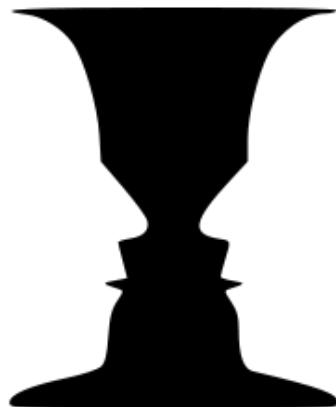
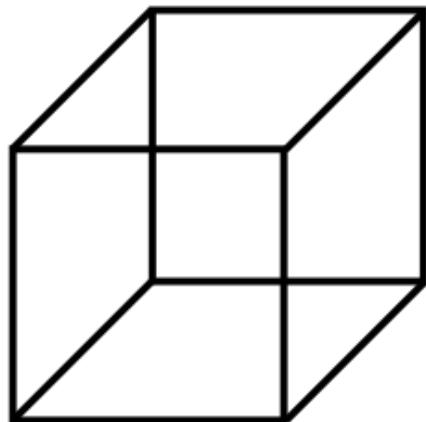


Mutual inhibition with weak self-connections

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

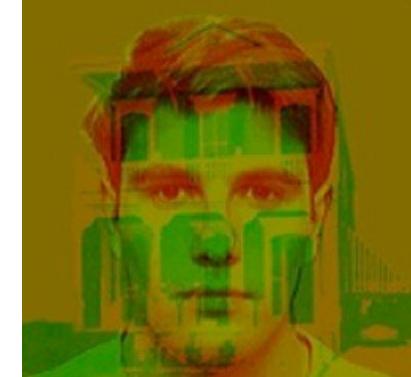
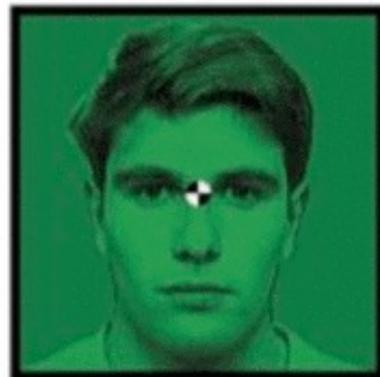
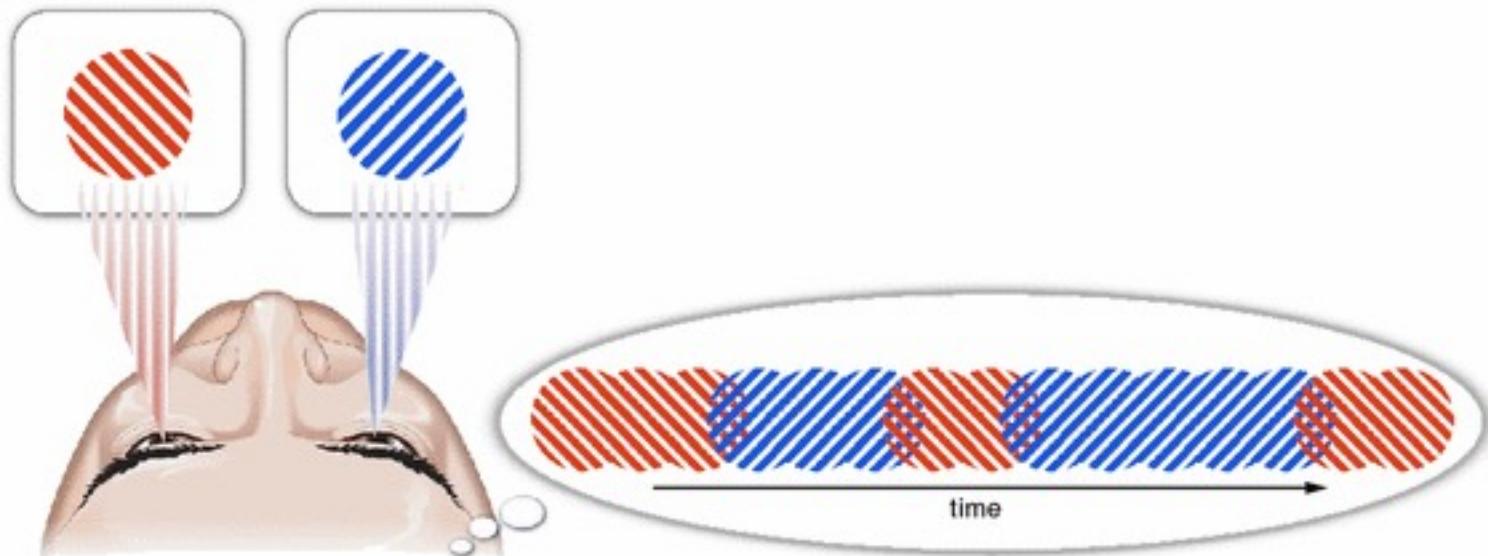
# Example: Perceptual oscillations – Binocular rivalry

Multiple states of the mind  
(for the same stimulus)

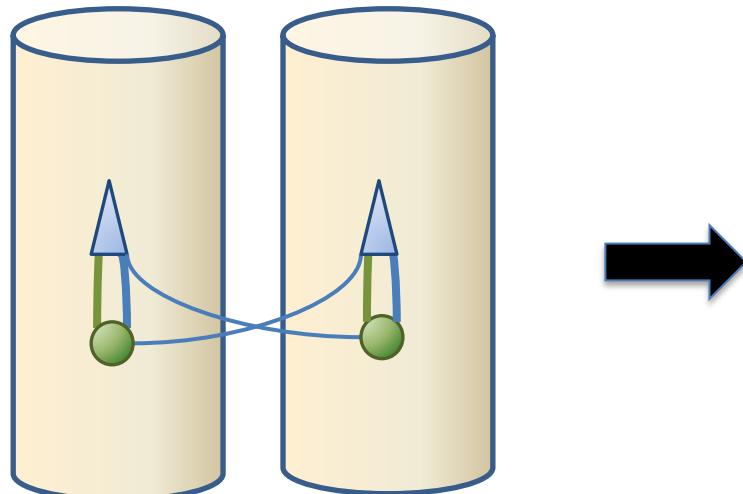


Necker cube

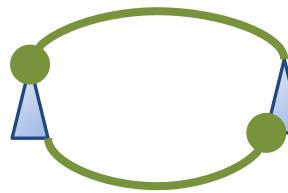
**Binocular rivalry: A phenomenon of visual perception in which perception alternates between different images presented to each eye.**



# A basic model for perceptual alternation phenomenon



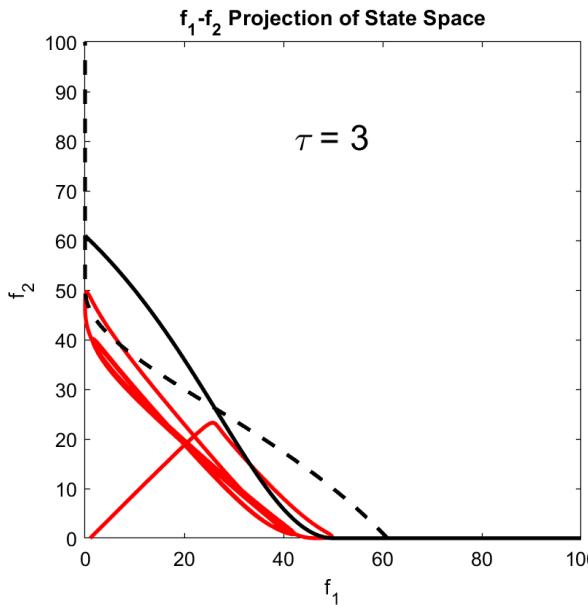
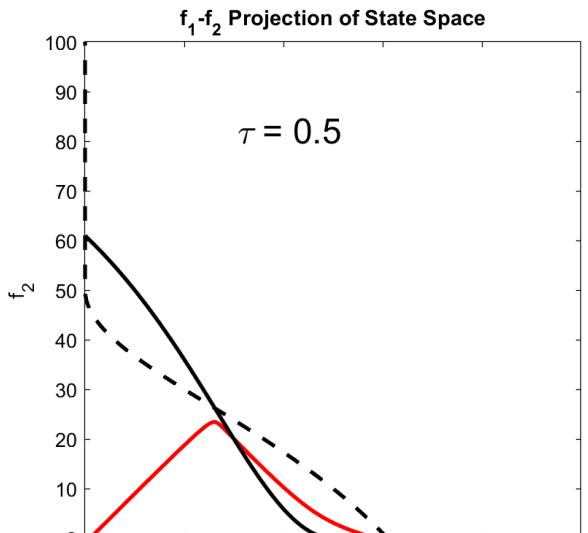
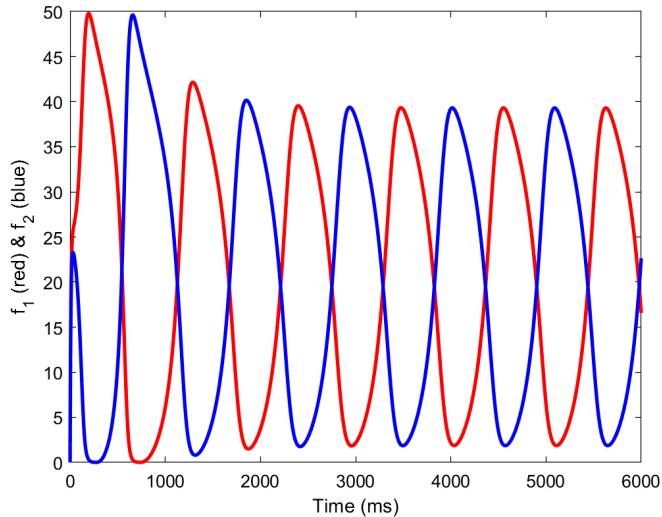
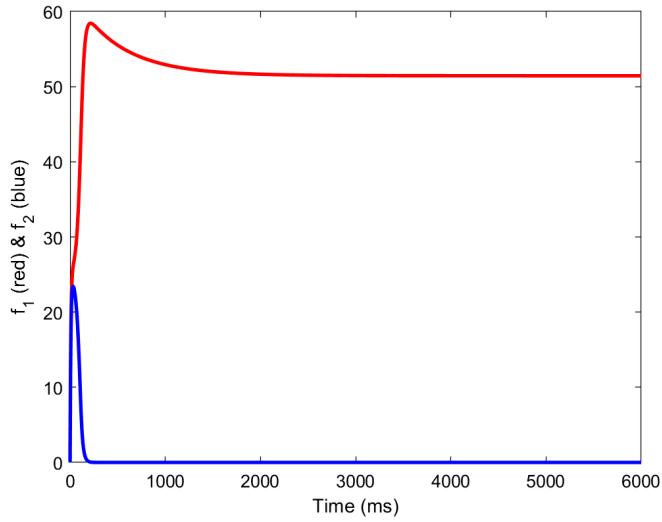
Mutual (effectively) inhibitory population  
- Implicitly incorporate inhibitory populations



Assume some slow adaption neural mechanism, A ( $\Rightarrow$  4 dyn equations)

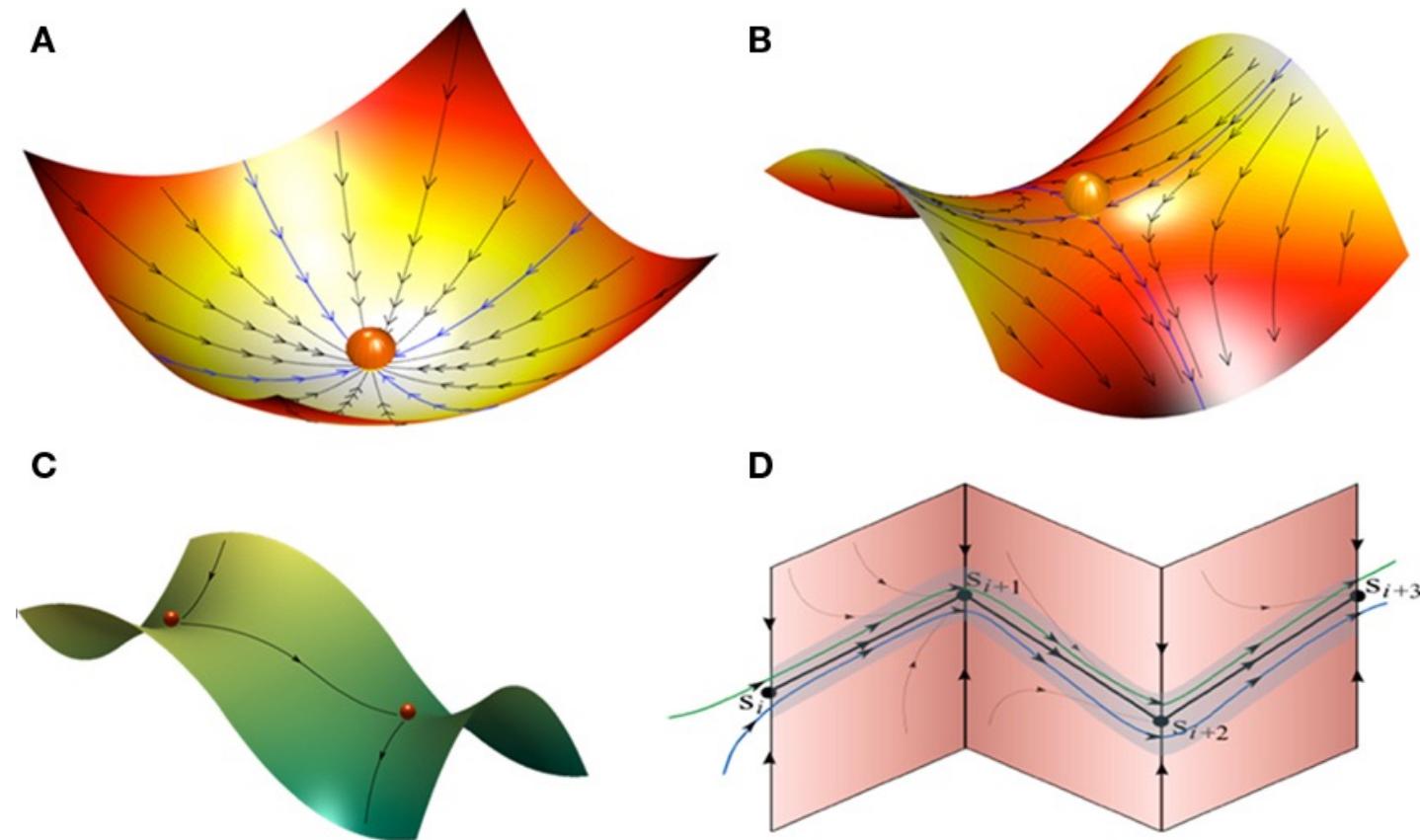
$$\begin{aligned} \frac{df}{dt} &= -f + F(W, A, B) \\ \frac{dA}{dt} &= -A + \beta f \end{aligned}$$

# A basic model for perceptual alternation phenomenon

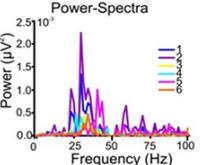
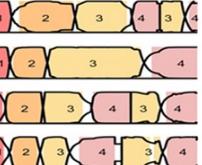
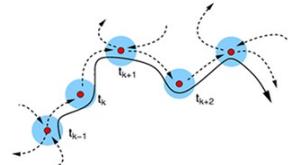
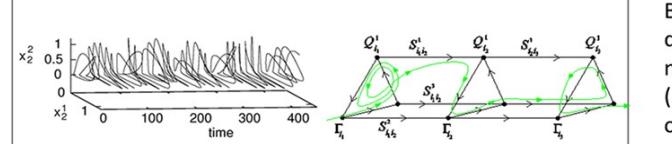
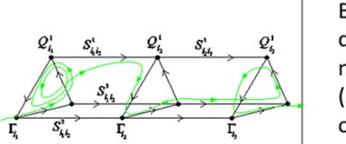
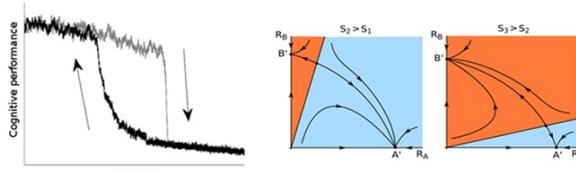
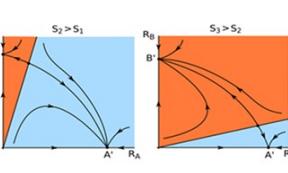
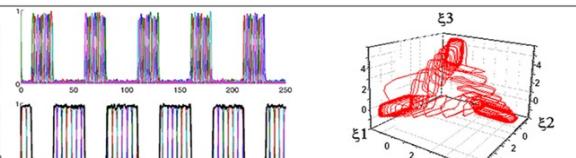
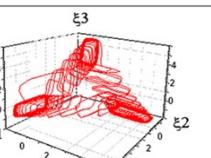
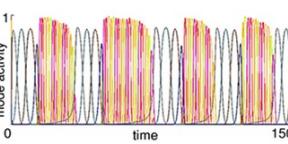
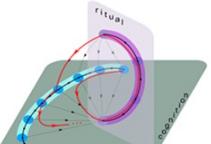


**Are there other types of neural  
network dynamics?**

**Landscape metaphors for brain dynamics (A–C).** (A) simple attractor (stable fixed point) in the phase space of a dynamical system. (B) a metastable state (saddle fixed point) with two stable and two unstable separatrices (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

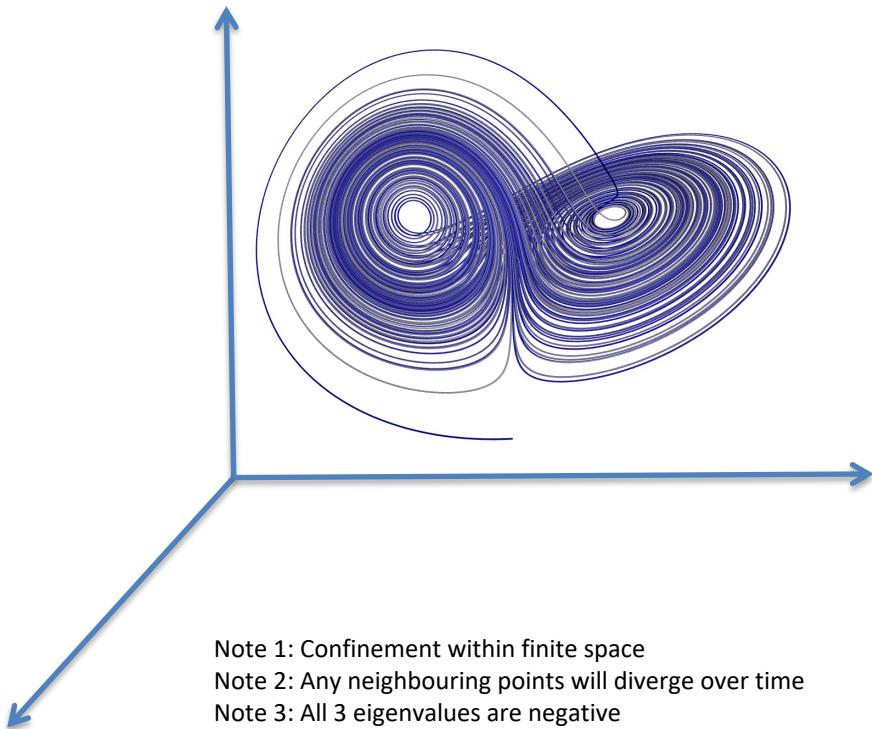
**Representative examples of dynamical images of brain functions.** (1) Rhythmic oscillations (adapted from Gloveli et al., 2005; Walling and Hicks, 2006). (2) Reproducible sequences of taste-specific switching patterns in the gustatory cortex (adapted from (Jones et al., 2007) and heteroclinic channel of saddle cycles (adapted from Rabinovich et al., 2008a). (3) Integration of different modalities – Heteroclinic Binding (Rabinovich et al., 2010a) for mutual modulation of coupled sequential dynamics. (4) Bistability and hysteresis (Jones and Hardy, 1990; Rabinovich et al., 2010b). (5) Low-frequency oscillations and modulational instability in a network with non-symmetric inhibition (WLC; Rabinovich et al., 2010b). (6) Intermittency of sequences (Rabinovich et al., 2010b).

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

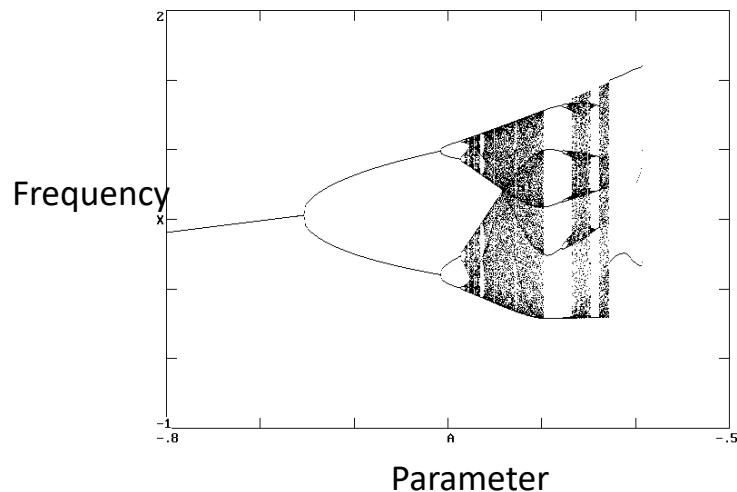
# Chaotic (strange) attractor

## - Deterministic chaos

Lorenz attractor (3D system)

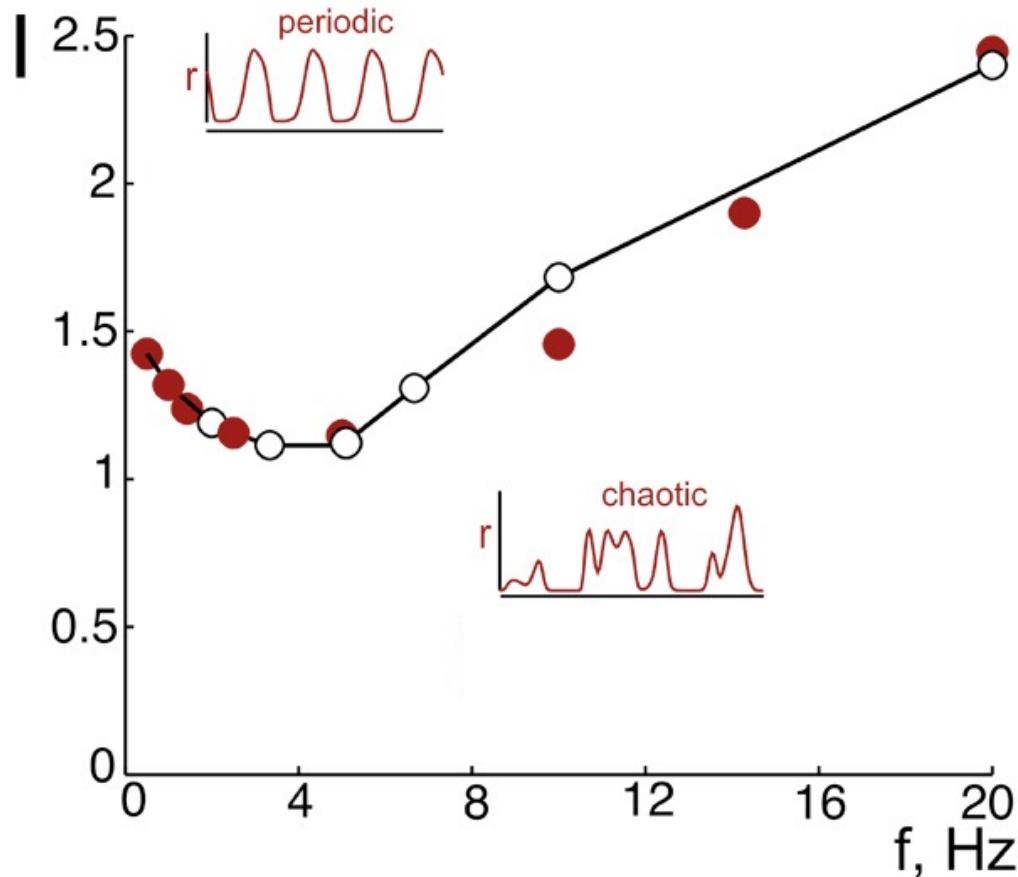


Period doubling leading to chaos



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

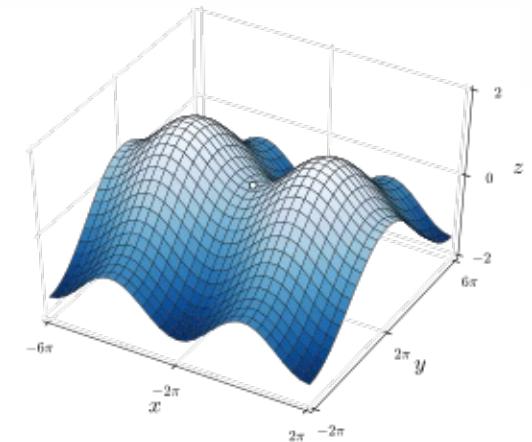
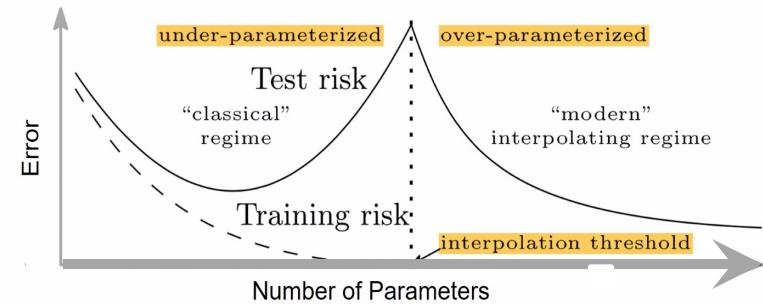
# Transition to periodic oscillations in a chaotic, randomly connected recurrent neural network



