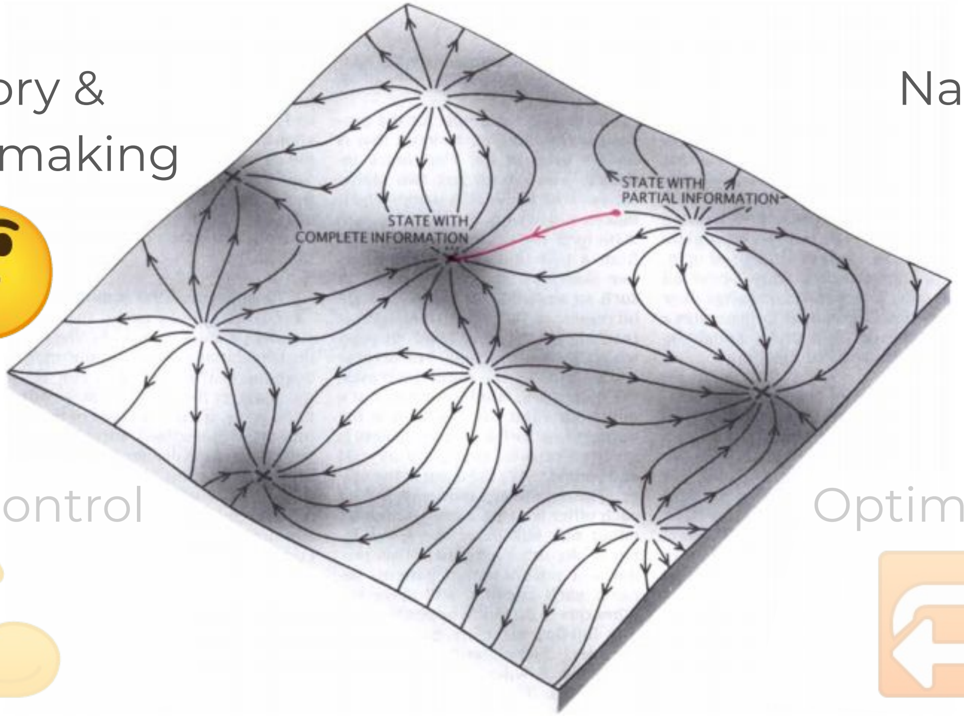
Computation through dynamics

Memory & decision making

Navigation



Motor control

Optimal feedback

There's lots of great lectures related to
this topic in this online course:
"Introduction to Neural Computation" by Michale Fee

The first half of this lecture in particular
draws from Lecture 19. Neural Integrators
as well as Mark Goldman's lecture How Neurons do Integrals

I also highly recommend Geoff Hinton's
lectures on [Hopfield Nets here]

Key concepts for today's lecture

- **Memory** is integration
  - **Dynamical systems can integrate**
- **Decision making** is integration + a threshold
- Attractor networks implement memory & decision making
- **Navigation** (and other tasks)
  - Require integration + feedback

$$\text{Memory} = \int \text{input dt}$$

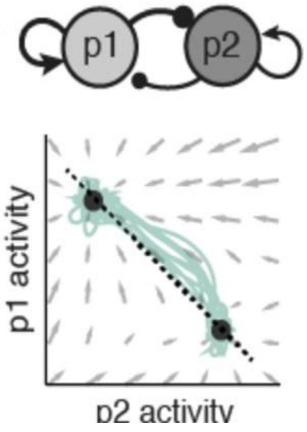
$$\text{Decision} = \boldsymbol{\theta}\left(\int \text{input dt}\right)$$

Dynamics - Lecture 1 review

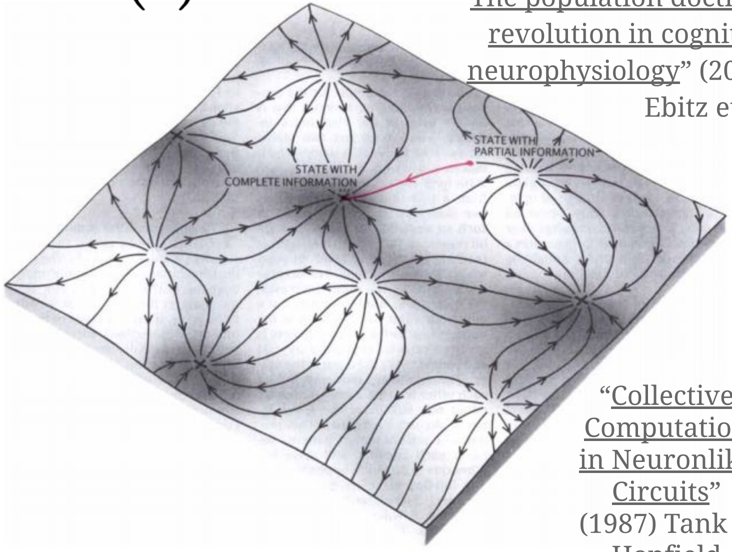
- What is an attractor?
- What do eigenvalues do?

$$\dot{\vec{x}} = \mathbf{A}\vec{x} + \mathbf{B}\vec{u}$$

$$\dot{x}(t) = \lambda x(t) + bu(t)$$

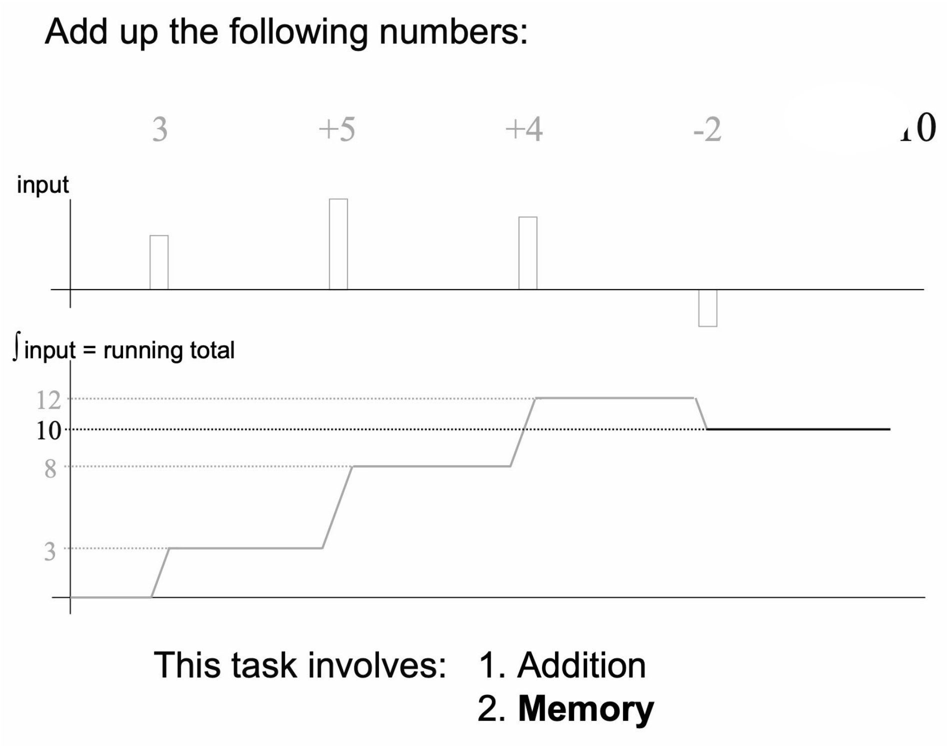


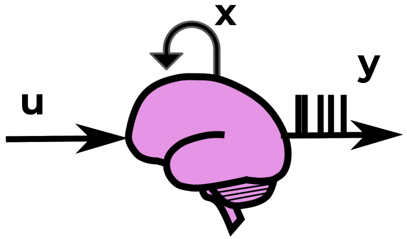
"The population doctrine revolution in cognitive neurophysiology" (2021) Ebitz et al.