*Input current suppresses chaotic behaviour*

# Excellent performance albeit “strange” behaviour in deep networks

- Remarkably good performance
- “Double descent” phenomenon e.g. Belkin et al. (2019) (overparametrisation)
- Local minima during learning rare as the high-dimensional parameter space consists mostly saddle points e.g. Pascanu et al. (2014) *On the saddle point problem for non-convex optimization.* arXiv:1405.4604.
- Degeneracy of solutions in high dimensions allow faster search for optimal solutions (Bartlett et al. (2019) *Benign overfitting in linear regression.* arXiv:1906.11300)



# 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)

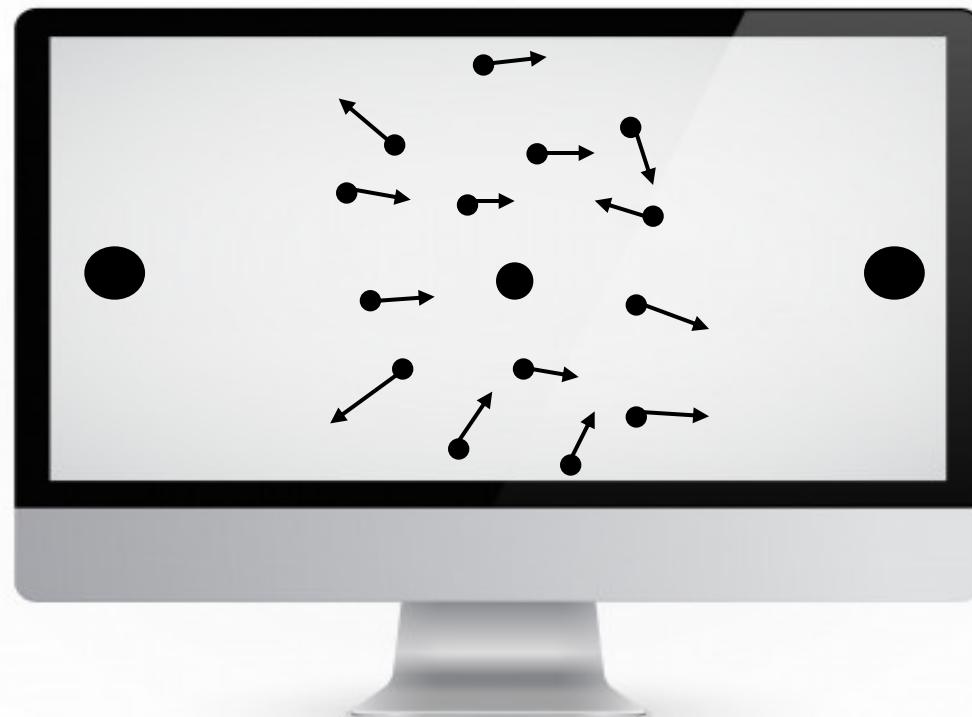
*Integrate sensory information*

*Select an action/choice among alternative competing options*

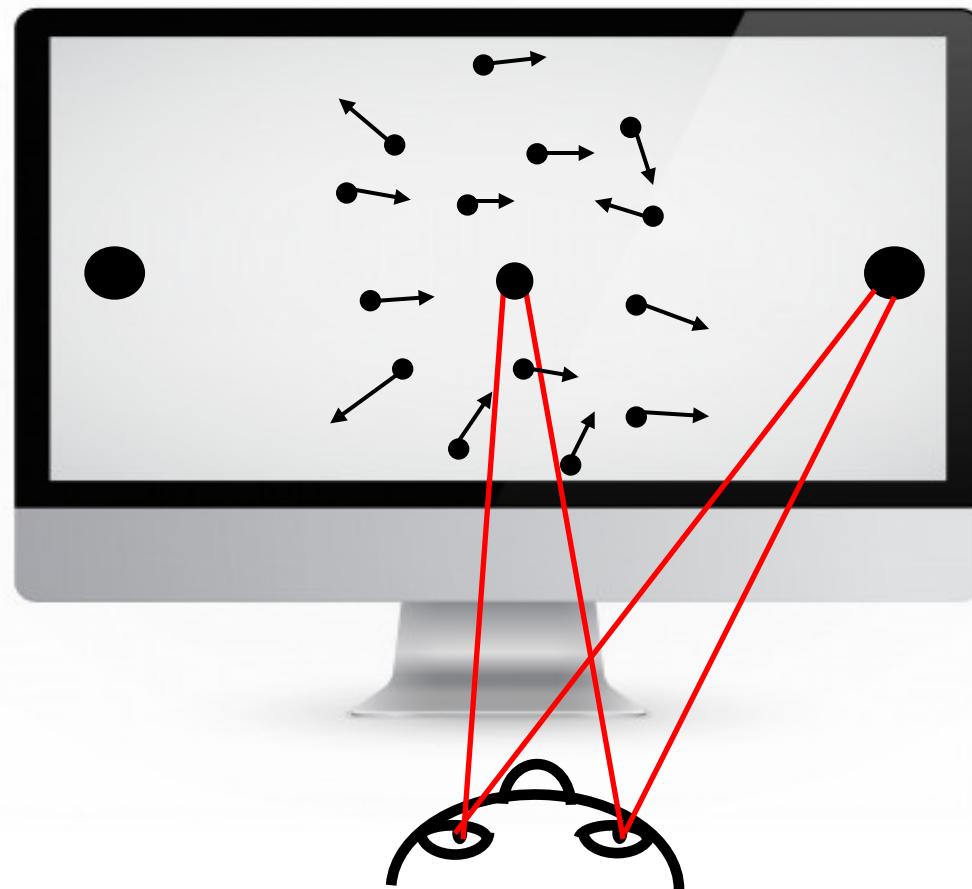
*Respond quickly and/or accurately*



# A visual motion direction discrimination task



# A visual motion direction discrimination task



# **Golden age of Mathematical Psychology**

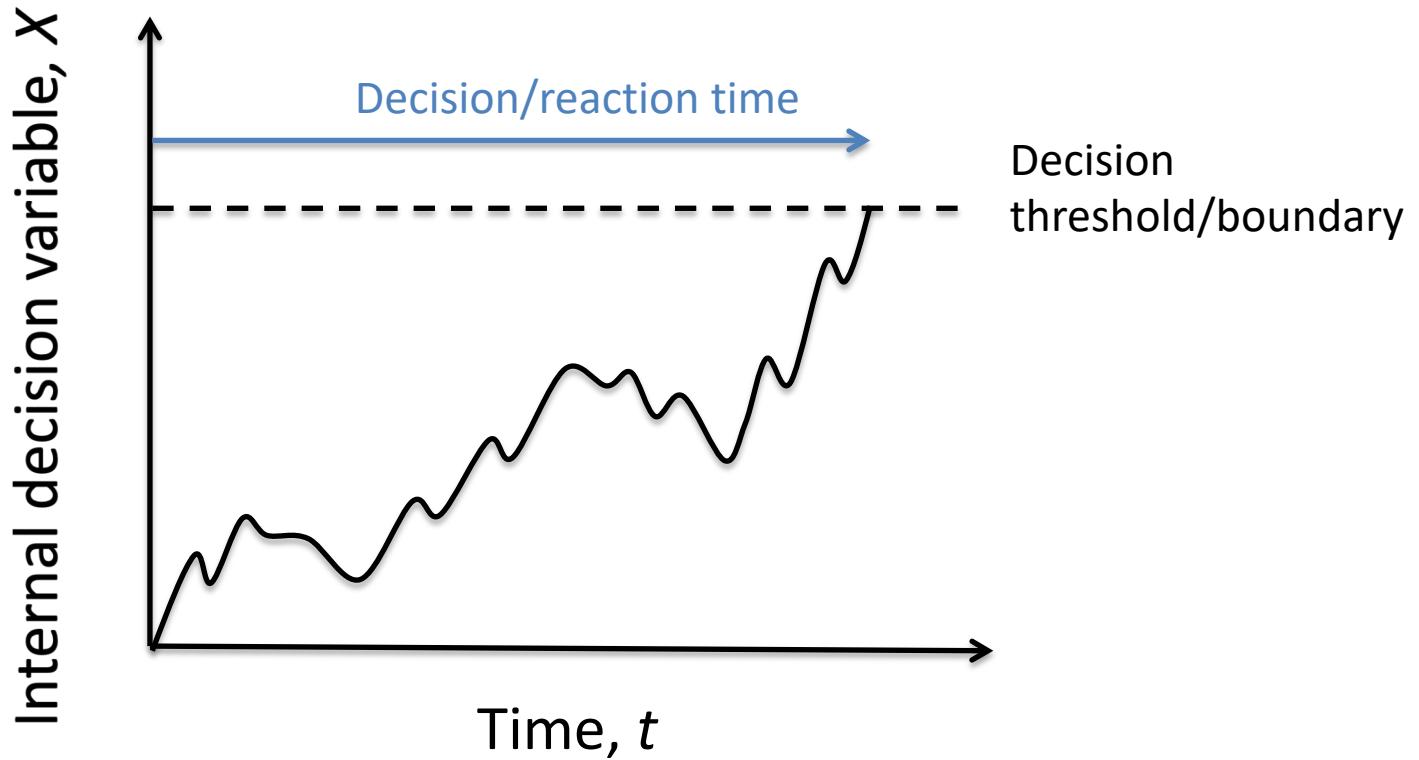
## **(1940's) ...**

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**

# Evidence accumulation

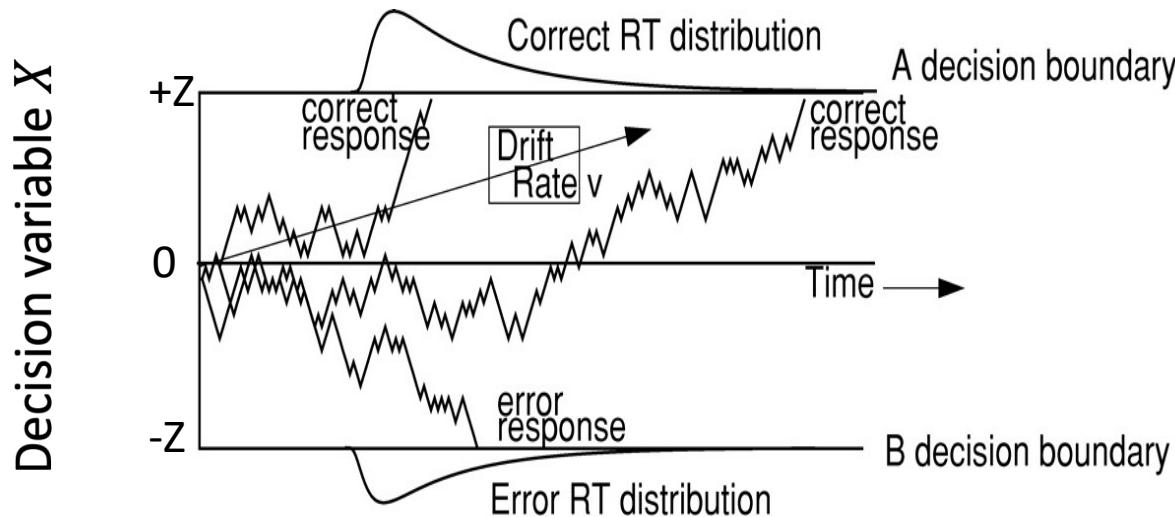
*Accumulator models*



Sequential sampling model framework

# Cognitive model: Drift-diffusion model

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

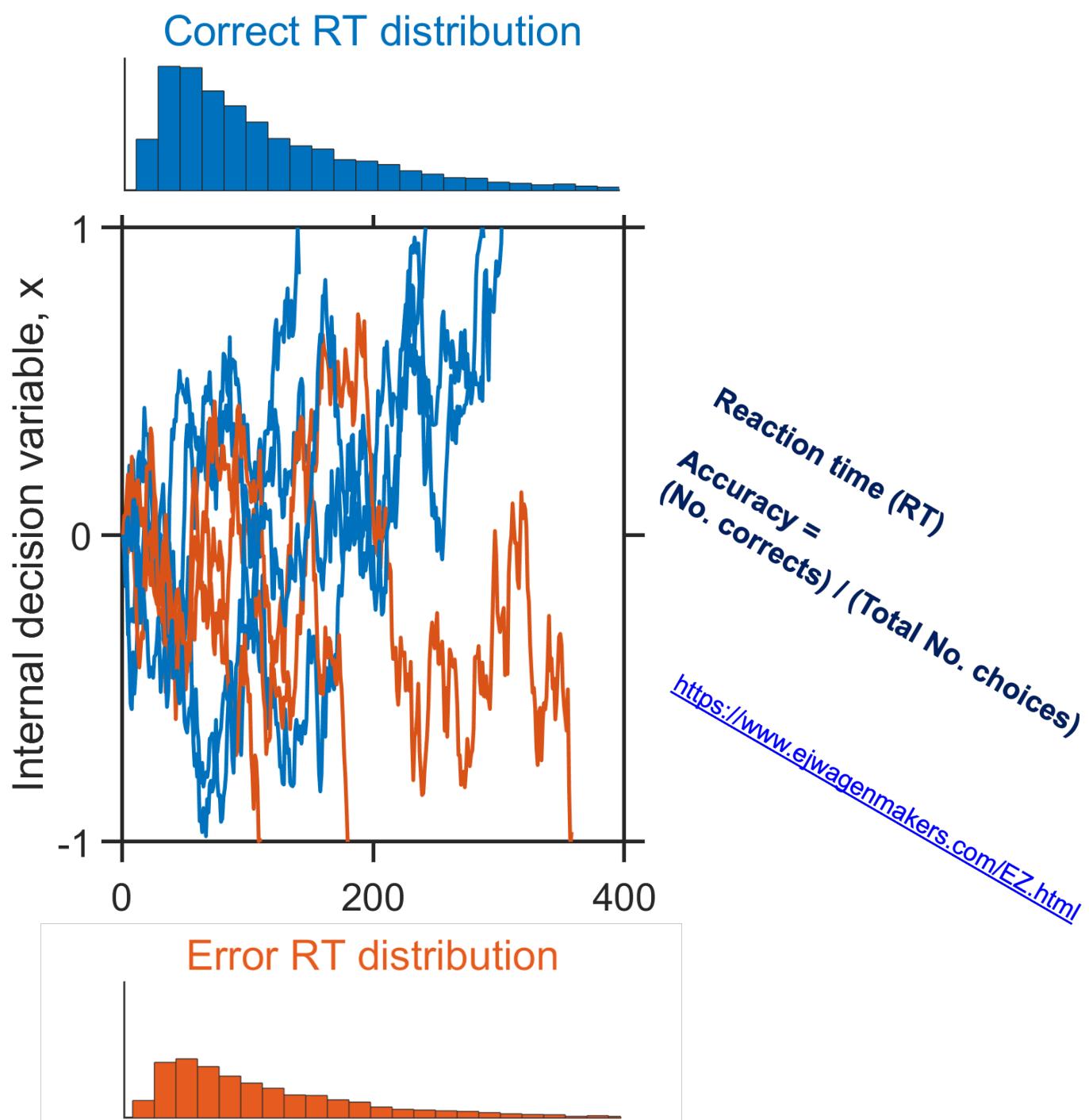


$$\begin{aligned} X = \int dX &= \int v dt + \sigma dW \\ &= \text{signal difference} + \text{noise} \end{aligned}$$

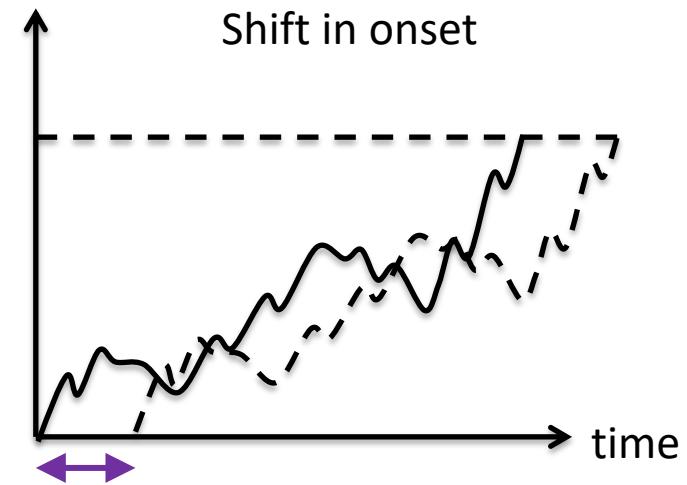
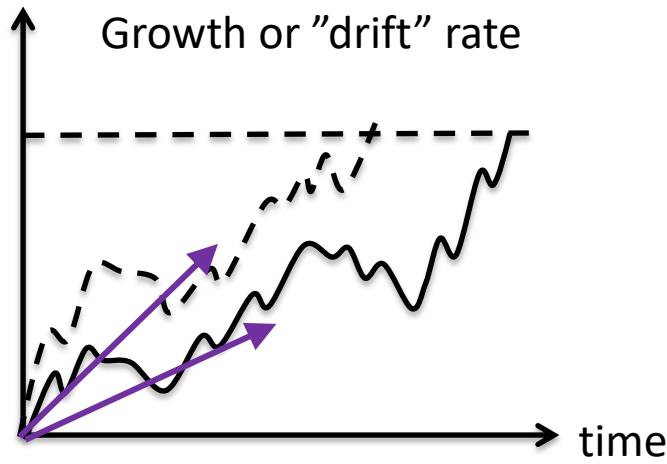
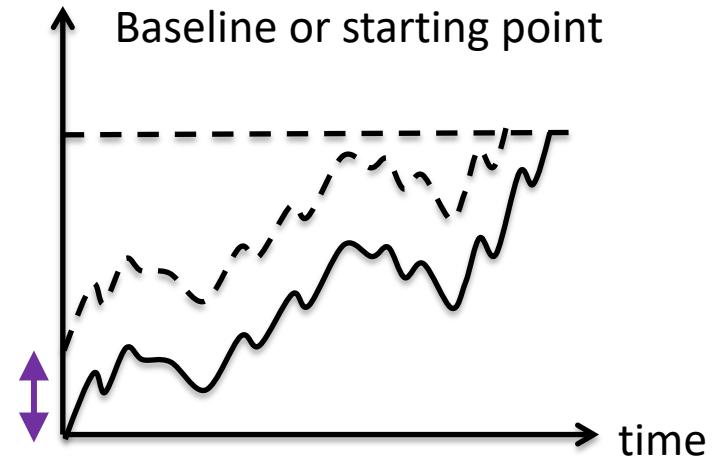
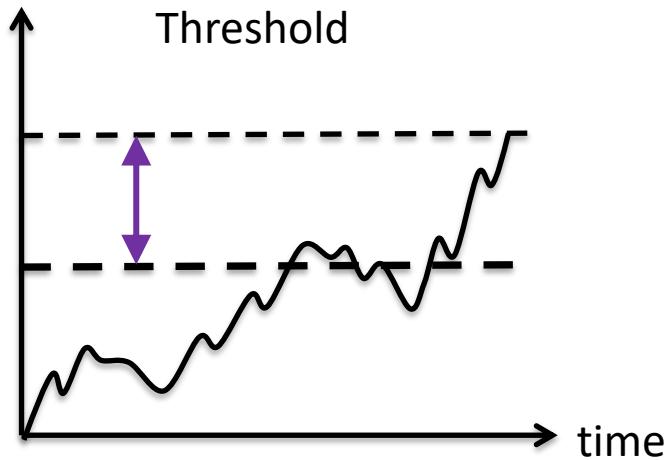
(Stochastic) Calculus

## Computer simulations

With upward drift rate (overall signal)



# “Biases” in decision making



*Drift rate and threshold can be time-dependent*

**Review**

# Bridging Neural and Computational Viewpoints on Perceptual Decision-Making

Redmond G. O'Connell,<sup>1,\*</sup> Michael N. Shadlen,<sup>2,3</sup> KongFatt Wong-Lin,<sup>4</sup> and Simon P. Kelly<sup>5,\*</sup>

**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

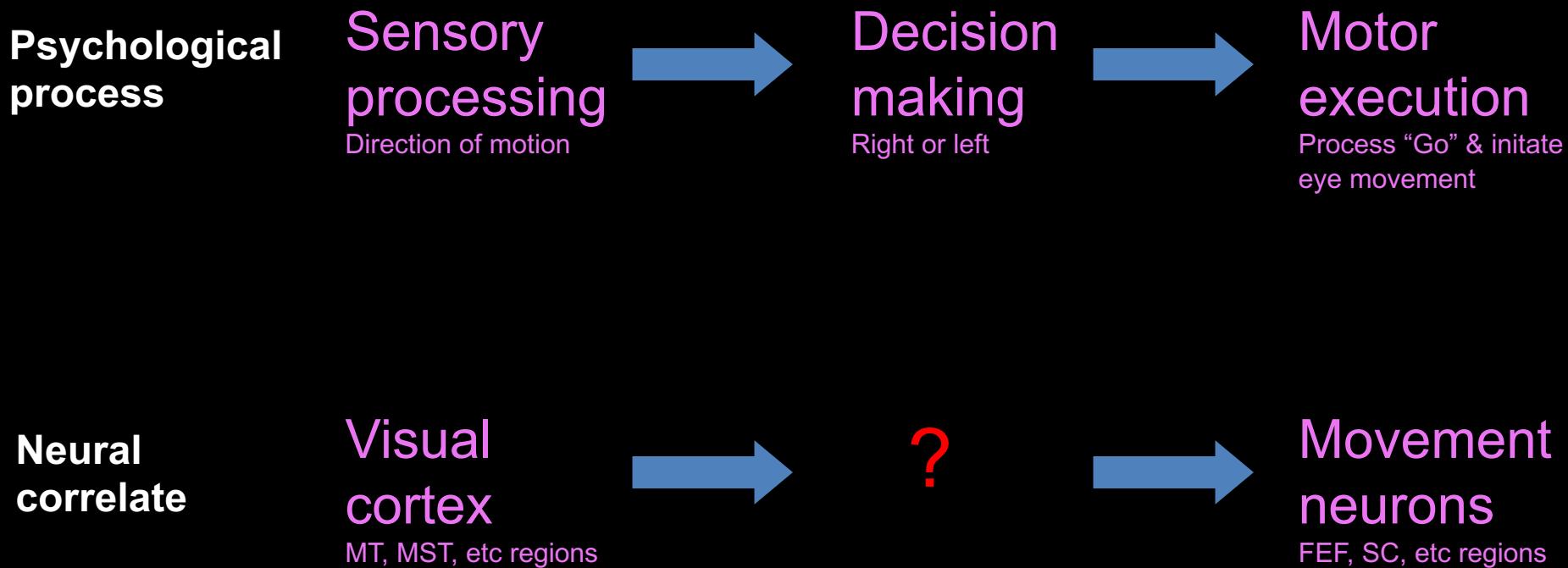
Sequential sampling models have been widely embraced in contemporary decision neuroscience. The models come in many forms that, despite containing fundamentally different algorithmic elements, can make highly similar predictions for behaviour. Consequently, it can be difficult to definitively adjudicate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

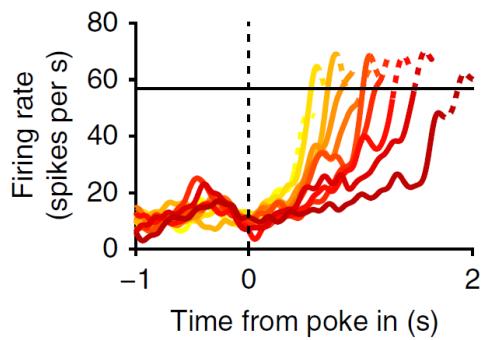
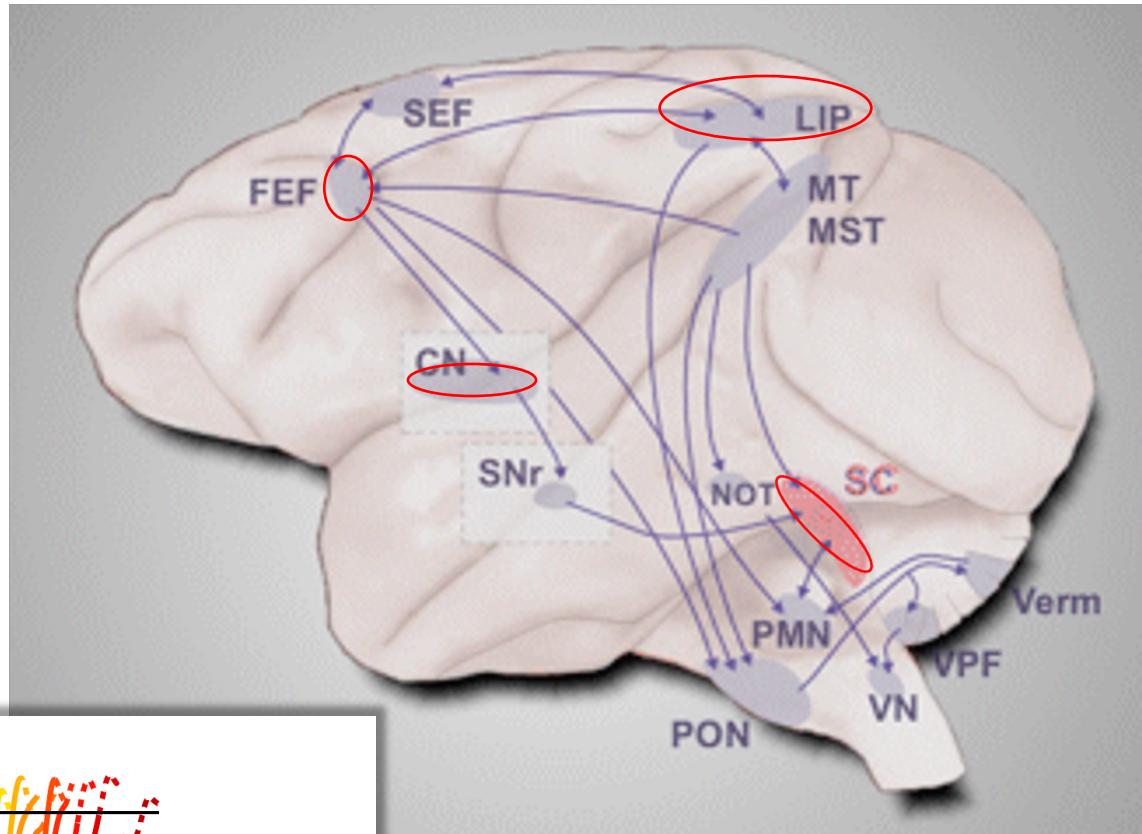
# Is there evidence in brain physiology of such processes in perceptual decision-making?

# Neural correlates of perceptual decision making



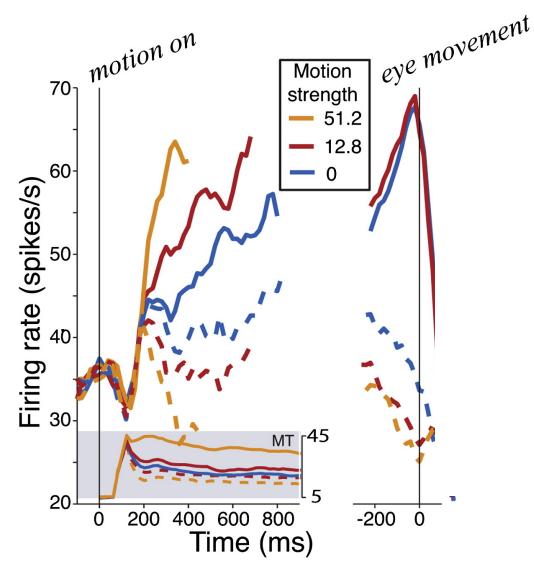
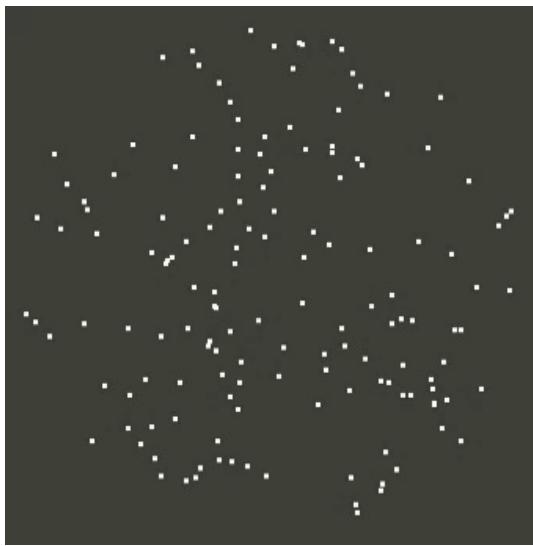
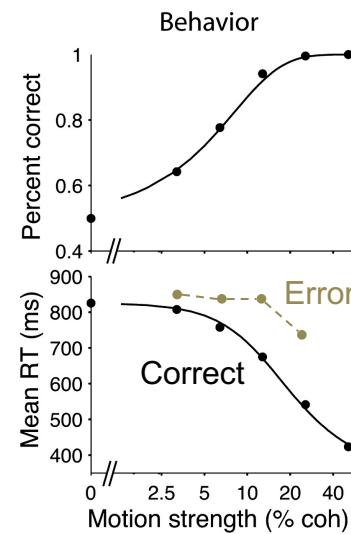
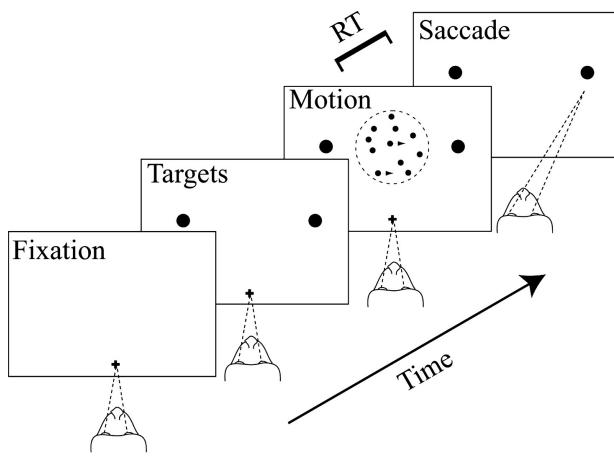
# Brain circuitry controlling (saccadic) eye movements

The search for “neural integrators” in the brain



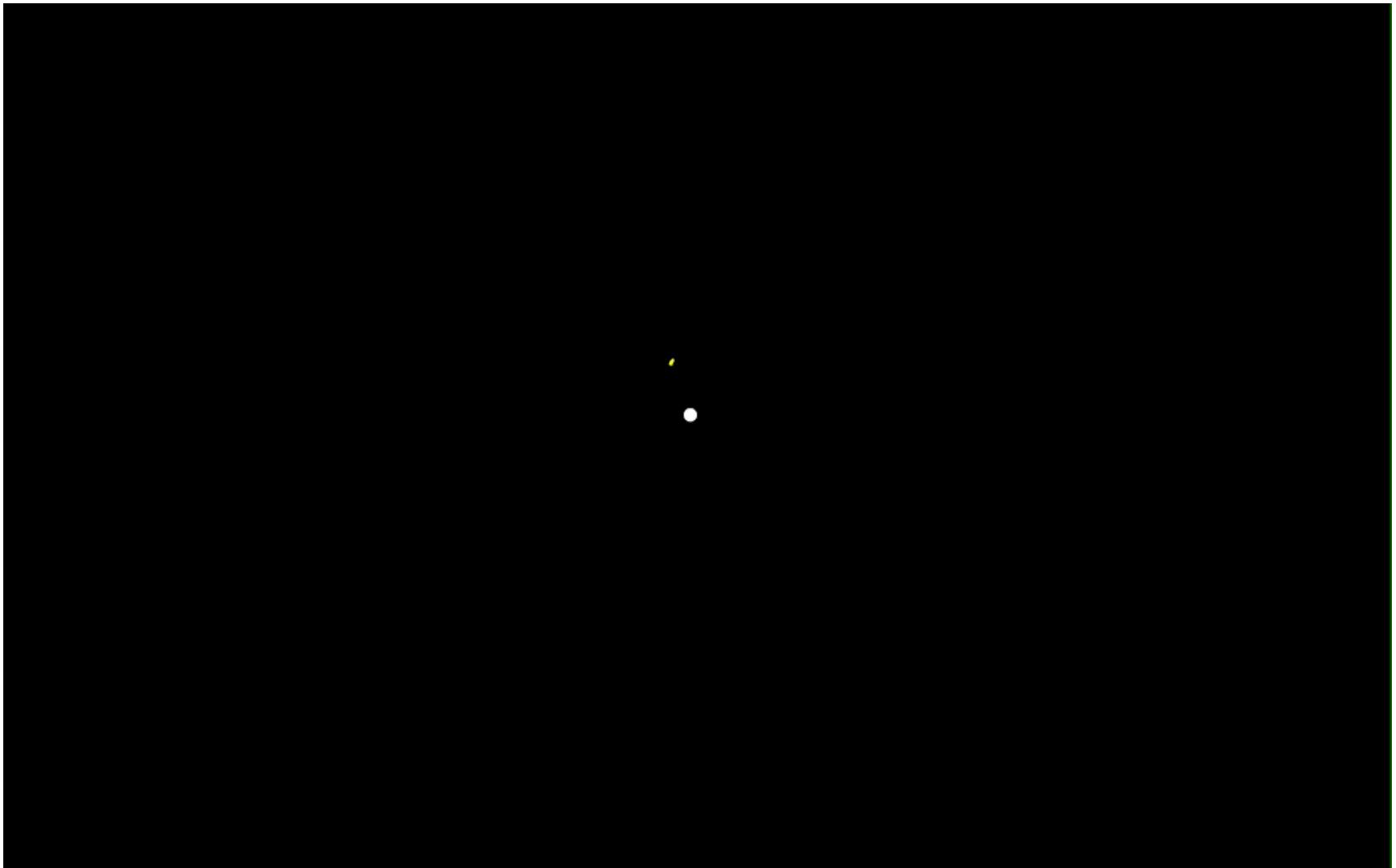
$$\int \dots dt$$

# Classic experiment

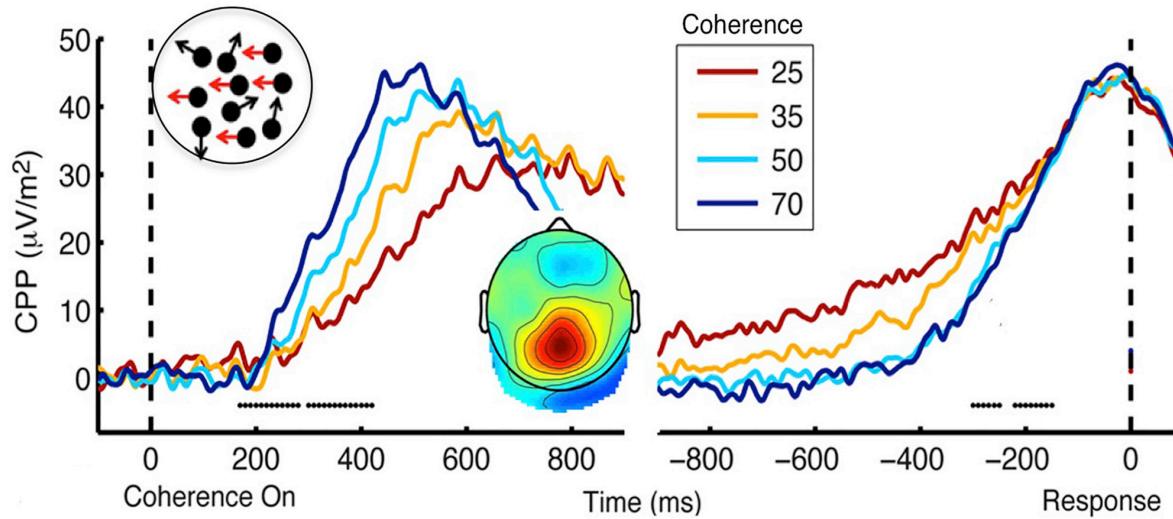


Neuronal population in area LIP (lateral intraparietal area)

## **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)?**

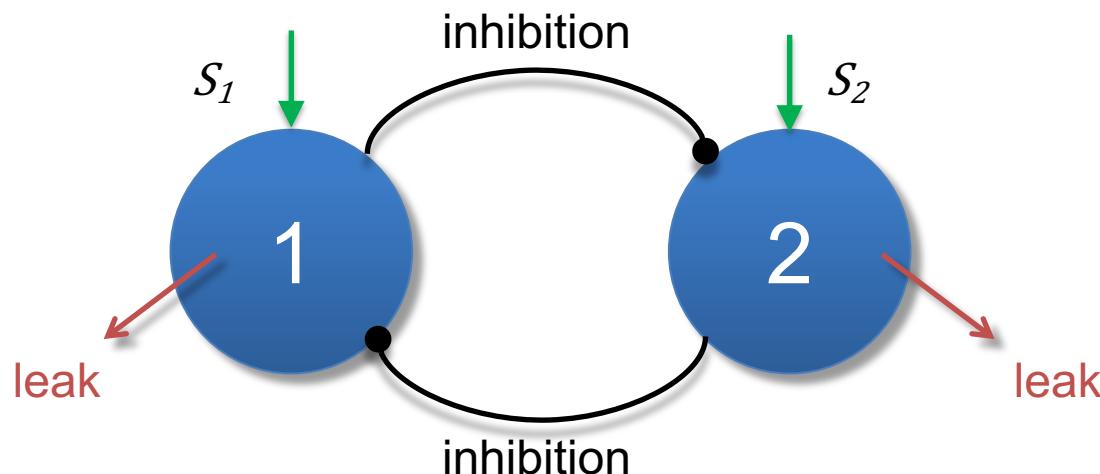
# A simple neural network model

Leaky Competing Accumulator (LCA) model

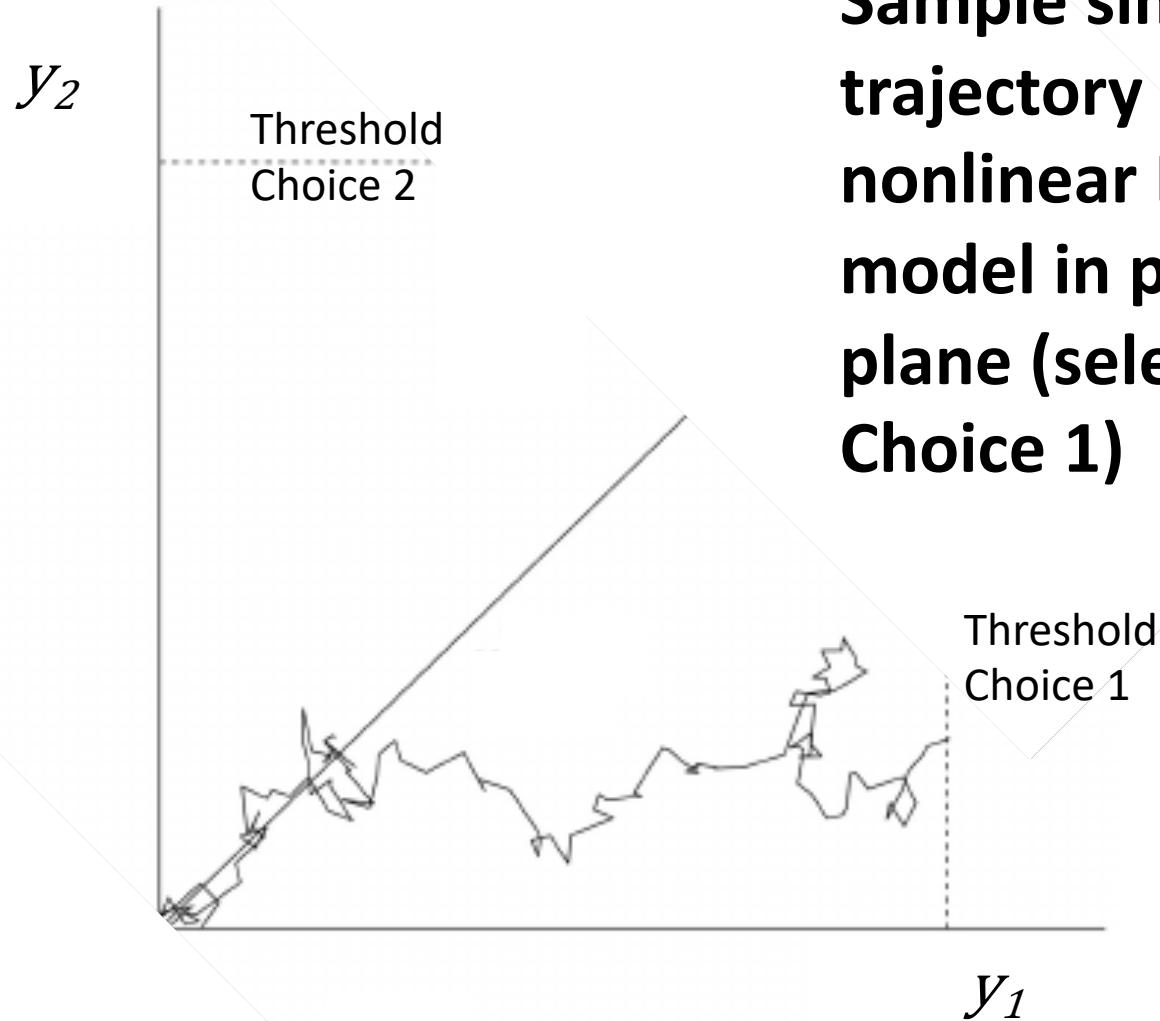
The decision process as the integration of evidence by competing accumulators – *winner-take-all* behaviour is necessary, or there will be conflict and indecisiveness.

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

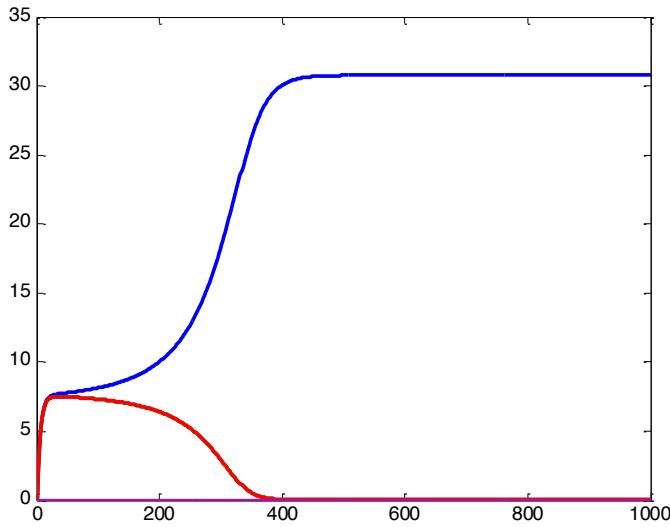
Usher & McClelland (1995, 2001)



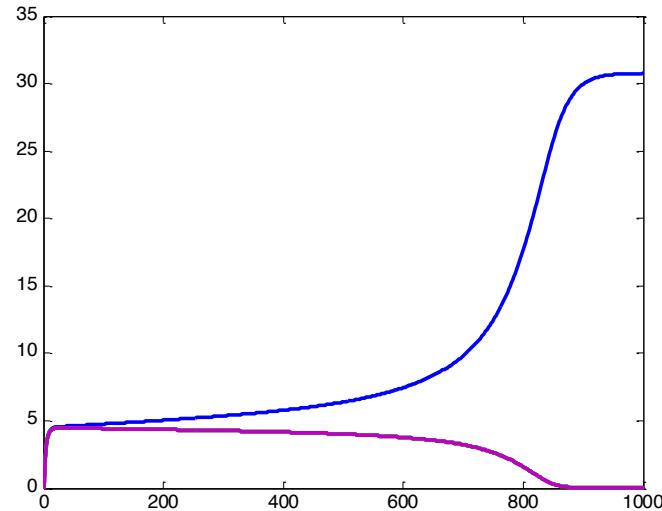
**Sample simulated trajectory of nonlinear LCA model in phase plane (selecting Choice 1)**



# 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

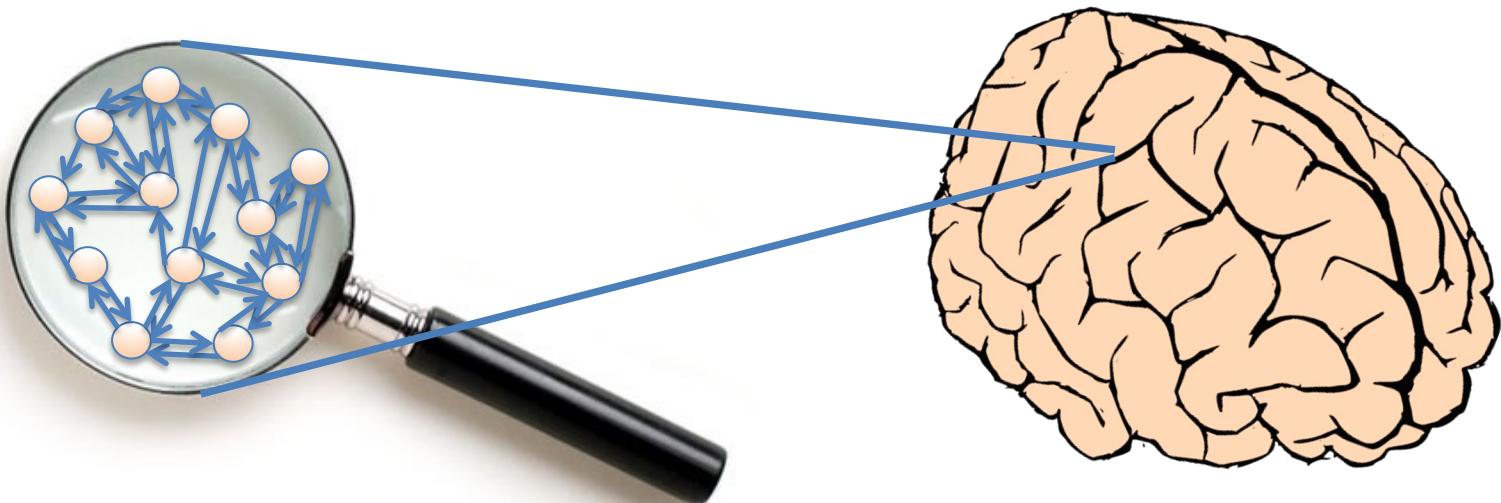


With 5 choices  
(long latency or  
response time)  
Note: The other 3 neural  
populations follow the  
same dynamics as purple

**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.

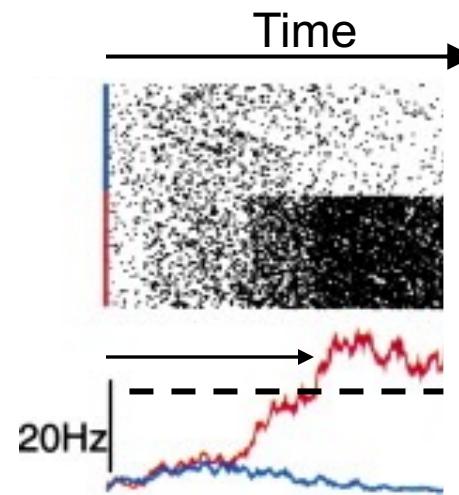
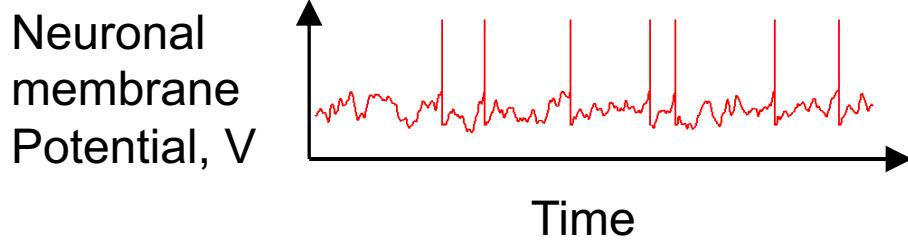
# A network of neurons and emergent behaviour



## 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

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

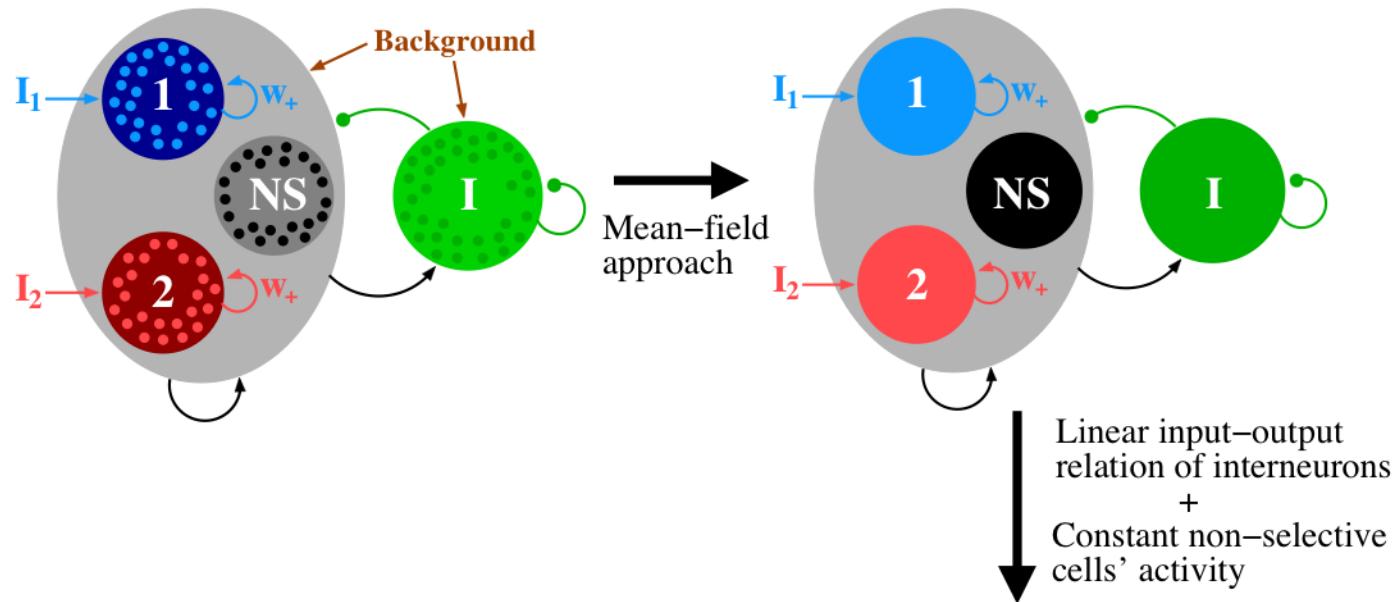
Dynamics describing the averaged (slow) synaptic dynamics for the neural population

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

(with interspike interval distribution  $\sim$  Poisson)