"Collective Computation in Neuronlike Circuits" (1987) Tank & Hopfield

Memory as Integration
a fundamental calculation

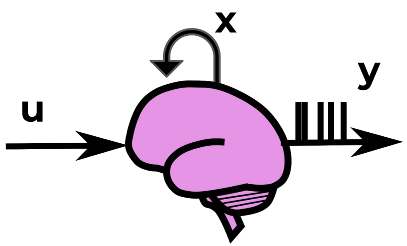




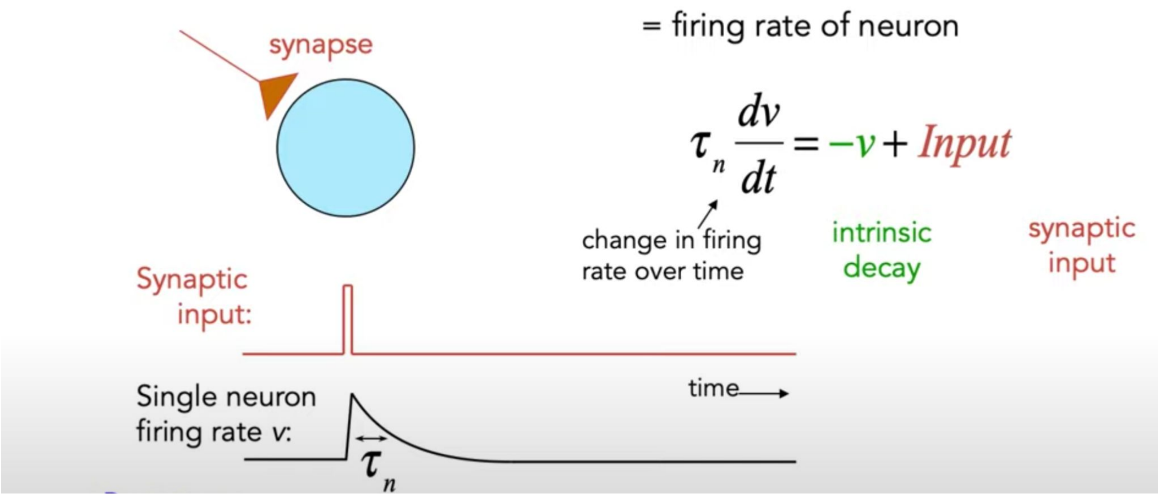
Memory = $\int$ input dt

“How Neurons do Integrals” Mark Goldman

Memory as Integration
- a fundamental calculation

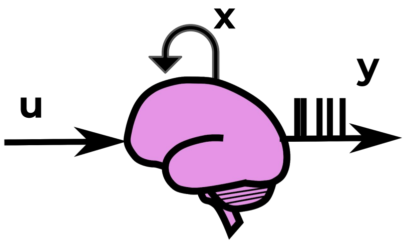


How to maintain a representation in the absence of input?