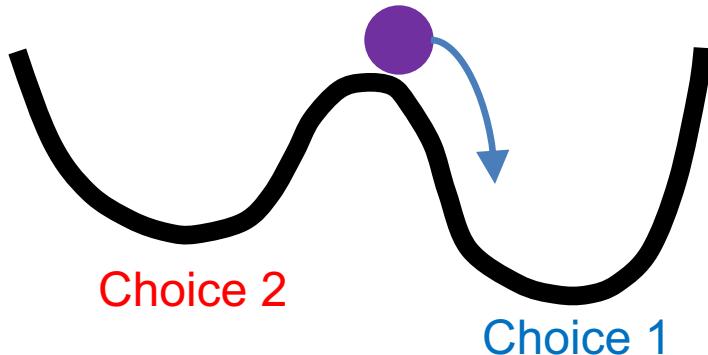
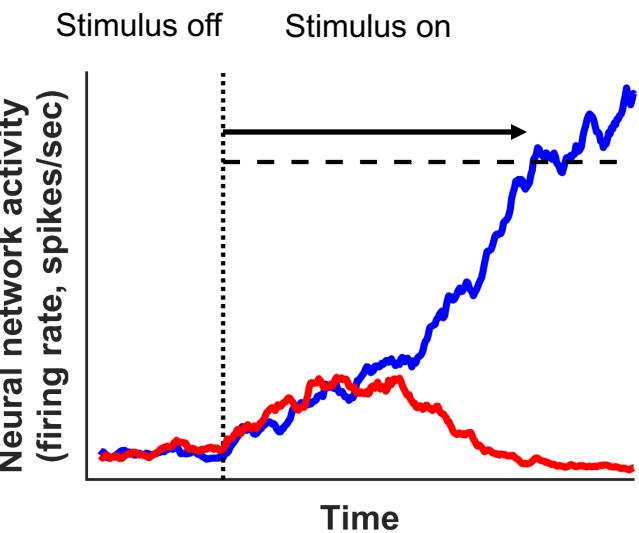
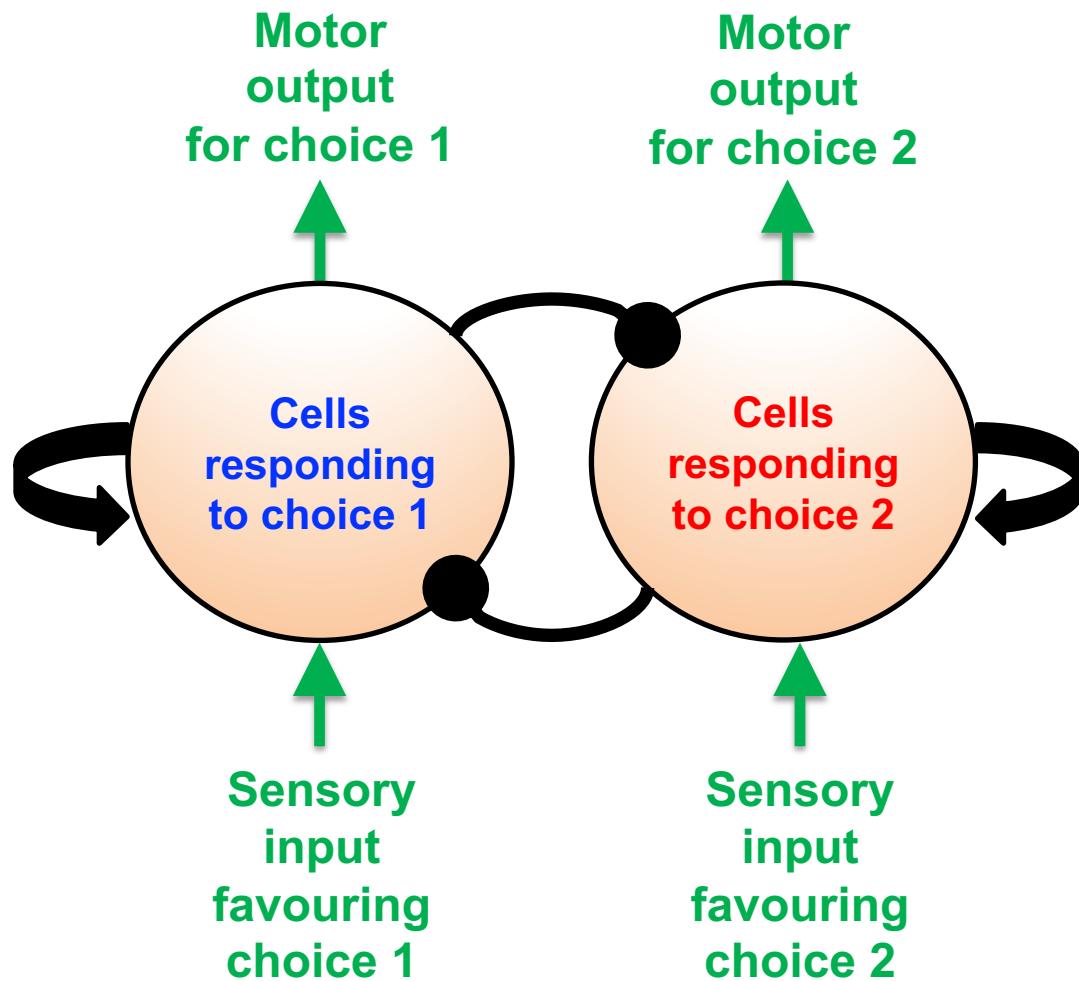
# Reducing a biophysical model of decision-making

Spiking neuronal network model



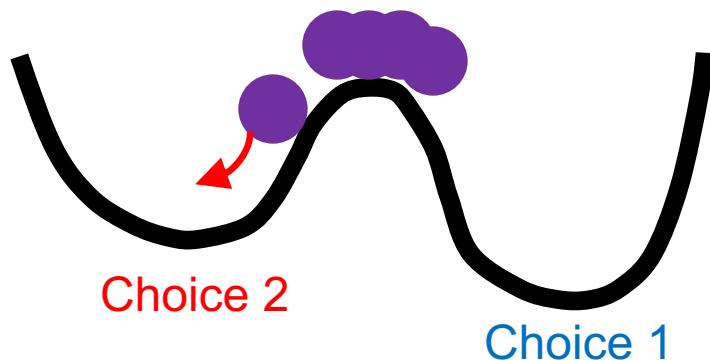
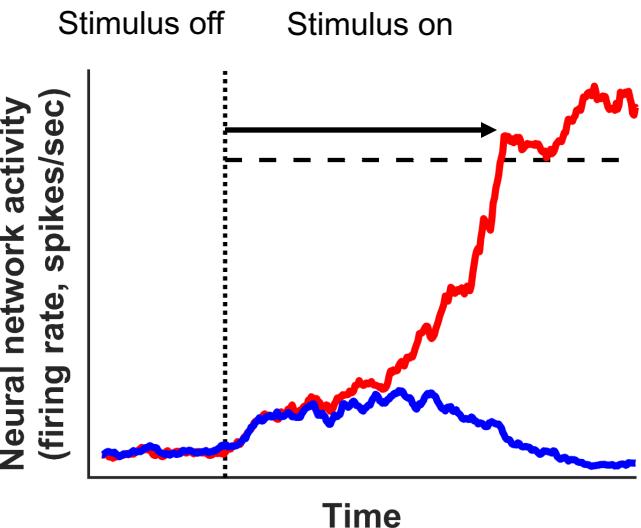
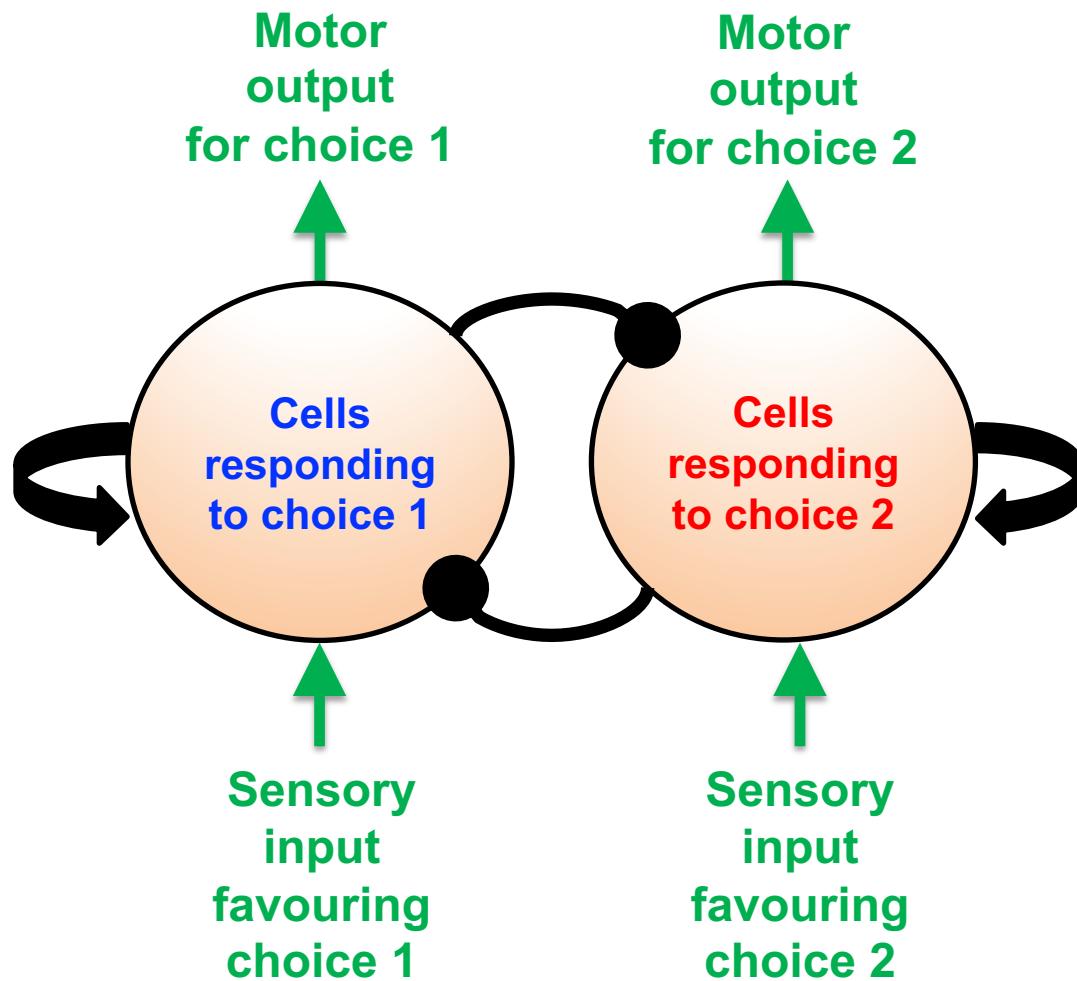
Reduced two-variable model

# A simpler biologically based neural network model



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

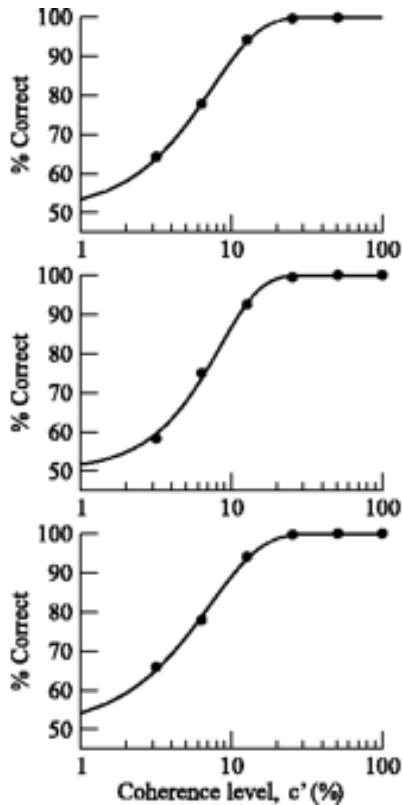
# A simpler biologically based neural network model



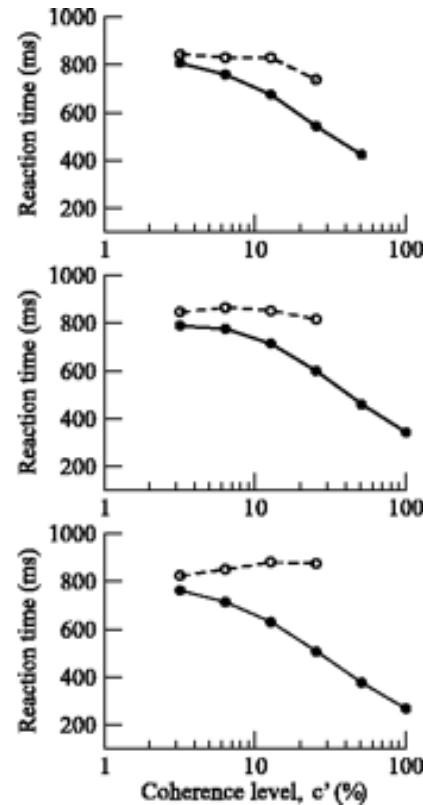
*Wong and Wang, J. Neurosci. (2006)*  
*Roxin and Ledberg, PLoS Comput. Biol. (2008)*

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

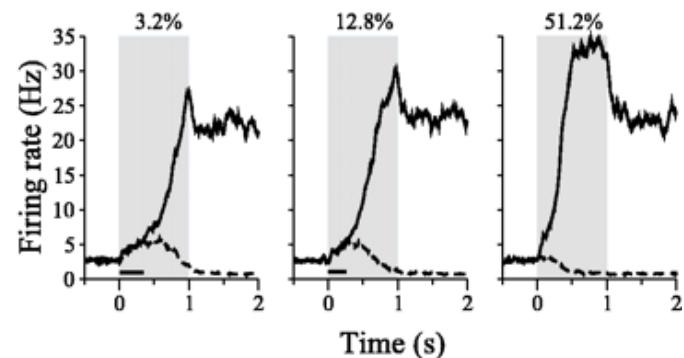
Experimental data



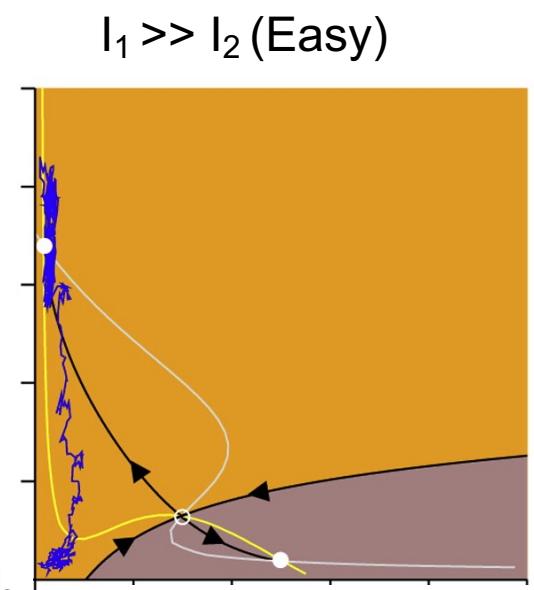
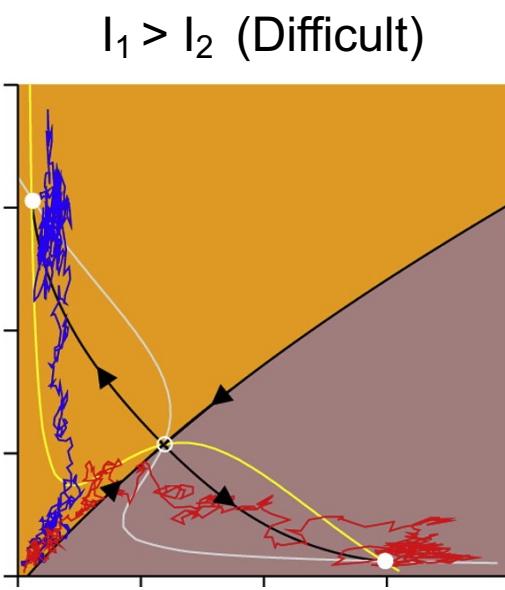
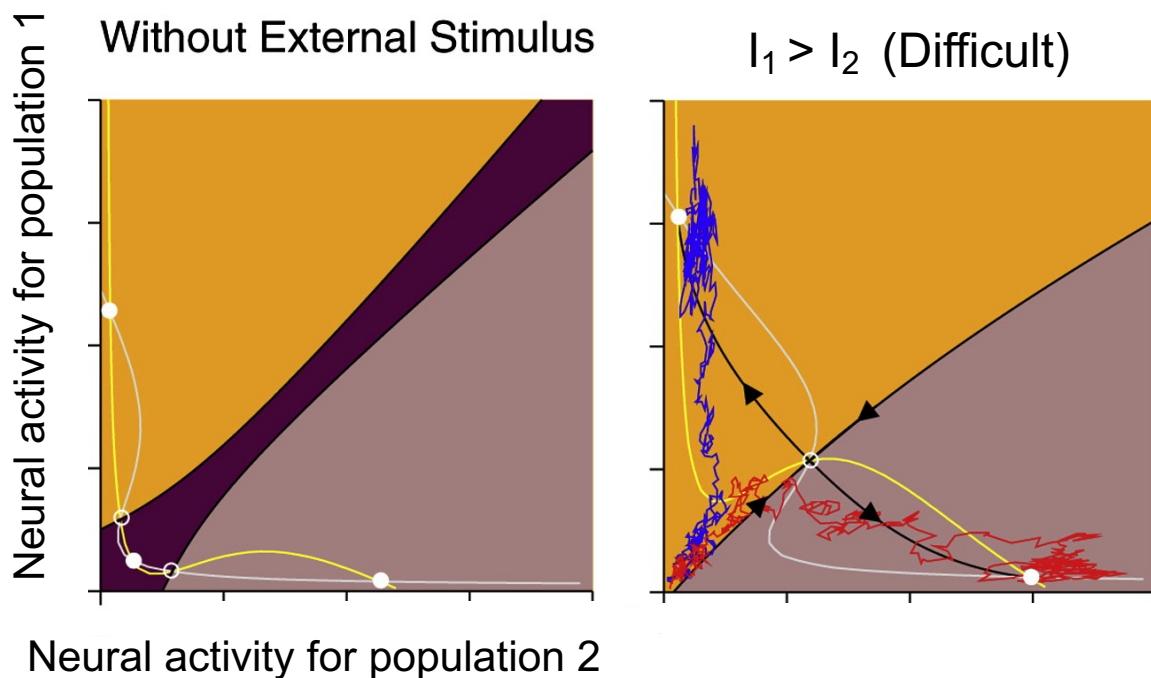
Spiking  
neuronal  
network  
model



Reduced  
two-variable  
model

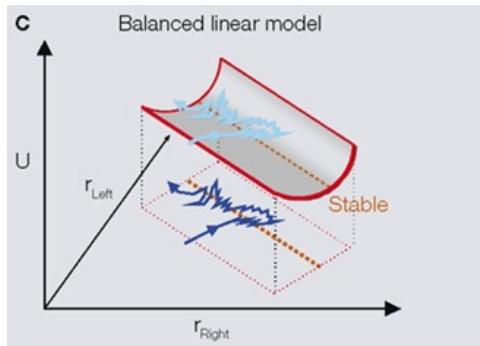
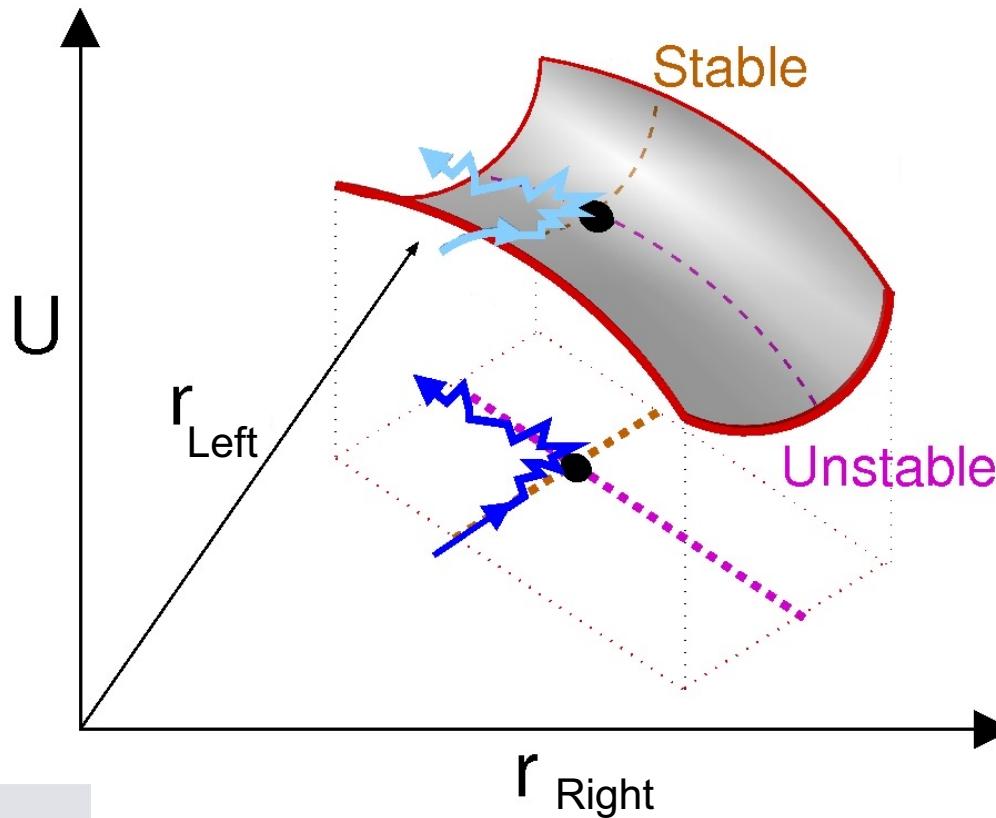


# Phase-plane analysis of attractor network model



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

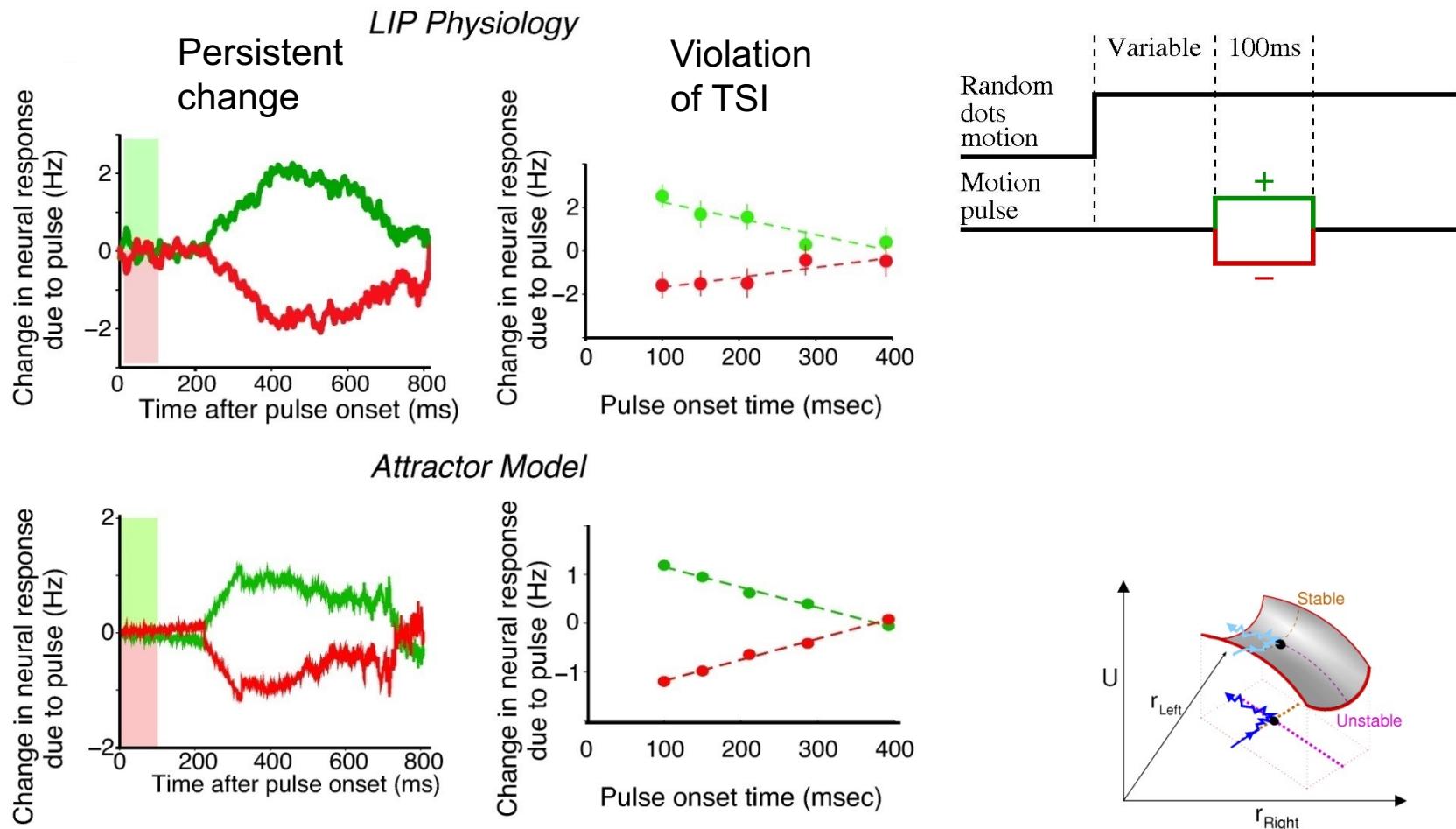
# “Potential energy” landscape in phase space



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

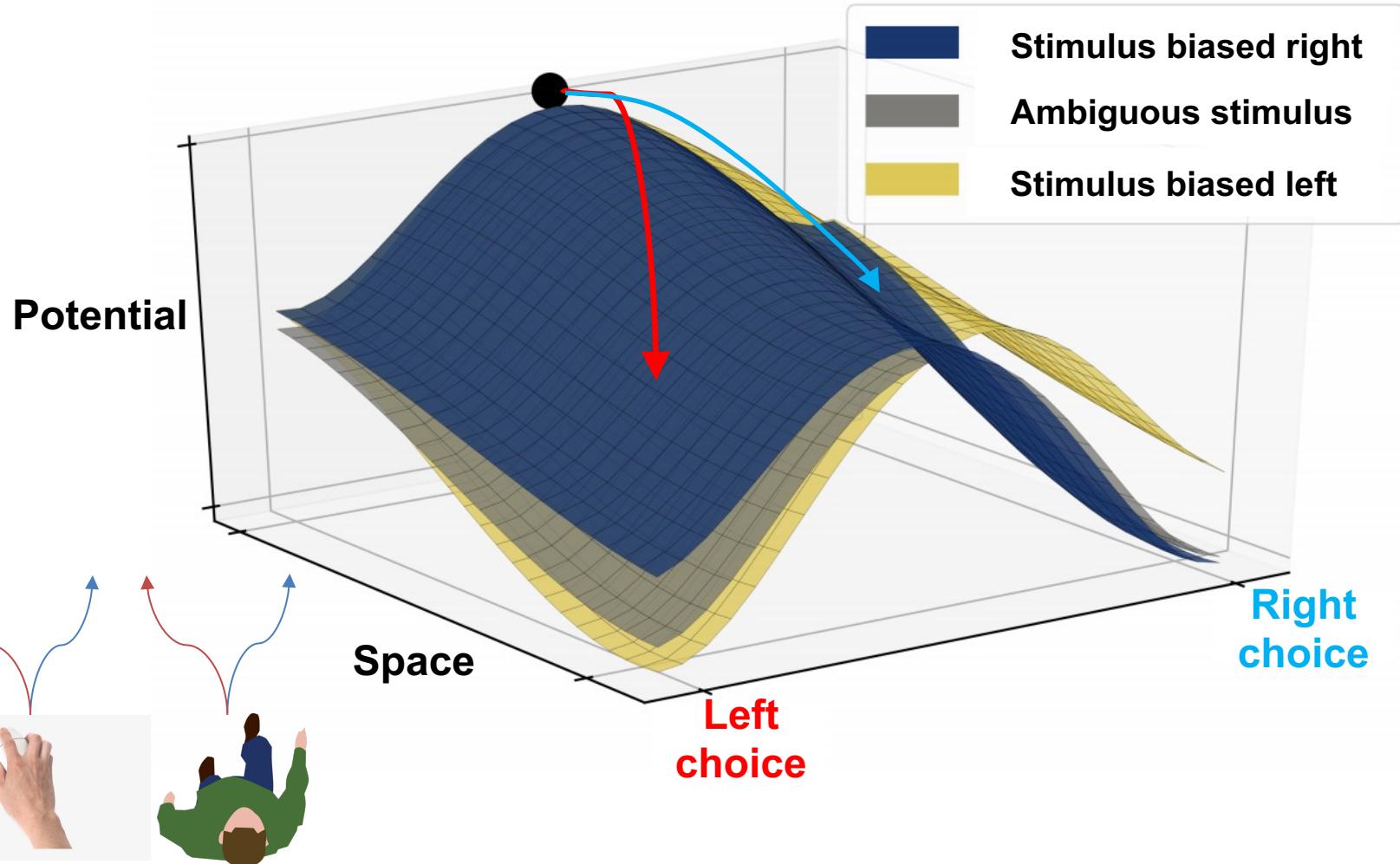
Wong & Huk, *Front. Neurosci.* (2008)

# Attractor network model with “runaway” temporal integration can account for violation of “time shift invariance (TSI)”



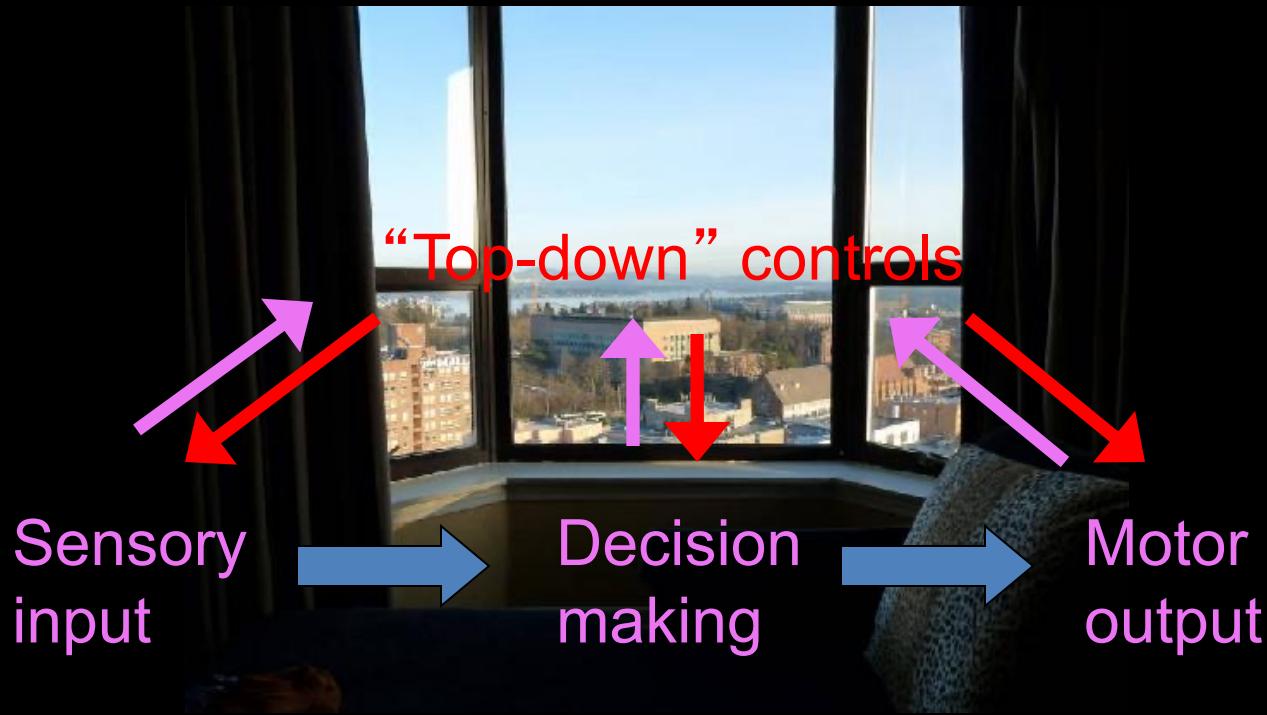
# “Potential energy” landscape in space

Reconstructed from walking or computer mouse trajectories



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

# 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**

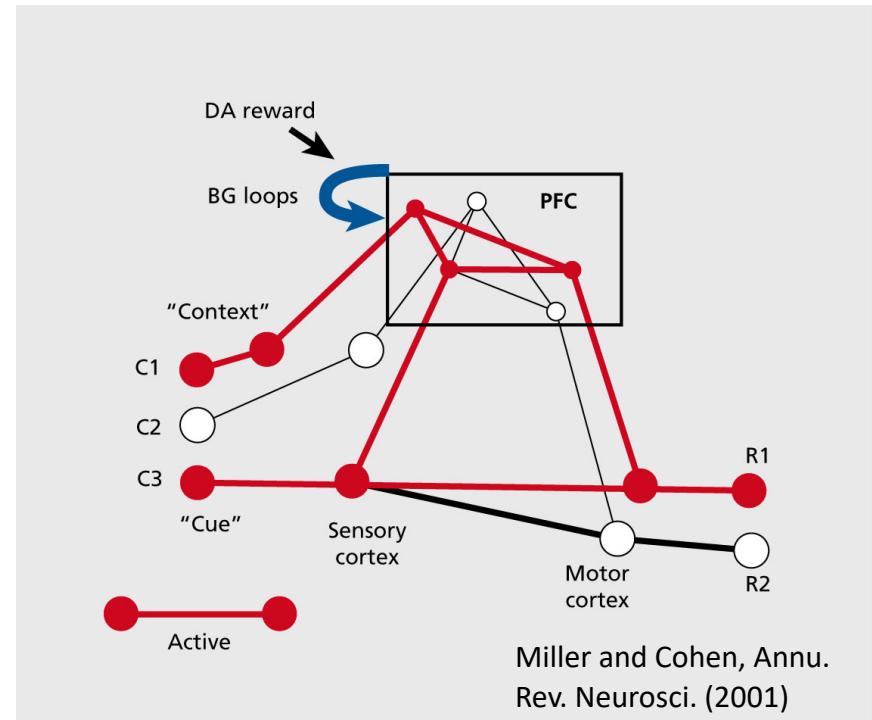
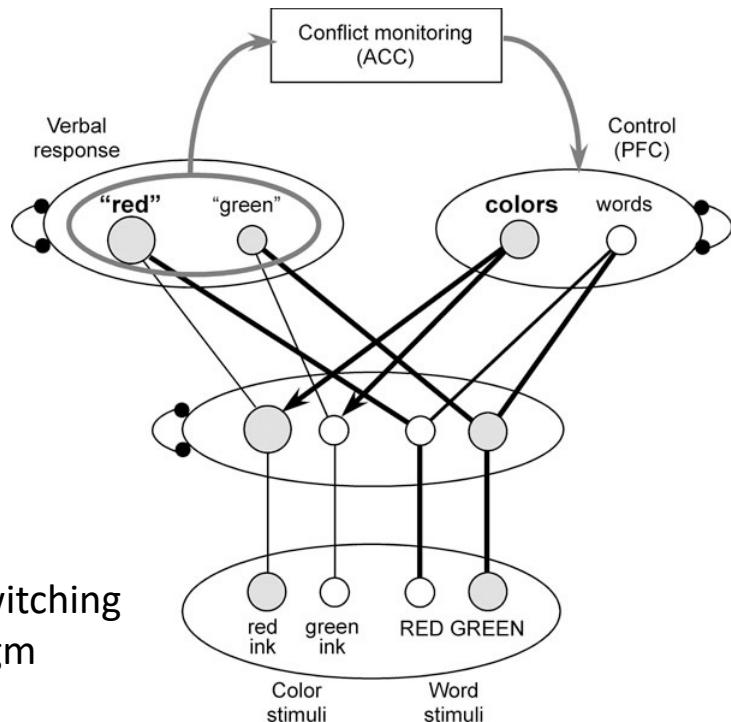
**WHITE**

**BROWN**

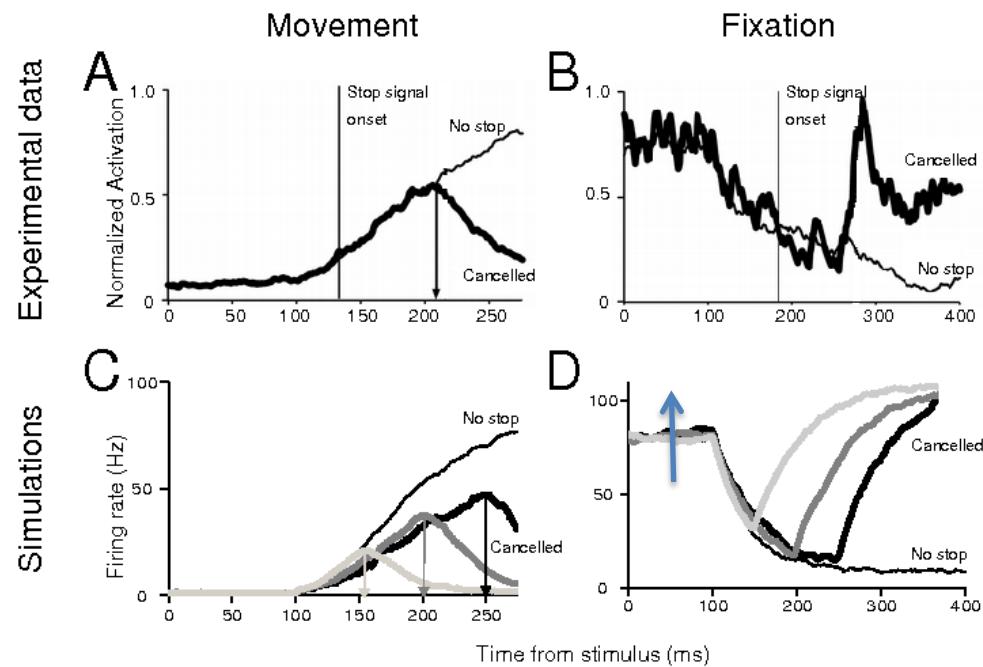
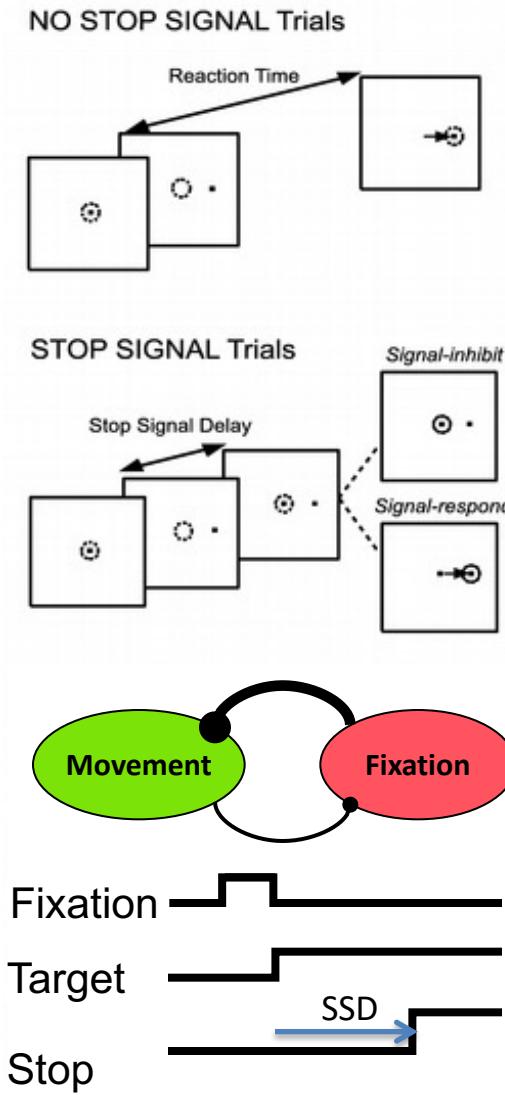
# Cognitive control

E.g. task-switching

- How do you learn the rules when they are not explicitly told?
- You make initial mistakes, and you learn from them. Reinforcement Learning. Dopamine (DA). Or you get supervised. You need to know or expect what choices are rewarded or valuable to make. Making choices/actions can enhance your knowledge about the underlying rule.



# Proactive inhibition of an impending decision



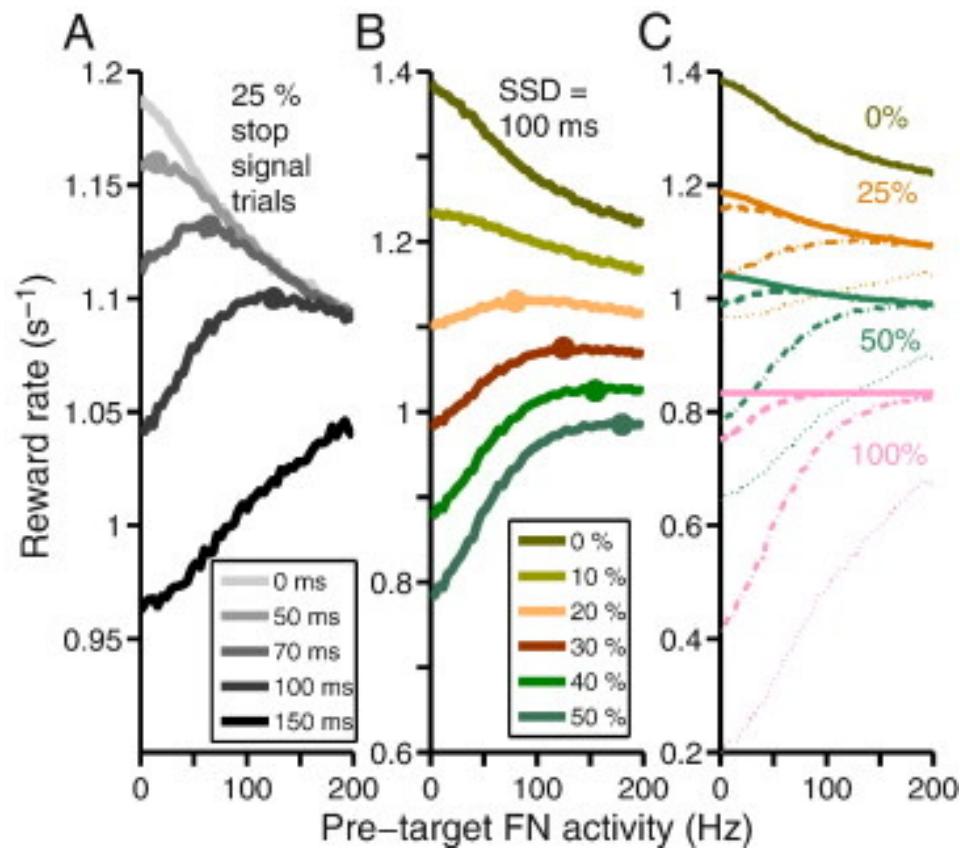
Wong-Lin, Eckhoff, Holmes & Cohen, *Brain Res.* (2010)  
Yang, McGinnity & Wong-Lin, *Front. Neuroeng.* (2012)

# Optimal inhibitory control

There is a speed-accuracy tradeoff!  
More stopping → more accurate, but  
slower response times.

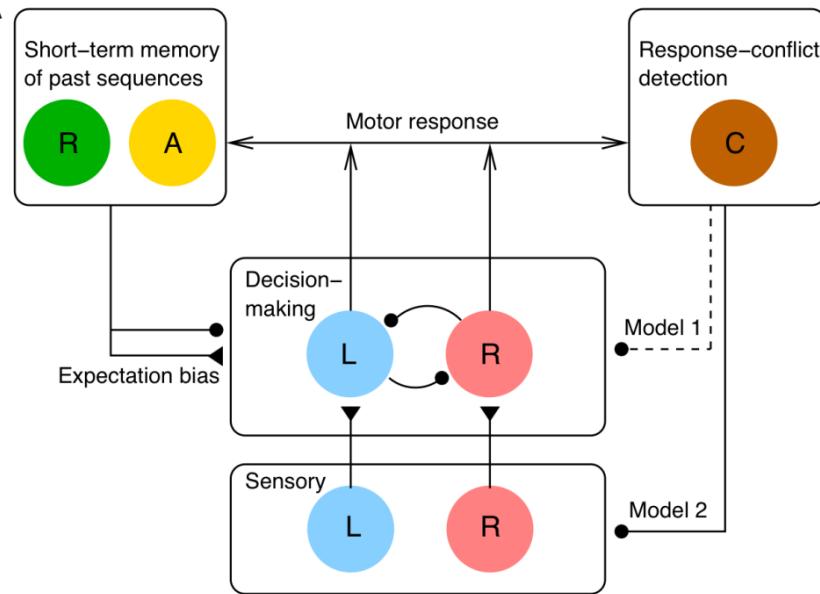
Reward rate, R, as a measure of  
inhibition control performance.

Optimal inhibitory control with  
respect to some model parameter  
(e.g. prior inhibitory strength) or task  
parameter (e.g. inter-trial interval, %  
stop signal trials) p:  $dR/dp = 0$ .