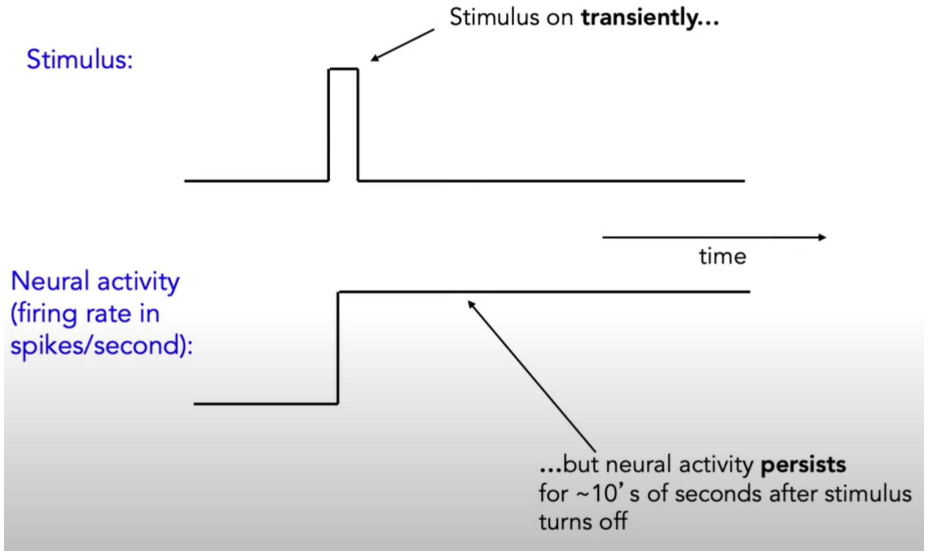


"Neural Integrators" Michale Fee

Memory as Integration
- a fundamental calculation



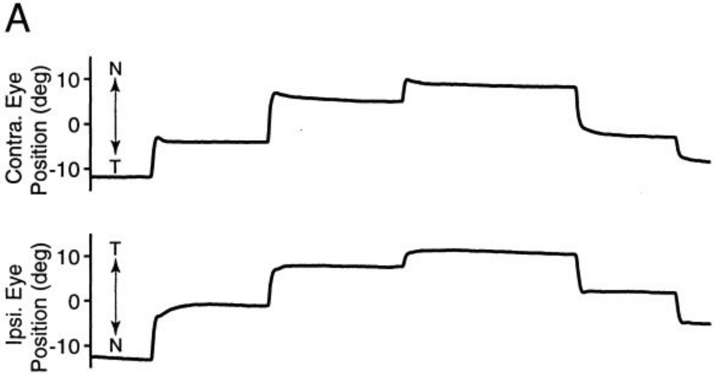
- Persistent activity is the neural correlate of short-term memory



Memory = $\int$ input dt

"Neural Integrators" Michale Fee

Oculomotor control in the goldfish
Integration via line attractor

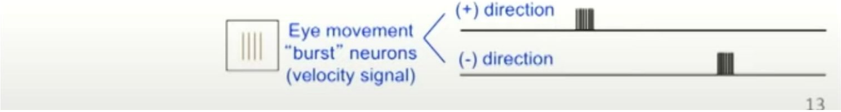


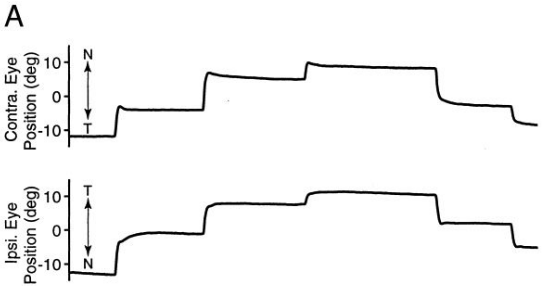
Position = ∫ velocity
Motor FR = ∫ Saccade-burst FR

"Anatomy and Discharge Properties of Pre-Motor Neurons in the Goldfish Medulla That Have Eye-Position Signals During Fixation" (2000) Seung et al.

Oculomotor control in the goldfish
Integration via line attractor

Burst neurons code eye velocity





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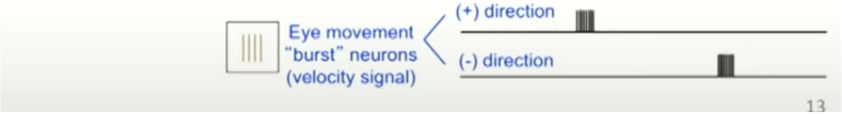

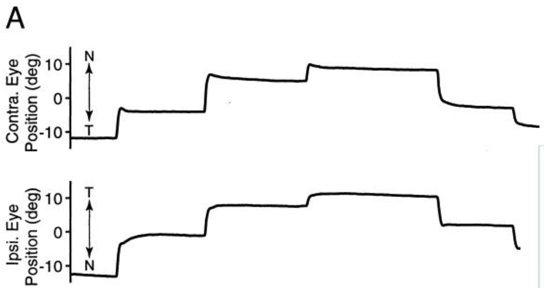

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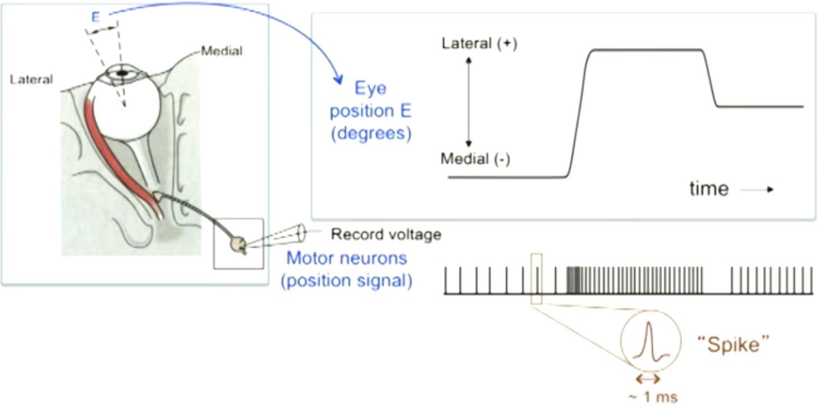