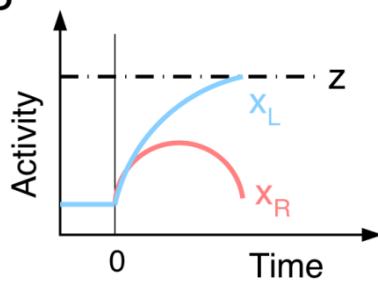


# Sequential effects in simple decisions

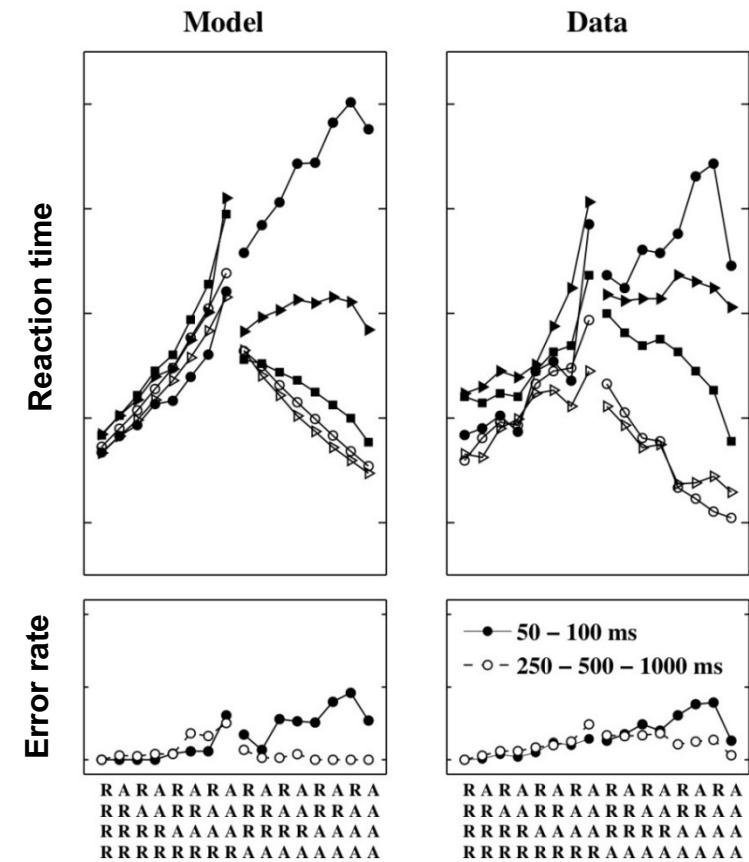
A



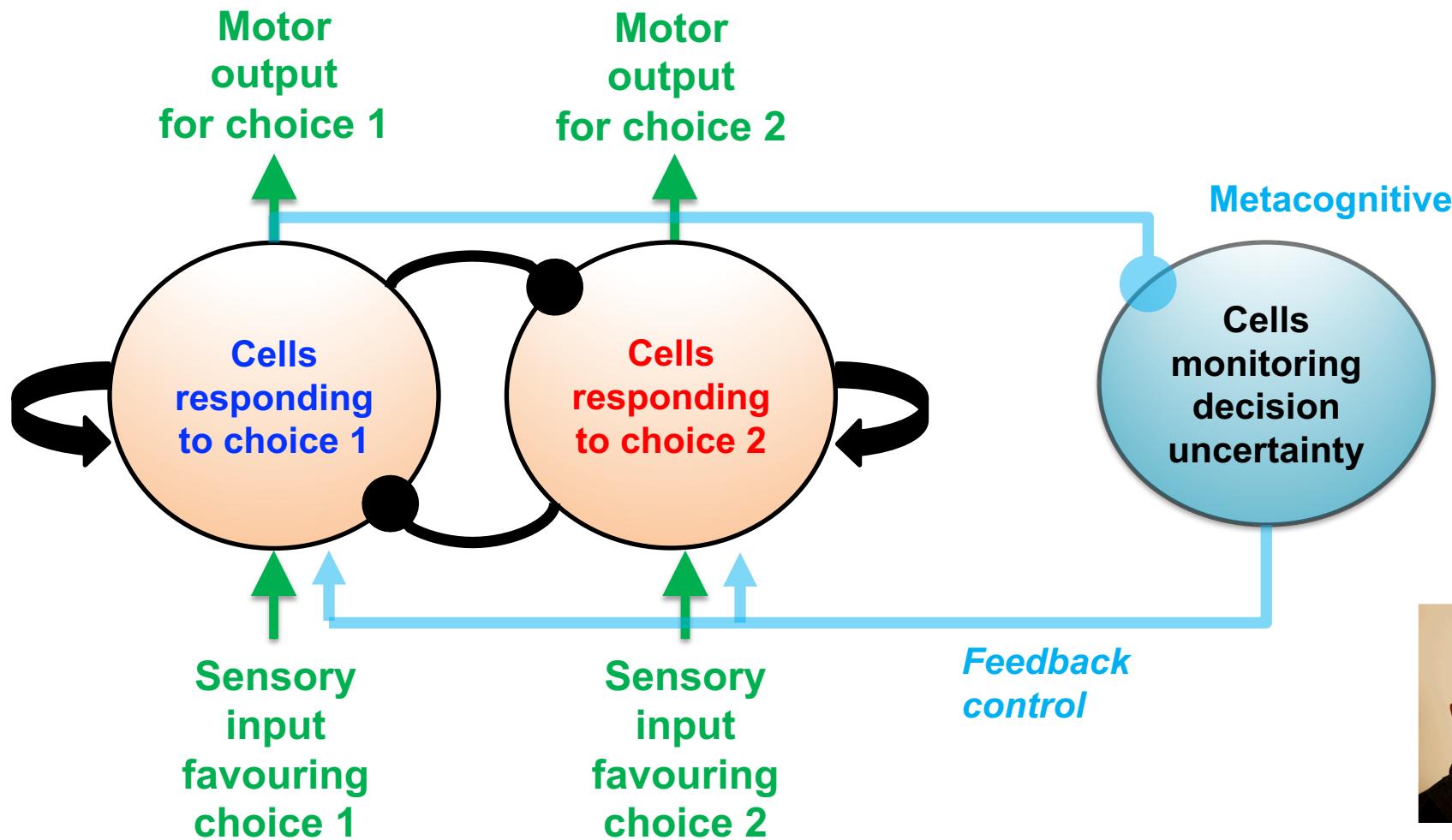
B



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



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

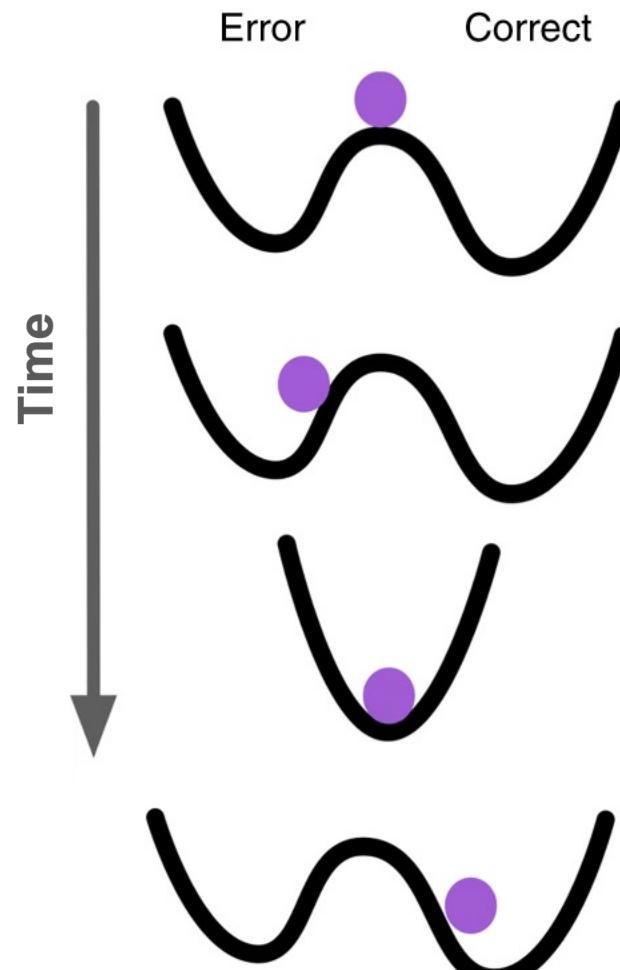
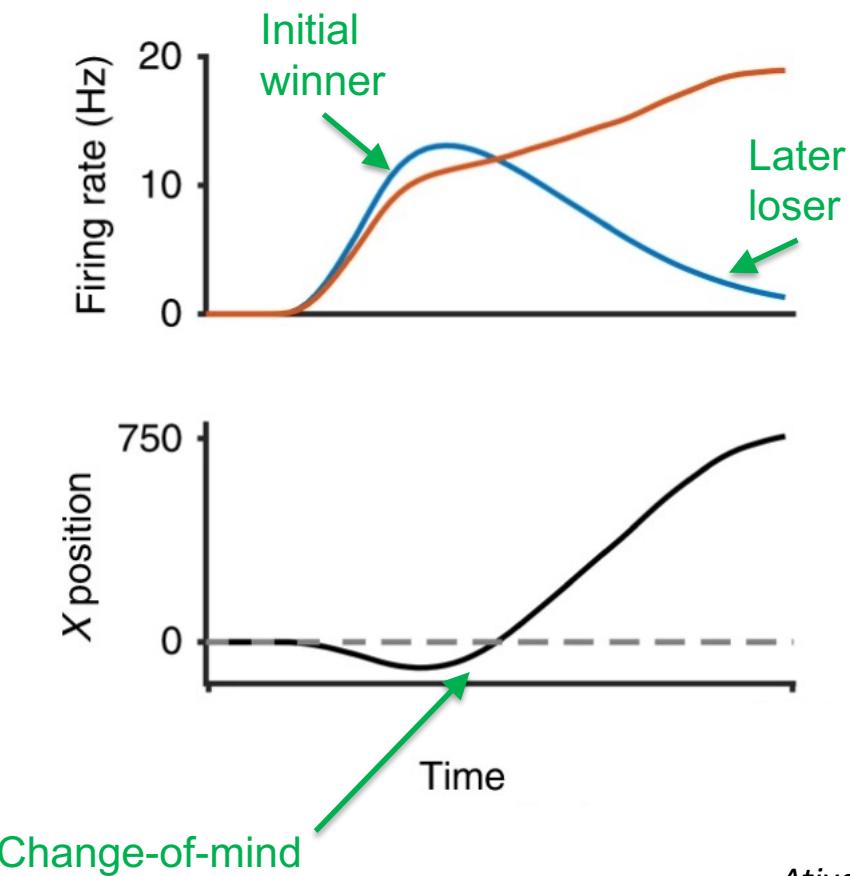


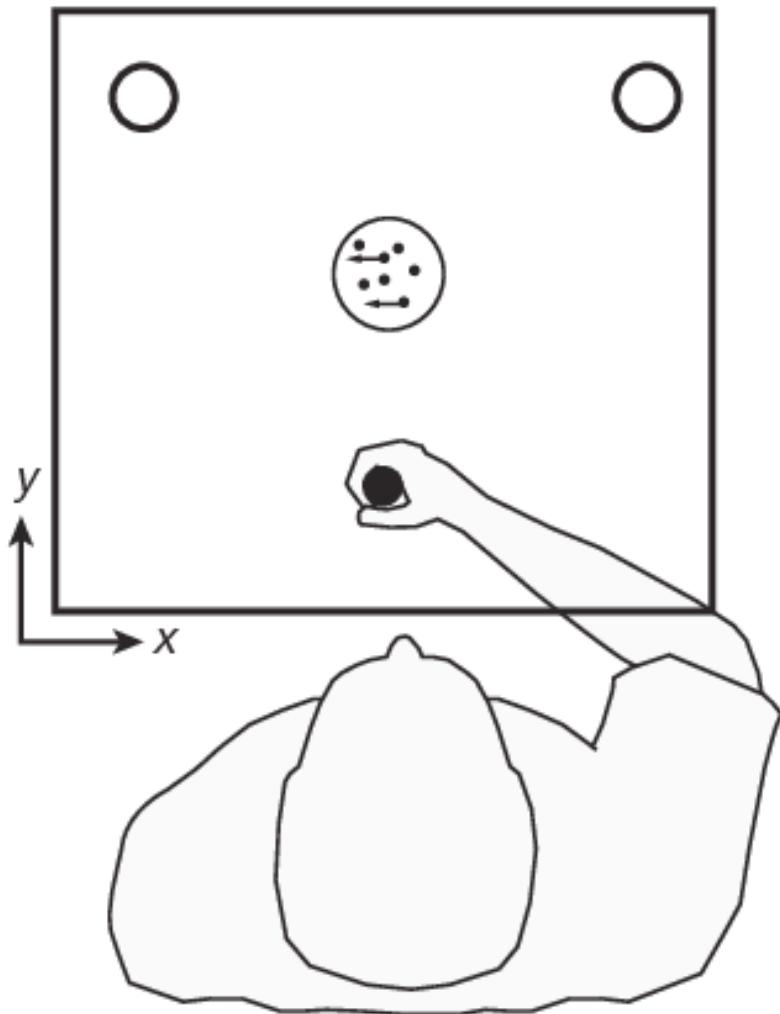
Nadim Atiya

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

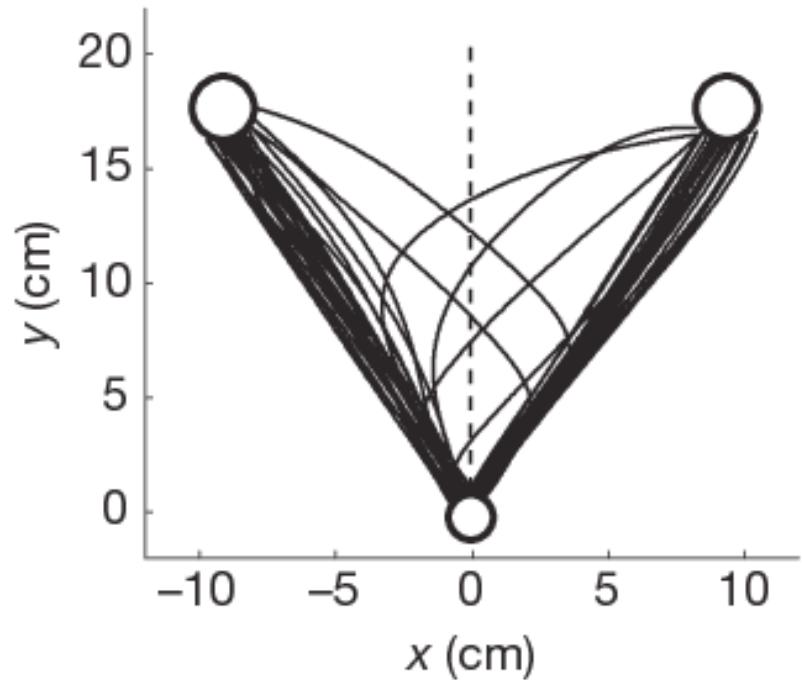
Atiya, Zgonnikov, O'Hora, Schoemann, Scherbaum & Wong-Lin, *PLoS Comput. Biol.* (2020)

# Model provides an explanation for change-of-mind





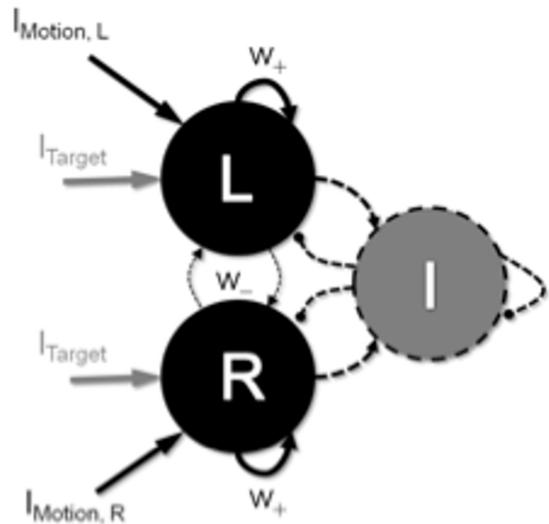
## Change-of-mind behaviour observed in experiments



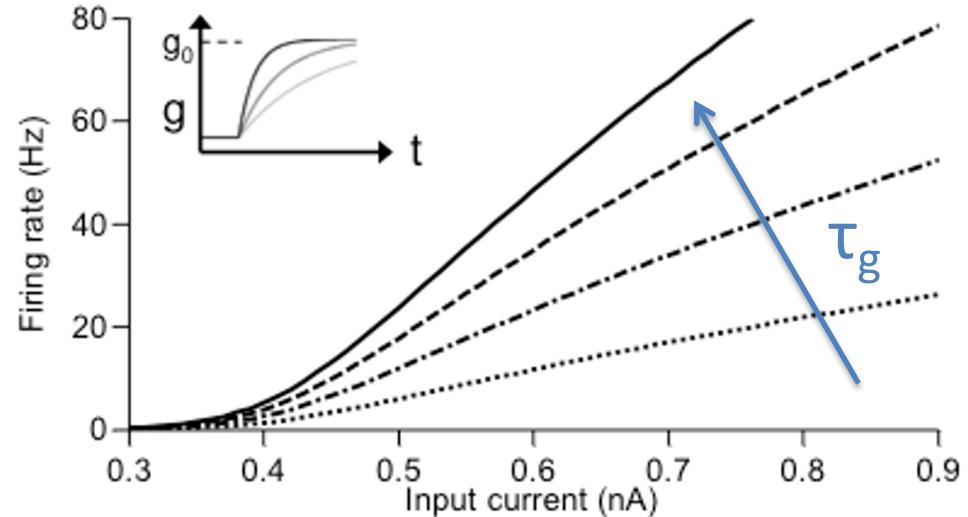
Resulaj, Kiani, Wolpert & Shadlen (2009) *Nature*

# Dynamic gain modulation on excitatory and inhibitory neurons

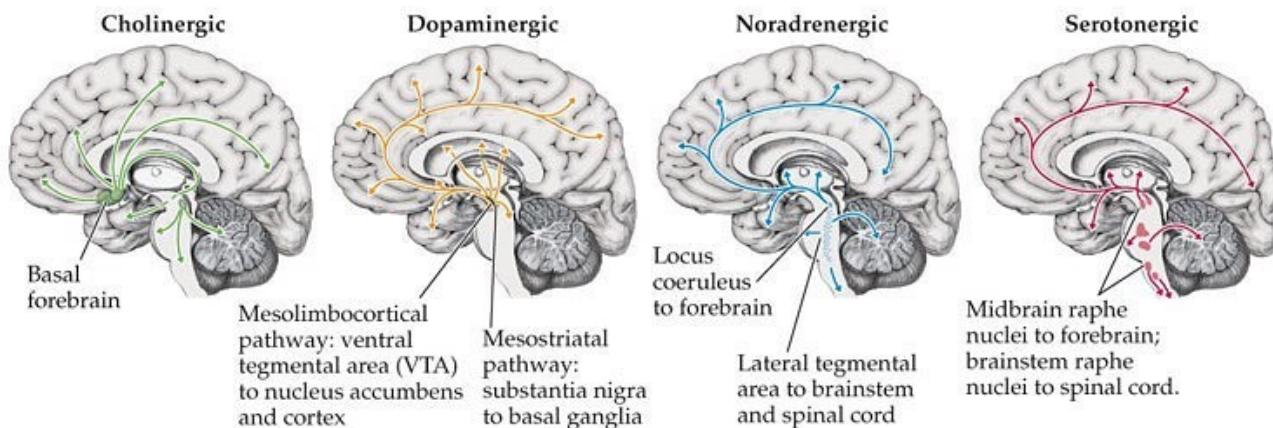
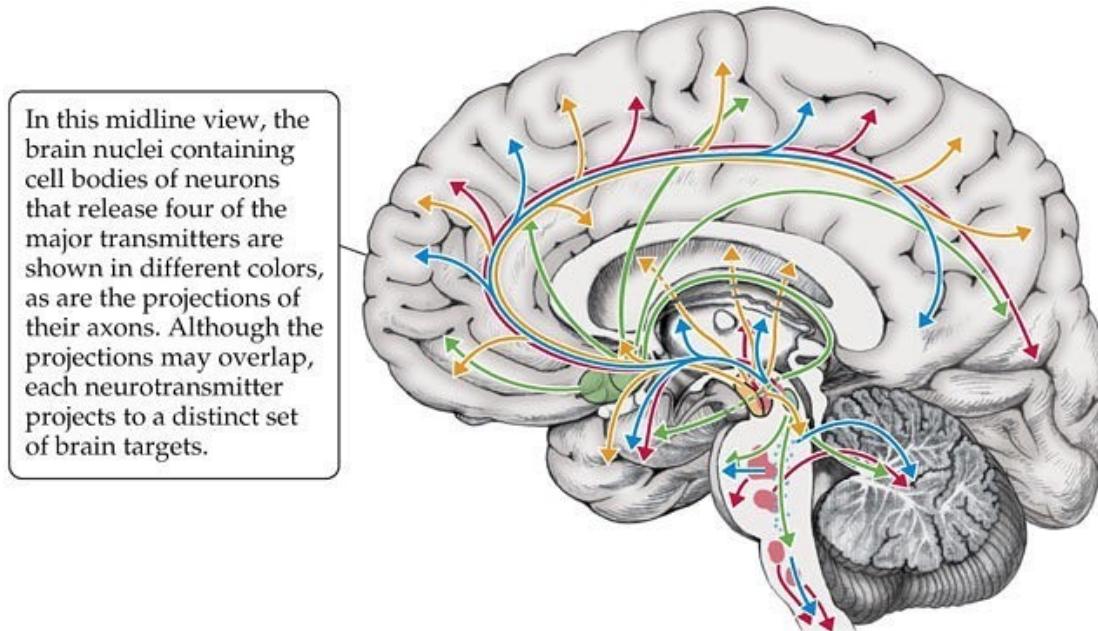
Motivated by attention-induced and urgency studies



Single-cell input-output (response) function with different gains

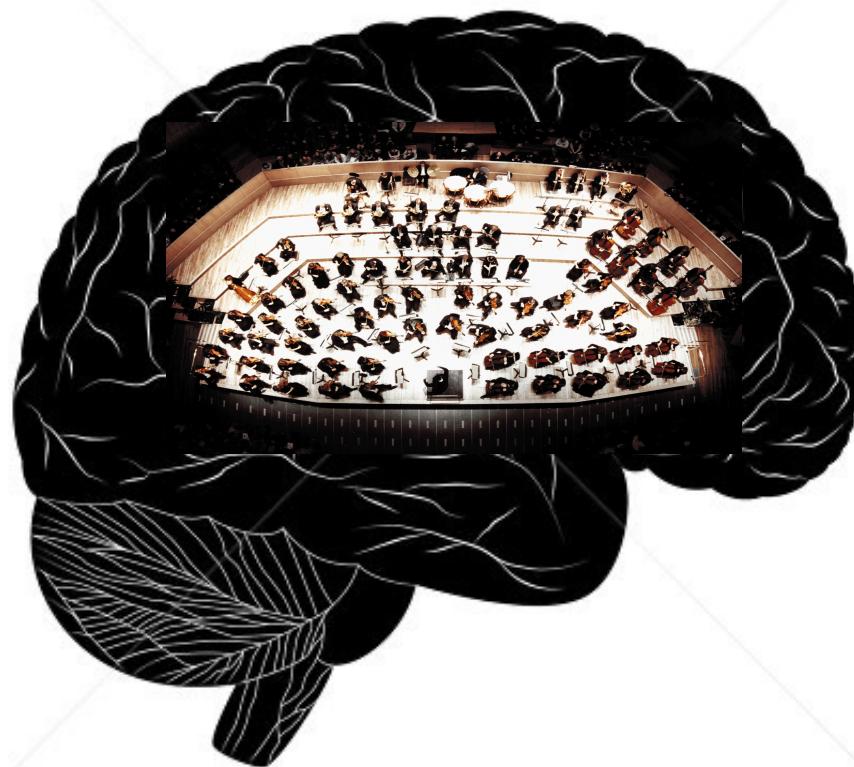


# Chemical neuromodulation

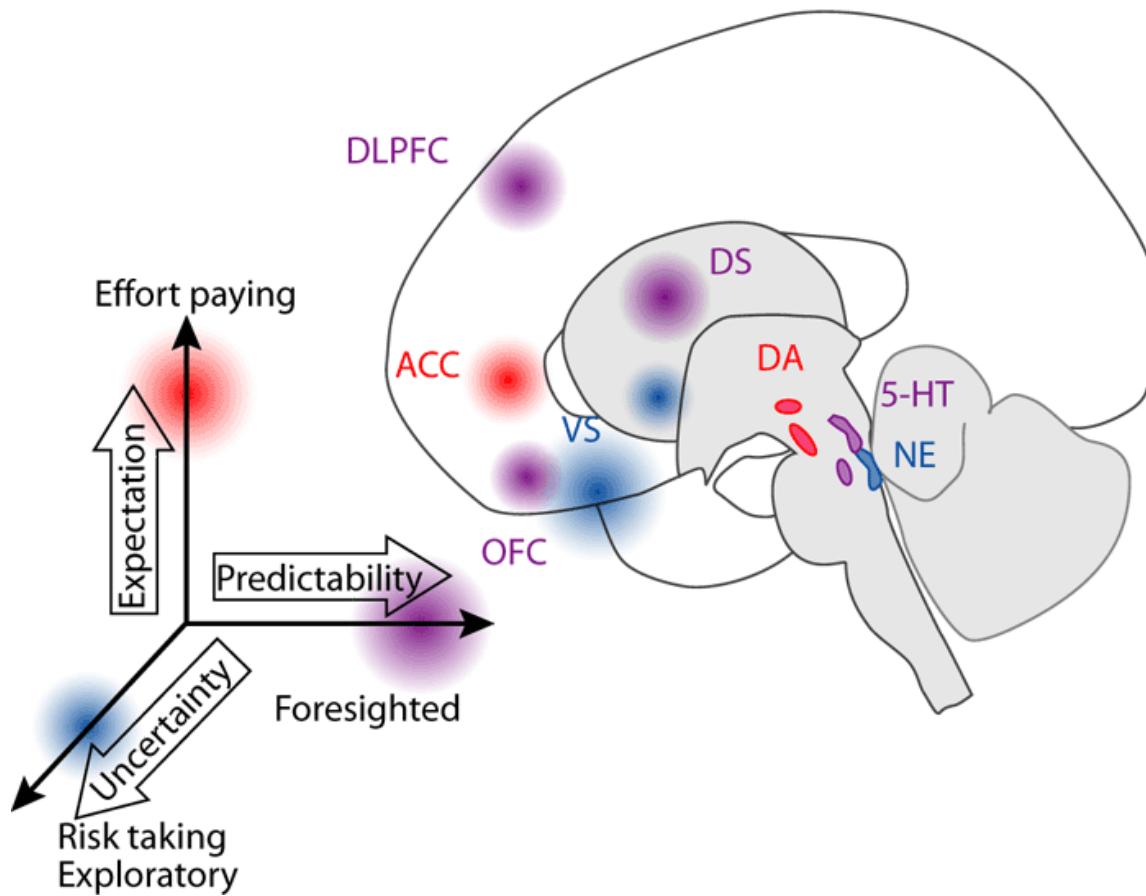


In addition to dopamine, other neuromodulators include: norepinephrine/noradrenaline, serotonin, acetylcholine, histamine, ... Many of these regulate the excitability of specific neurons and synaptic strengths (e.g. indirectly on certain ion channels and receptors). Some can affect gene transcription.

<http://en.wikipedia.org/wiki/Neuromodulation>



# Theories of chemical neuromodulation on decision-making

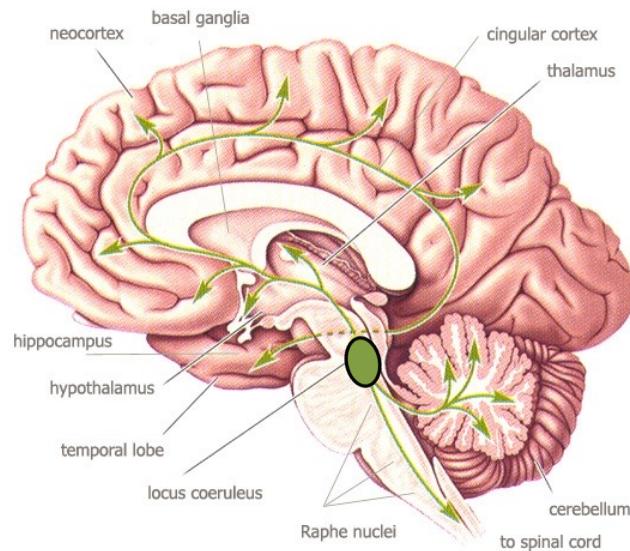


*Kenji Doya, Modulators of decision making, Nat. Neurosci. (2008)*

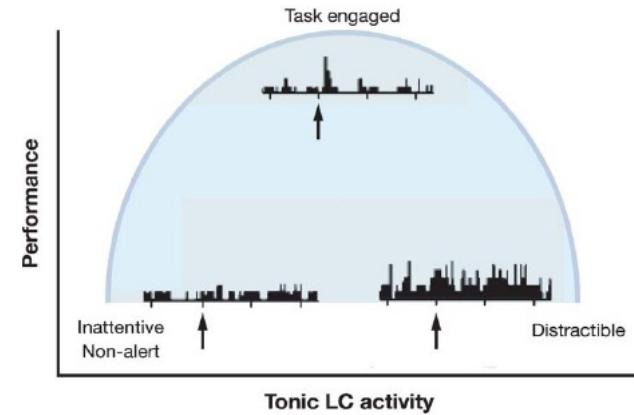
# Norepinephrine / noradrenaline (NE / NA)

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

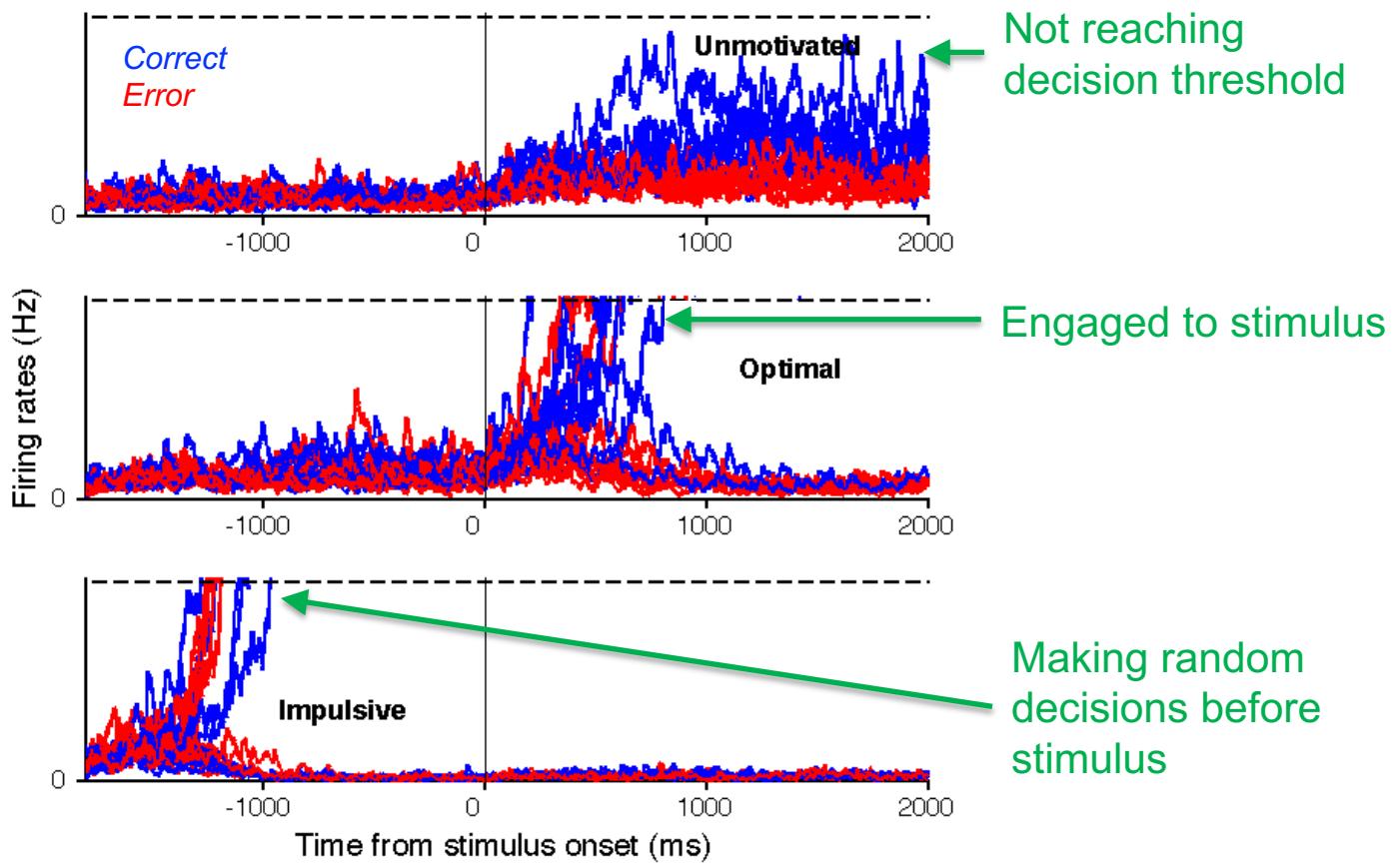


Aston-Jones et. al (1999); Aston-Jones and Cohen (2005)

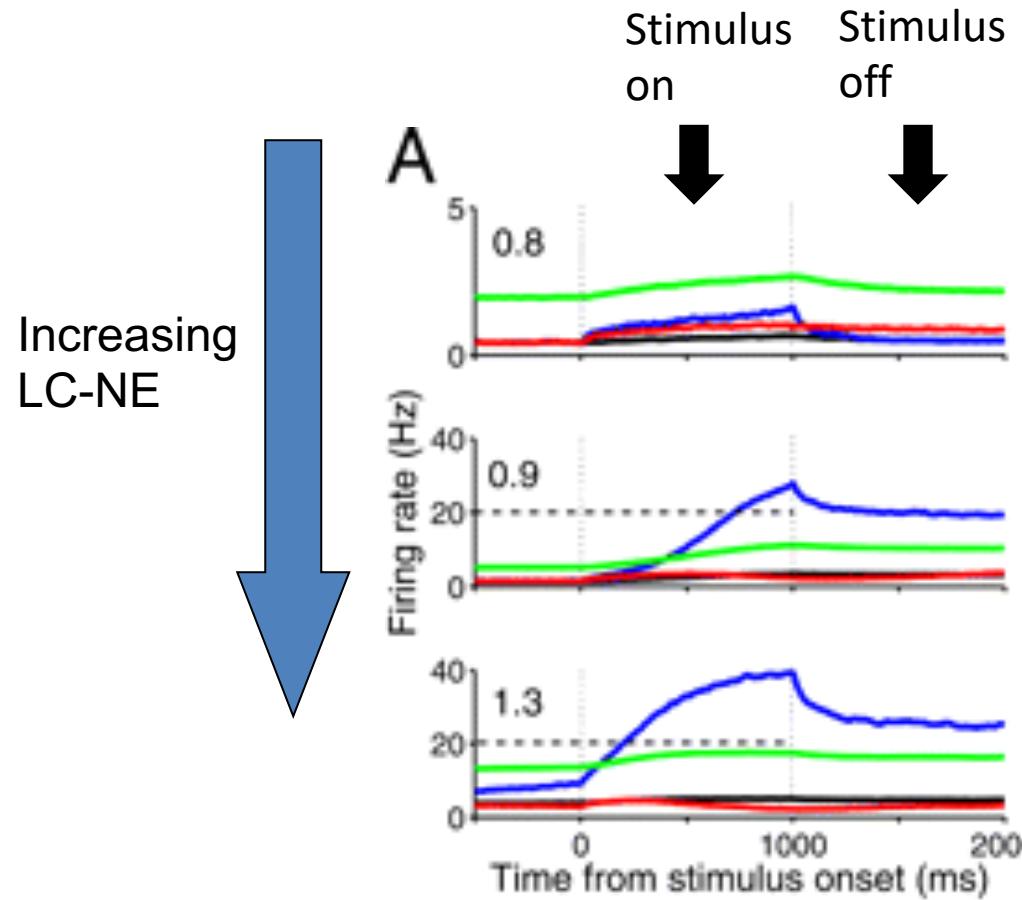
# Change in model decisions under “chemical” modulation of internal state

10 sample trials with the same external stimulus.

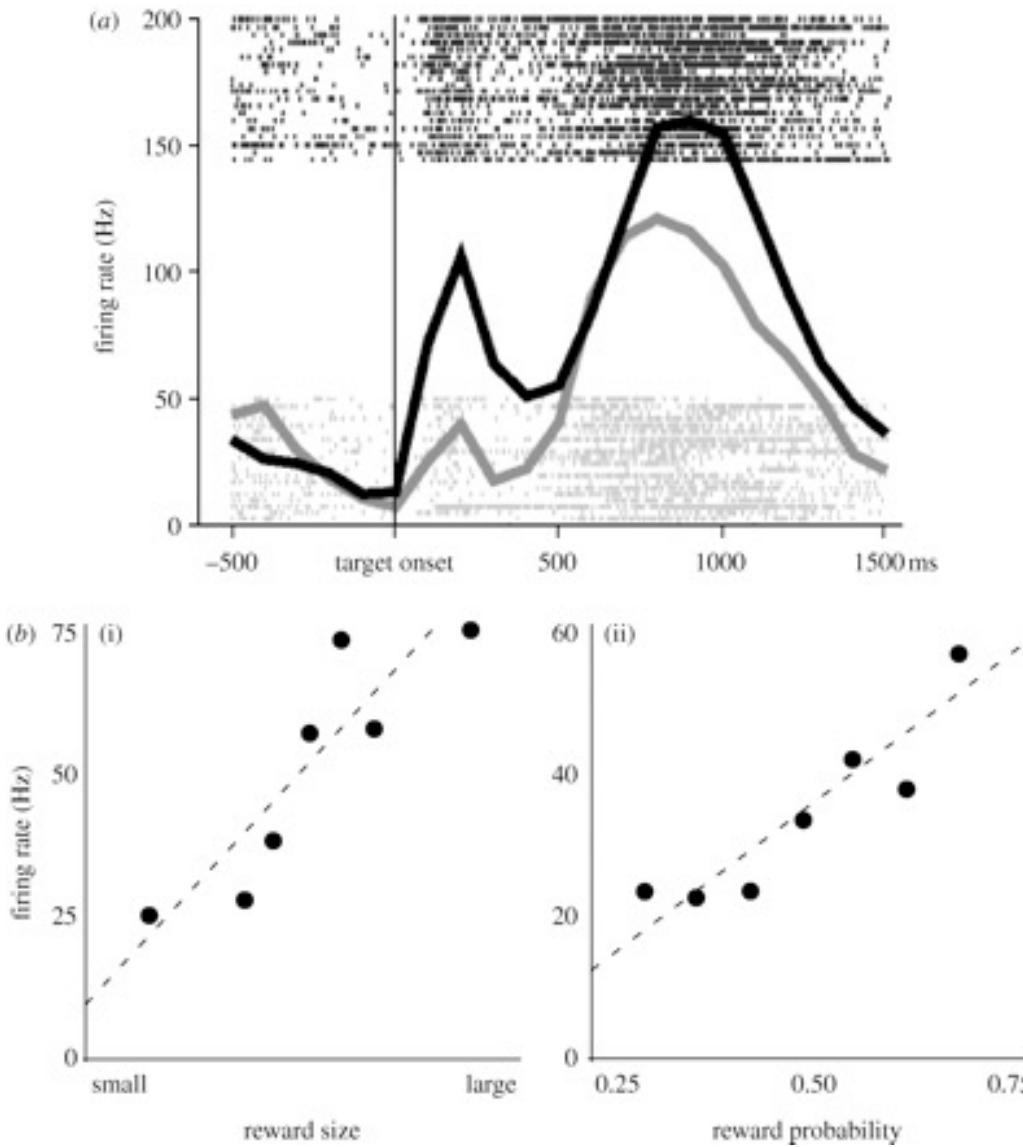
Increasing  
LC / NE



## Modulate storage (working memory) of decisions



# Neural correlates of value-based choice: Neuroeconomics



Neural representation of value (e.g. parietal cortical neurons)

Related to the neurochemical dopamine?

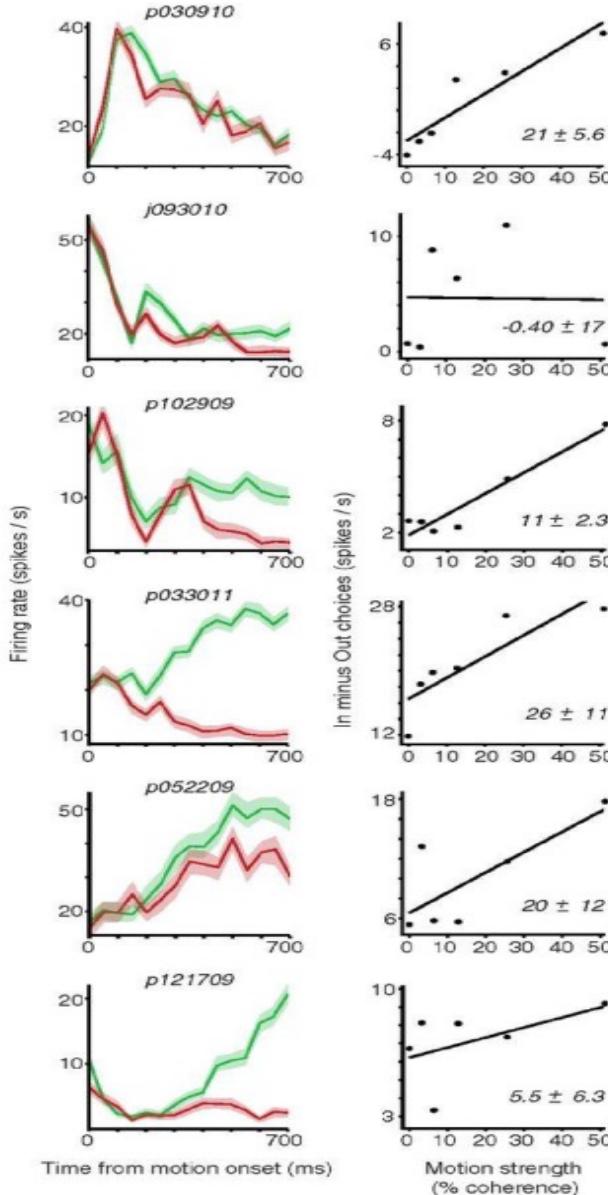
Work by research groups including that of Paul W. Glimcher, Michael Platt, and William T. Newsome, etc

# Some recent challenges: Neuronal heterogeneity

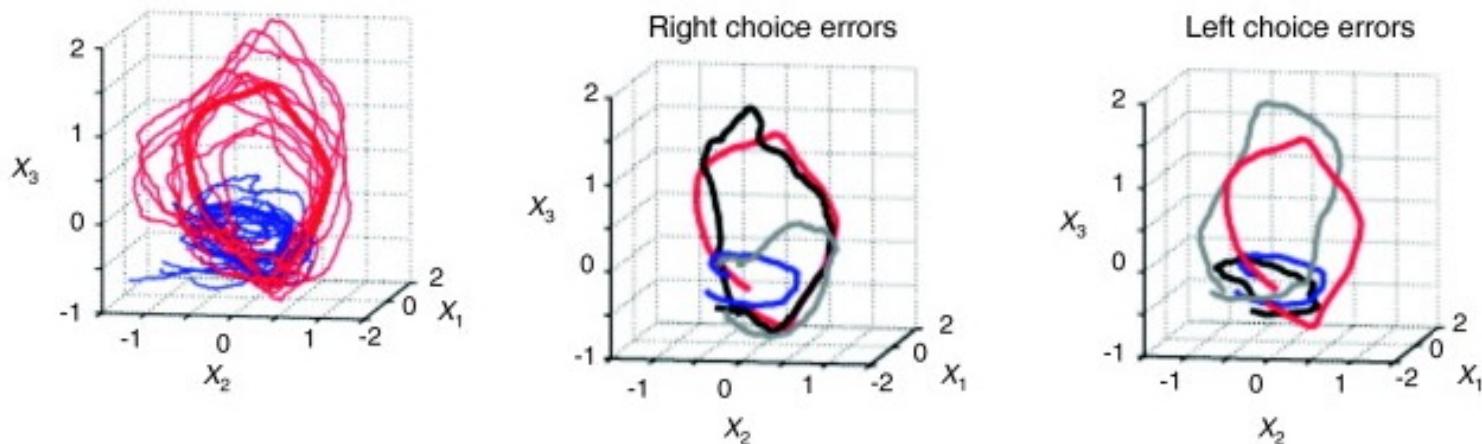
*Heterogeneous activities among different LIP neurons.*

*Activity timecourse (left) and activity-vs-directional motion coherence (right).*

*Meister, Hennig & Huk,  
J. Neurosci. (2013)*



# Neural dynamics in high dimensions



Population dynamics of 65 cells recorded from PPC in mice performing virtual-navigation decision task.

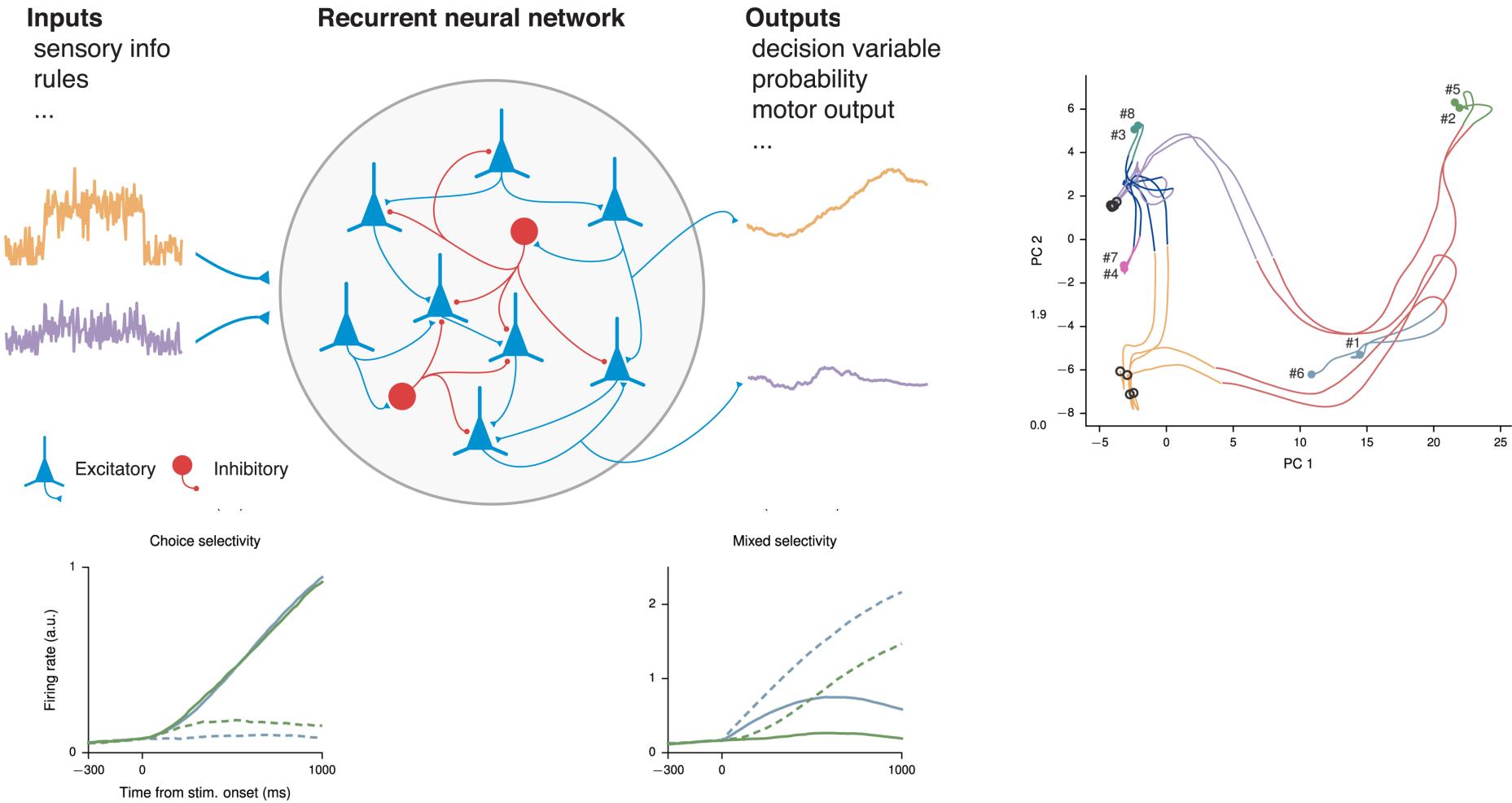
Red: right choice, blue: left choice.

Left: Sample correct trial trajectories.

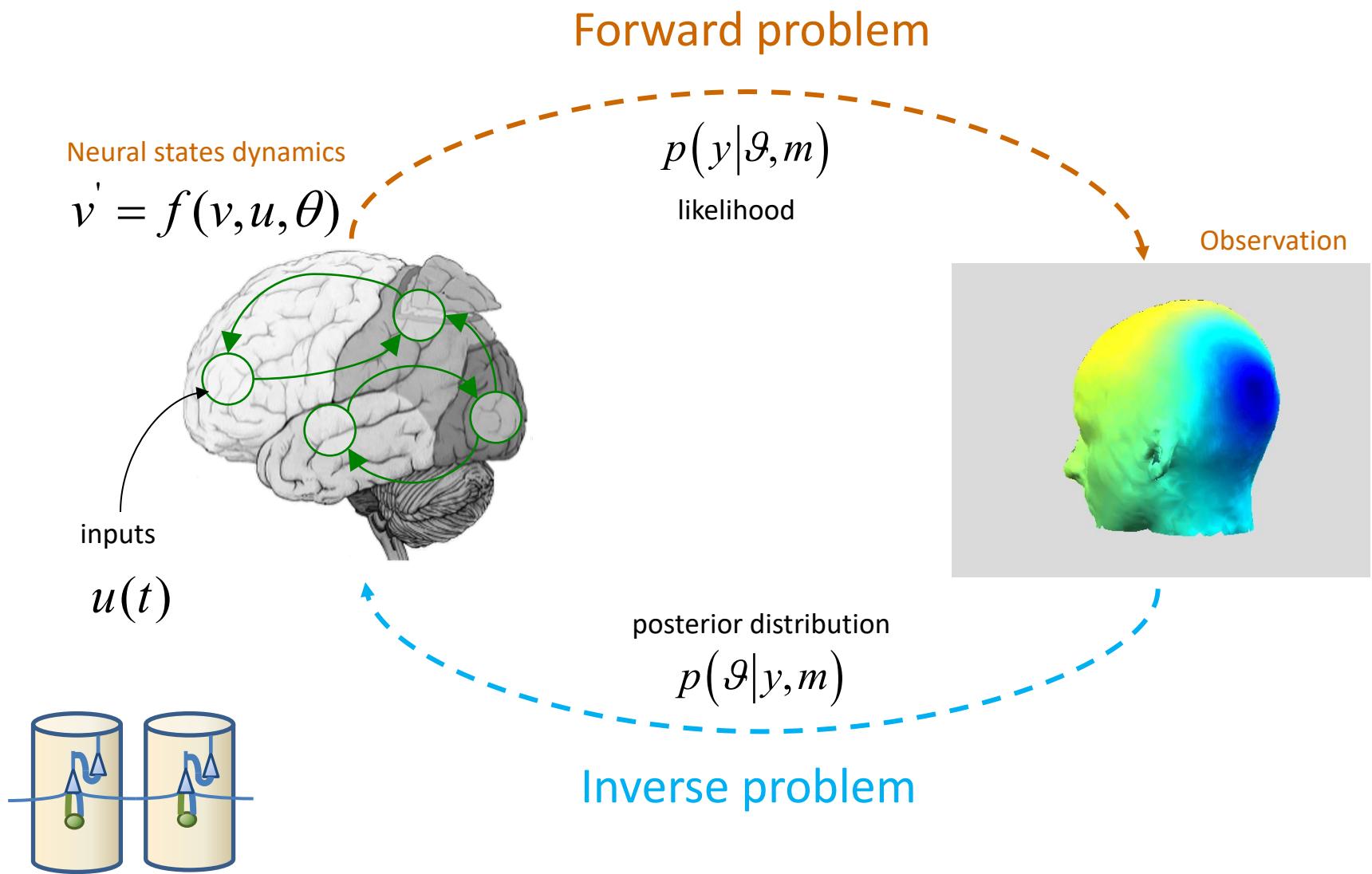
Middle and Right: individual trial trajectories (grey & black) on erroneous right choice & left choice trials.

*Harvey, Cohen & Tank, Nature (2012)*

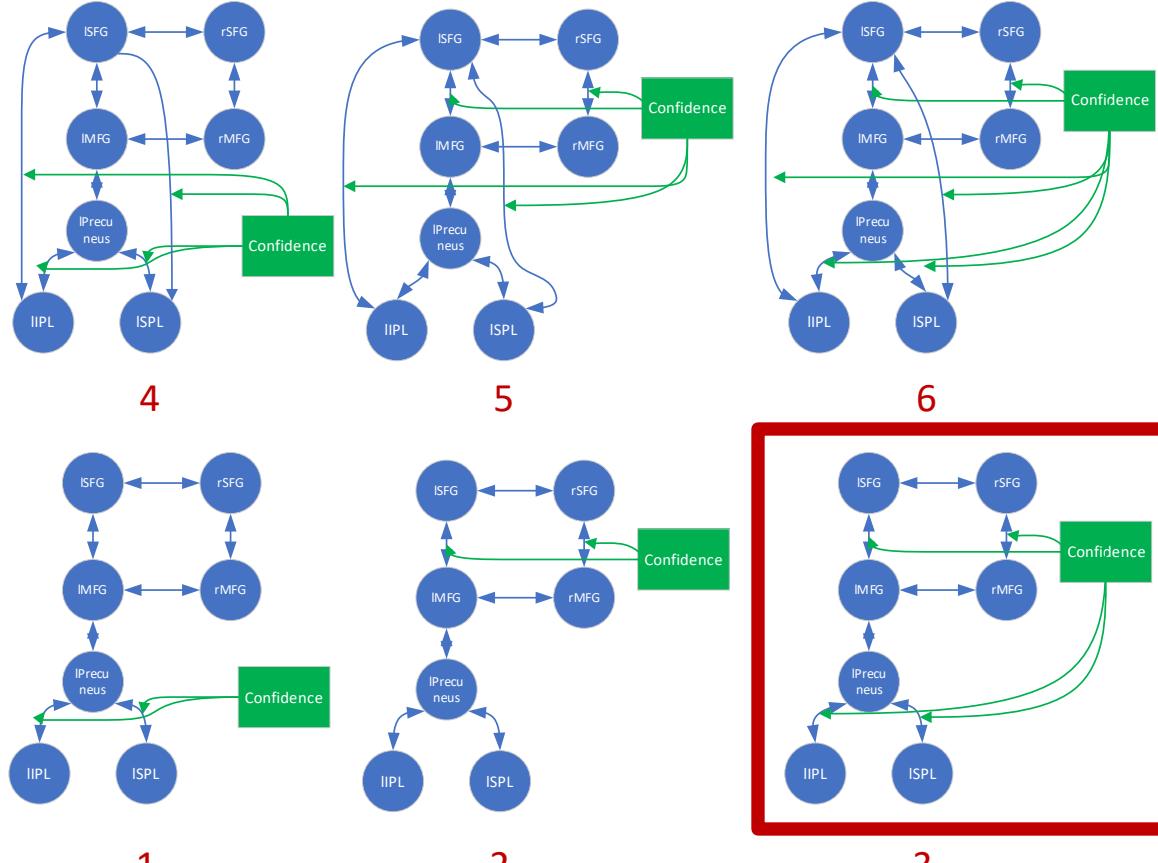
# Training recurrent neural network model