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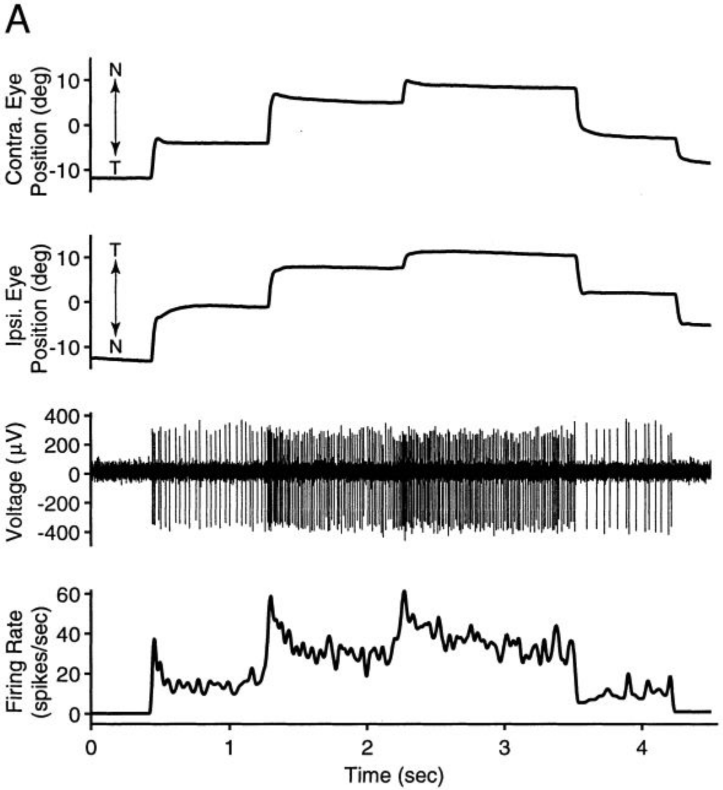

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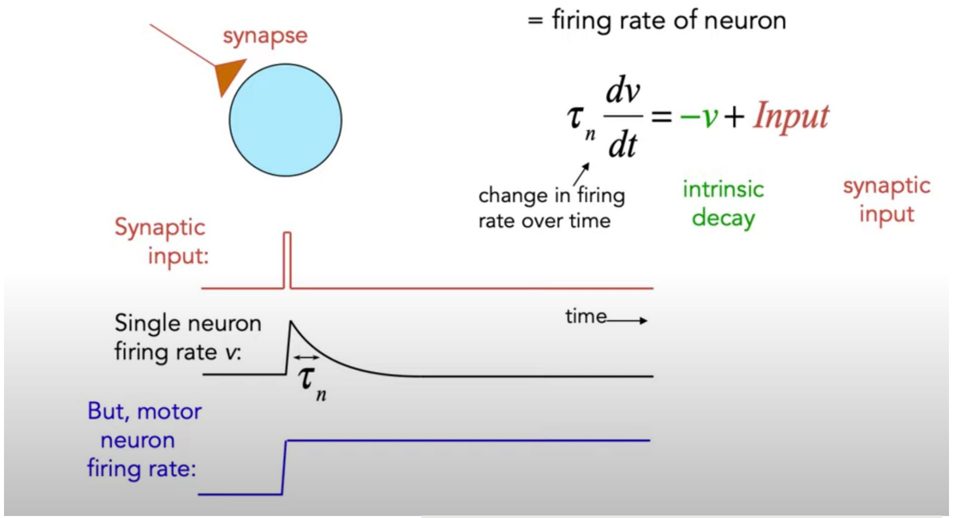
Timescale of integration extended by recurrent connectivity