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



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



Confidence  
affects both  
top-down and  
bottom-up

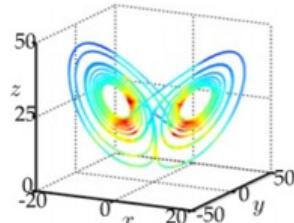


Abdoreza  
Asadpour

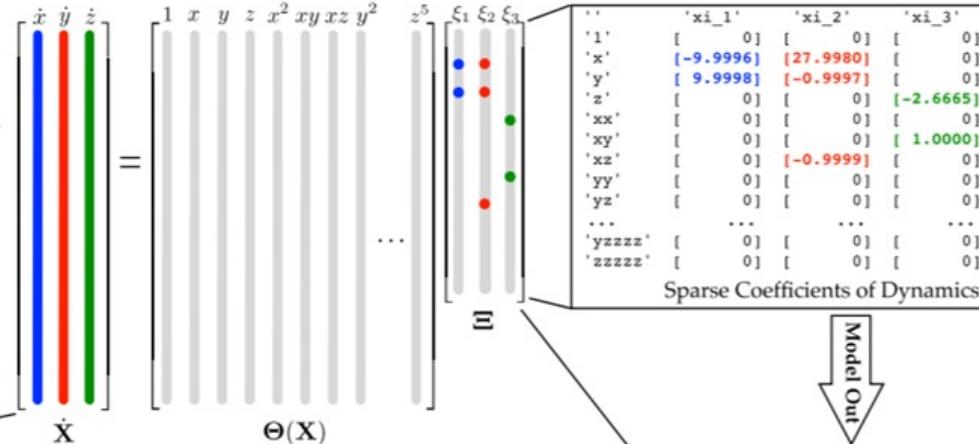
# Using machine learning to elucidate the underlying decision dynamics

## I. True Lorenz System

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



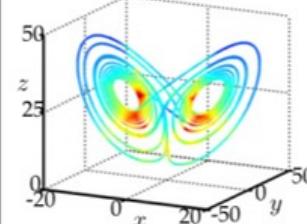
Data In



Model Out

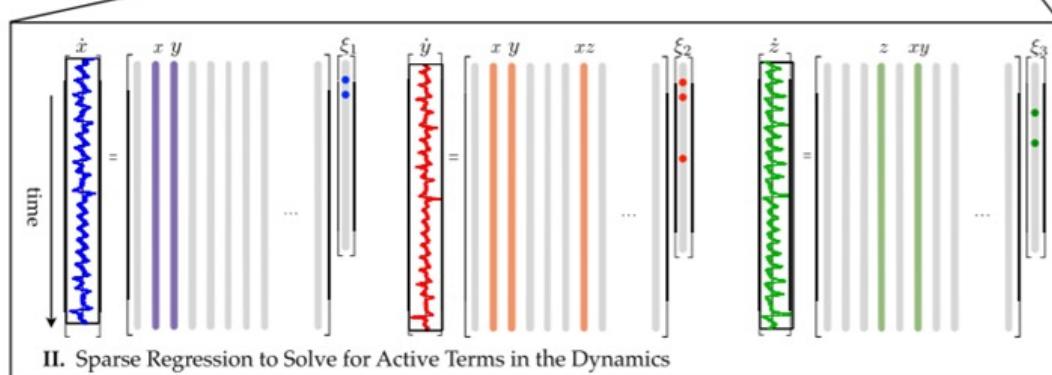
## III. Identified System

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



time

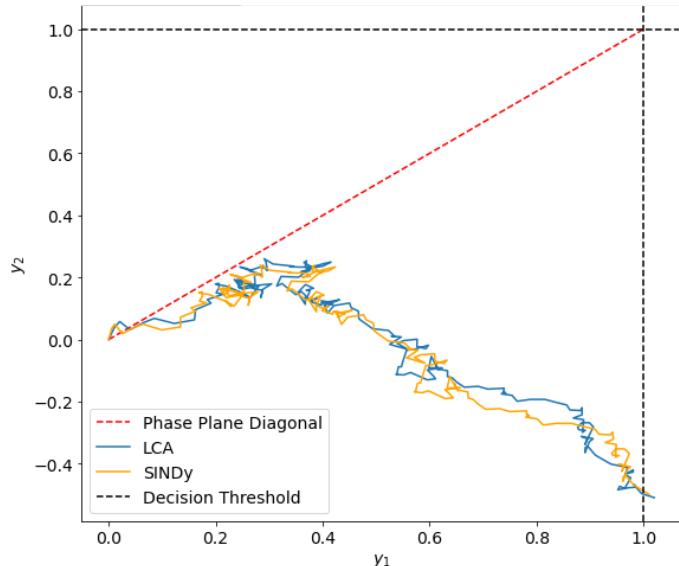
## II. Sparse Regression to Solve for Active Terms in the Dynamics



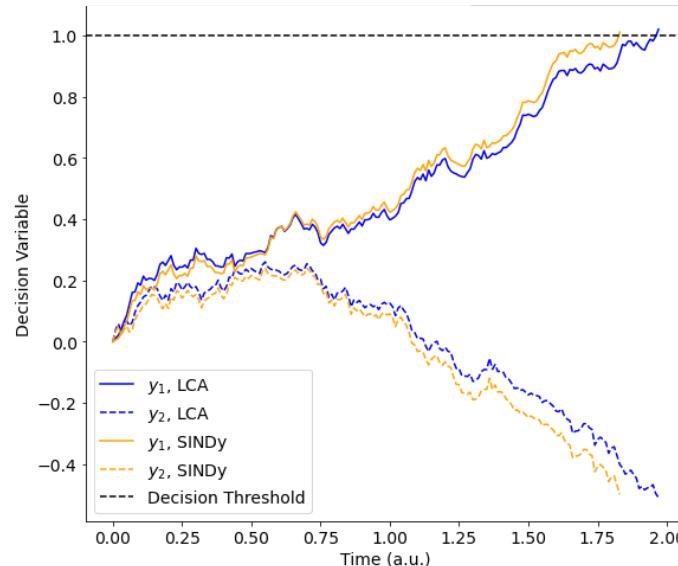
Sparse identification of non-linear dynamics (SINDy) to rediscover governing equations

# Using machine learning to elucidate the underlying dynamical equations

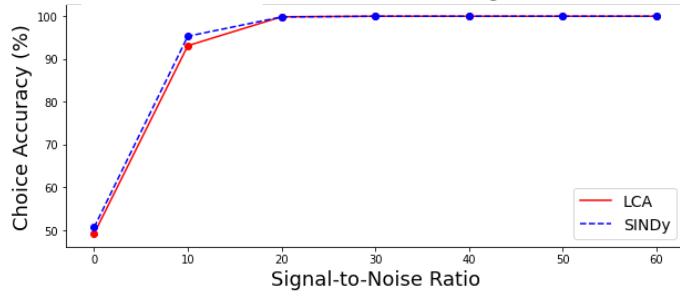
Phase space



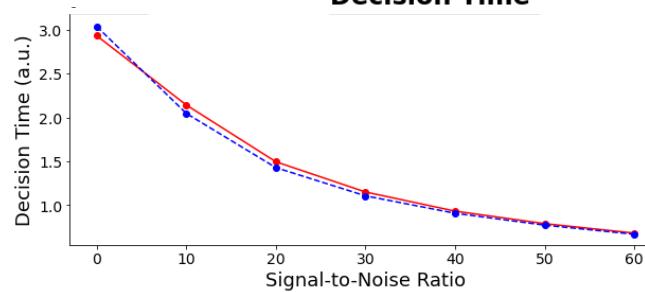
Activity time course



Choice Accuracy



Decision Time

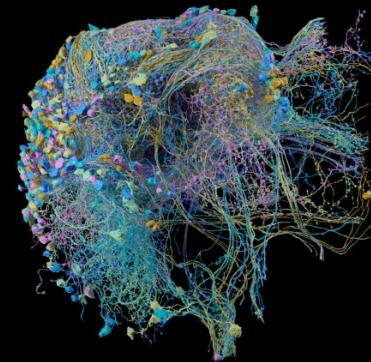


Brendan  
Lenfesty

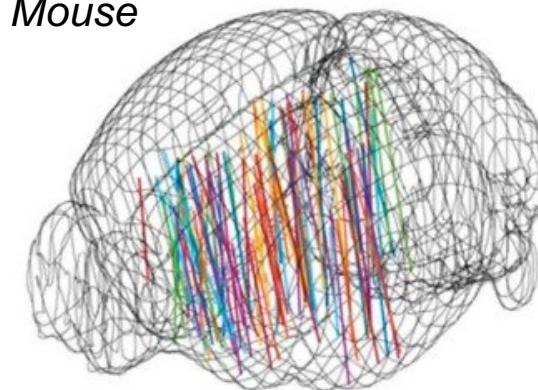
## Some Challenges

- More general, natural decisions, disorders
- New (neuro)technology. E.g. recording several neurons, brain regions & behaviour simultaneously
- Big, distributed, complex data handling, & computational (machine learning) algorithms needed to analyse
- New theories &/or new mathematical methods to understand underlying mechanisms & computational principles?

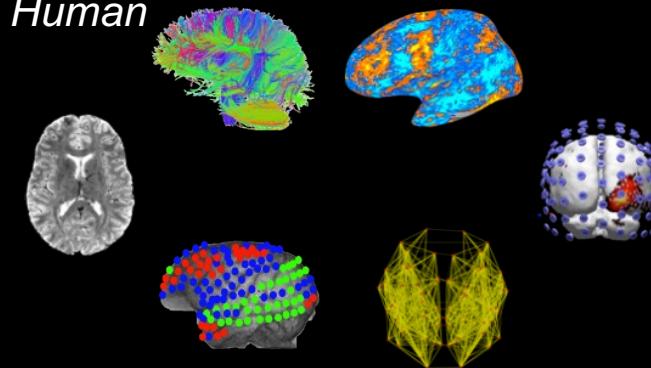
*Fly*



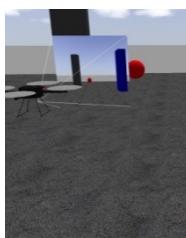
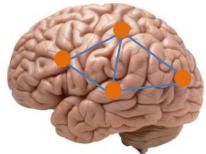
*Mouse*



*Human*



# Applications to Intelligent Systems



```
INCLUDE evbu.hdr
MAC_APPEVENT (EVBU) i Indicate that the GBR is connected to a connection (Event)
EVBU_TxData (EVBU) i Indicate that a position has been updated (Data)

REGISTER EVBU_Example
    MAC
        MAC
            MAC
                MAC
                    MAC
                        MAC
                            MAC
                                MAC
                                    MAC
                                        MAC
                                            MAC
                                                MAC
                                                    MAC
                                                        MAC
                                                            MAC
                                                                MAC
                                                                    MAC
                                                                        MAC
                                MAC
                            MAC
                        MAC
                    MAC
                MAC
            MAC
        MAC
    MAC

```



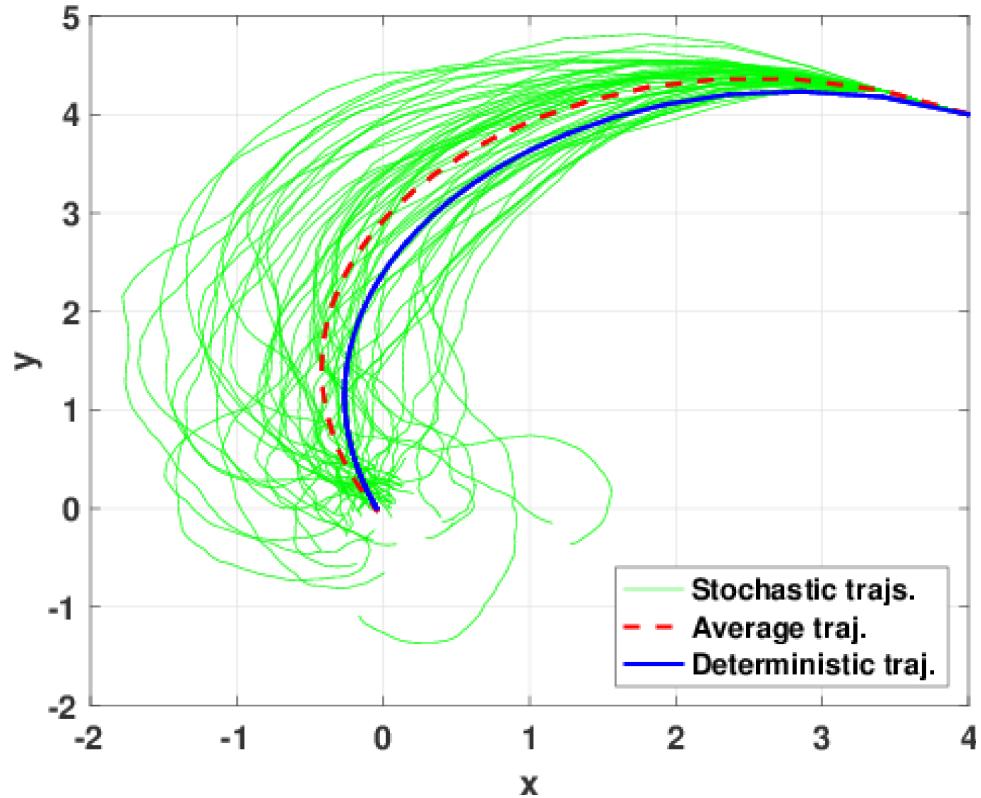
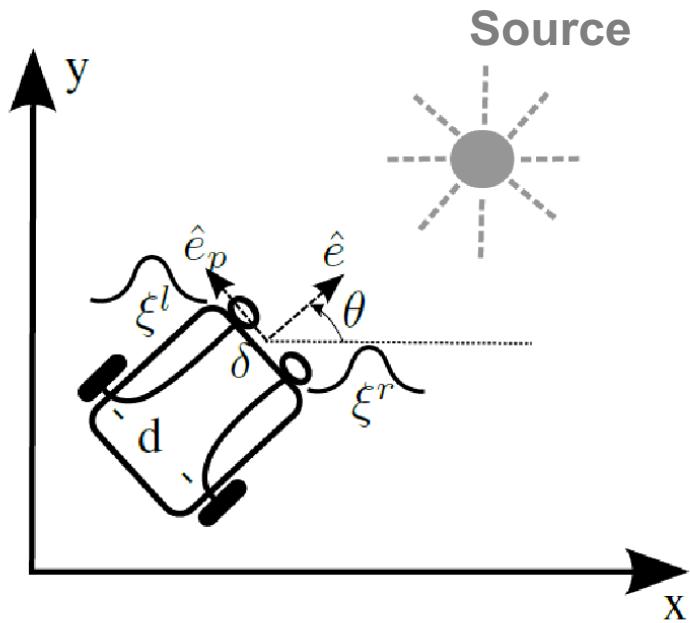
Computational  
cognitive  
neuroscience

Computational  
models, novel  
algorithms, &  
simulations

(Neuromorphic)  
Implementations  
in hardware for  
real-time  
applications

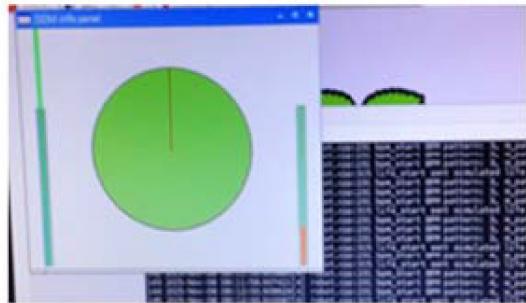
Implementation in  
physical intelligent  
machines & robots

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



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

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



(A)



(B)



(C)



(D)

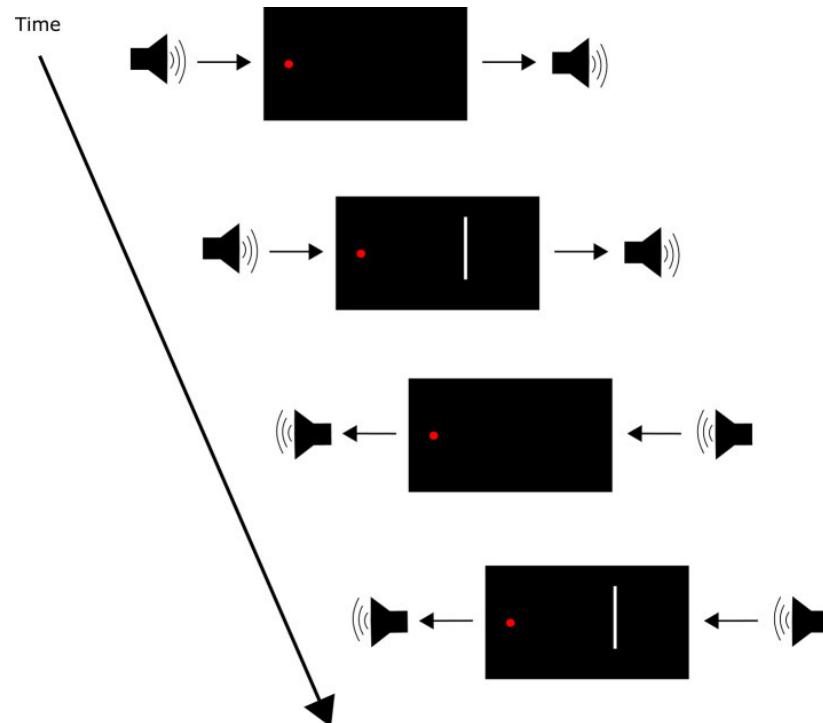


(F)

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

# Illusions as a by-product of optimal information fusion

The same “best” (optimal) computational model can lead to illusory perception and decisions – Caution!

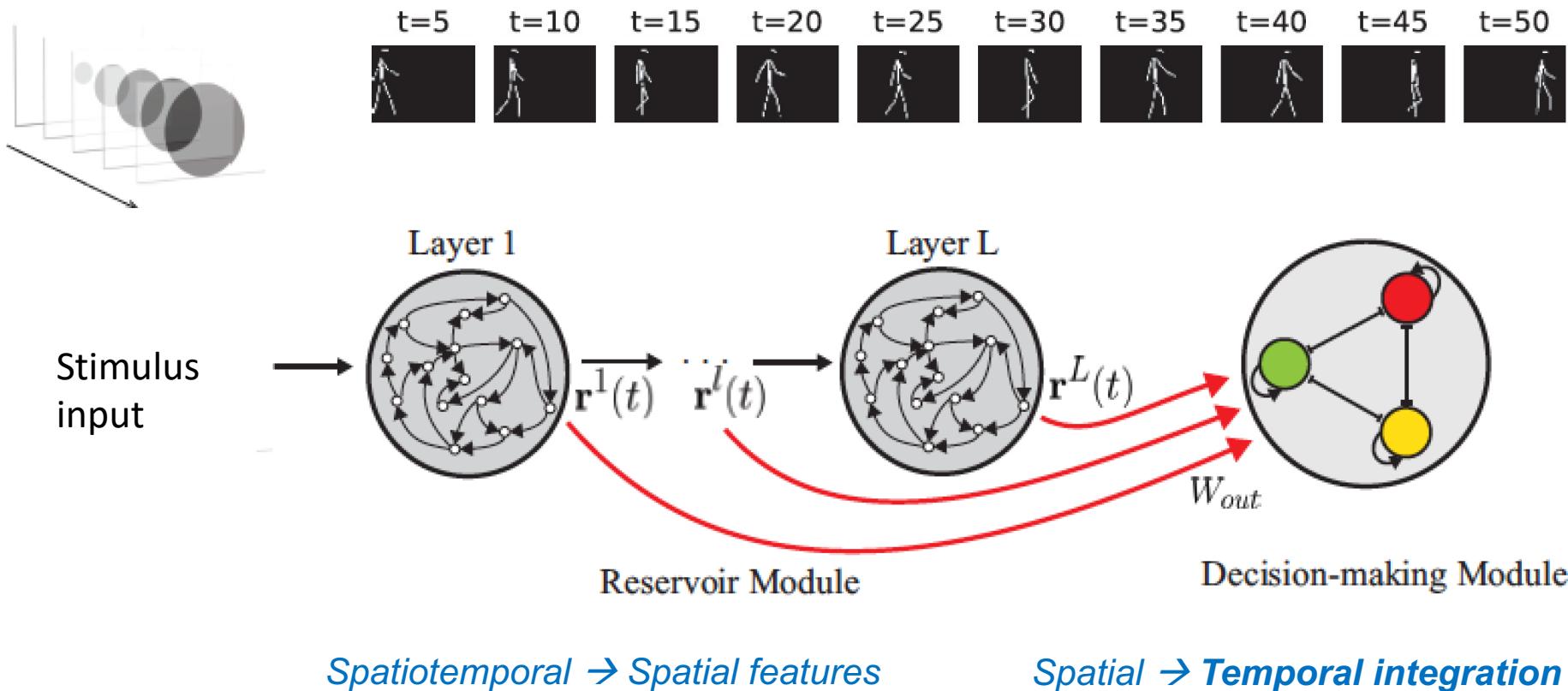


Sound-induced  
illusory visual  
motion paradigm

# Information processing over space & time

*Looming pattern detection*

*Individual's gait identification*



Mi, Lin, Zou, Ji, Huang & Wu (2019) arXiv:1907.12071v1;  
Lin, Zou, Ji, Huang, Wu & Mi Neural Netw. (2021)

# Neuromorphic computing



*Pei et al., Nature (2019). Towards artificial general intelligence(?) with hybrid Tianjic chip architecture*

# Final message

- 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 generalizable to novel (testable) predictions.
- Understanding brain mechanisms can lead to or inspire novel computational algorithms and intelligent machines.

## People

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- Nadim Atiya, Inaki Rañó (now USC), W. Paul Boyce (now UNSW), Anthony Lindsay, Girijesh Prasad, Brendan Lenfesty, Abdoreza Asadpour, Hui Tan, Saugat Bhattacharyya, Vahab Youssofzadeh

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- Ritwik Niyogi (now MediaTek Research)

### **National University of Ireland Galway, Ireland**

- Denis O'Hora, Arkady Zgonnikov (now Delft U of Technology), Petri Piiroinen (now Chalmers U Technology)

### **Technische Universität Dresden, Germany**

- Martin Schoemann, Stefan Scherbaum

### **University of Wolverhampton, UK**

- Shufan Yang (now Edinburgh Napier U)

### **Institut des Systèmes Intelligents et de Robotique, Université Pierre et Marie Curie, France**

- Mehdi Khamassi (now ISIR, Sorbonne Université)

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- Redmond O'Connell

### **University College Dublin, Ireland**

- Simon Kelly

### **Beijing Normal University, China**

- Da-Hui Wang

### **Brandeis University, USA**

- Xiao-Jing Wang (now NYU)

### **Hofstra Northwell School of Medicine; Feinstein Institute for Medical Research**

- Stefan Bickel

### **University of Texas at Austin, USA**

- Alexander Huk

### **Columbia University, USA**

- Michael Shadlen

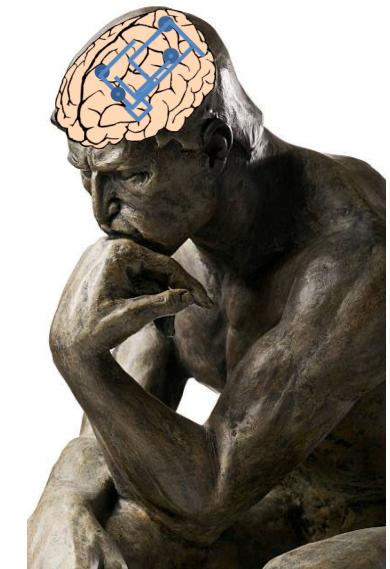
### **Princeton University, USA**

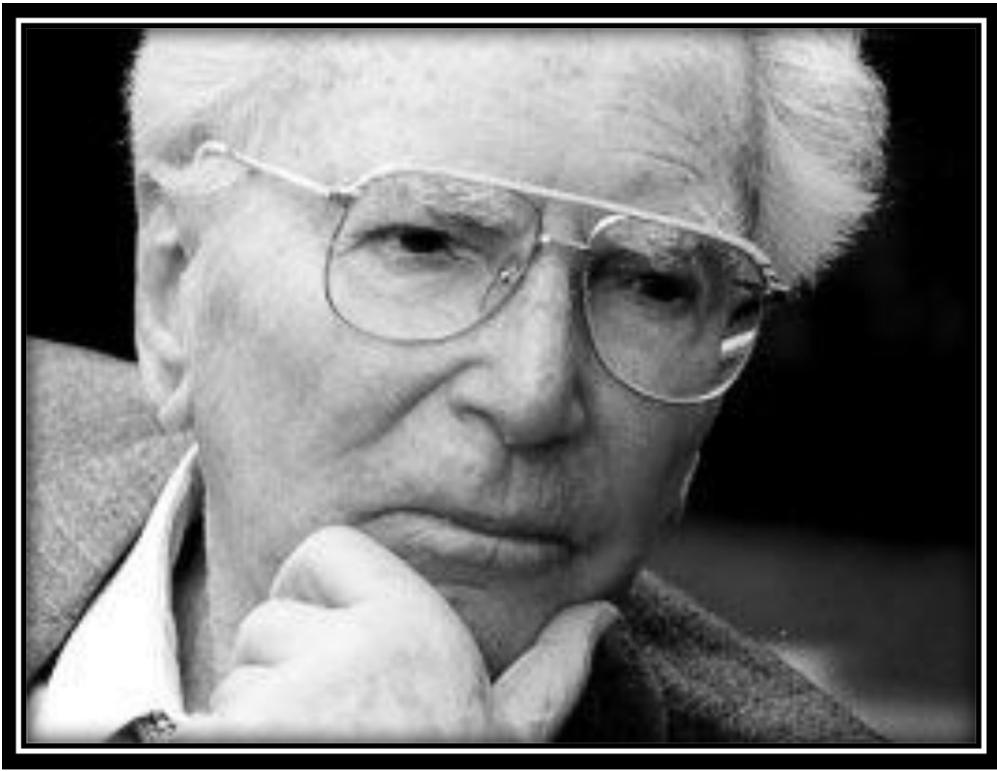
- Philip Holmes, Jonathan Cohen, Philip Eckhoff, Juan Gao, Xiang Zhou, Stephanie Goldfarb

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**Viktor E. Frankl**  
*Psychologist and  
Holocaust Survivor*

***Between stimulus and response there is a space.  
In that space is our power to choose our response.  
In our response lies our growth and our freedom.***