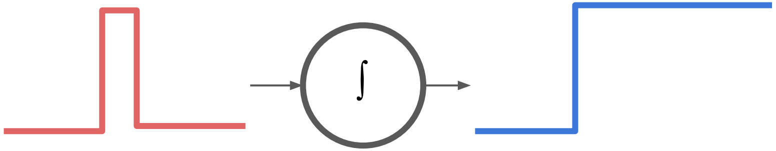


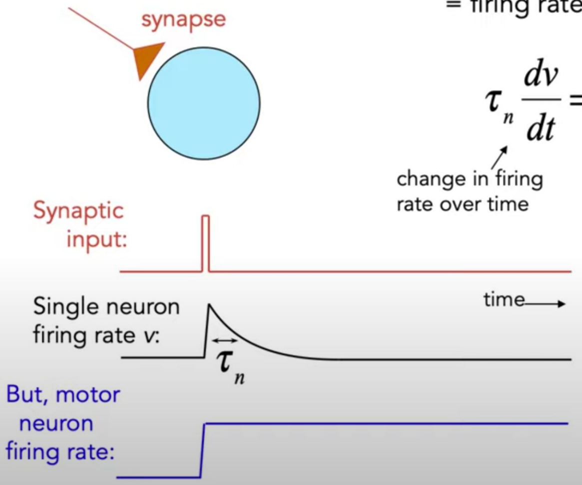
Single isolated neuron: $\tau_n \approx 10 - 100$ ms

Integrator circuit: $\tau_{network} = \frac{\tau_n}{|1 - \lambda|} \approx 30$ sec

“Neural Integrators”
Michale Fee

Timescale of integration extended by recurrent connectivity

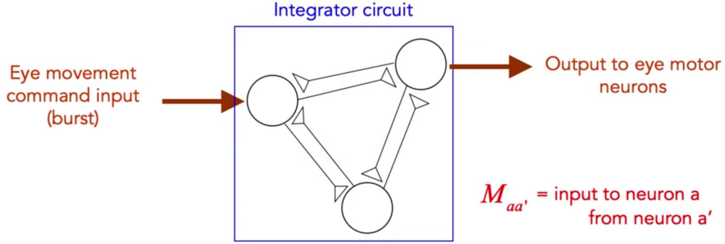




v = firing rate of neuron

$$\tau_n \frac{dv}{dt} = -v + Input$$

change in firing rate over time — intrinsic decay — synaptic input



$$\tau_n \frac{dv_a}{dt} = -v_a + \sum_{a'} M_{aa'} v_{a'} + burst\ input$$

Single isolated neuron: $\tau_n \approx 10-100\ \text{ms}$

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"Neural Integrators"
Michale Fee

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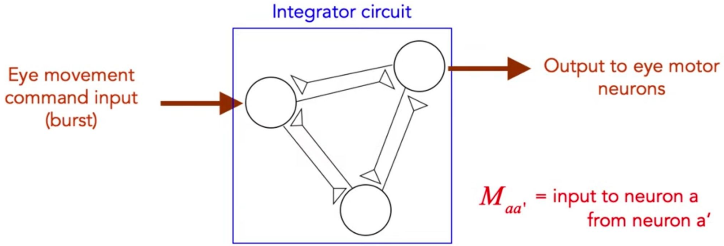

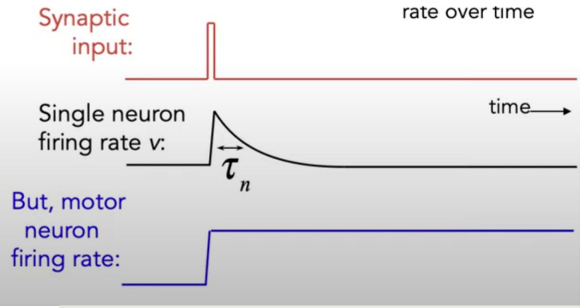

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$$\tau_n \frac{dc_1}{dt} = -c_1 + \lambda_1 c_1 + \textit{burst input}$$

"Neural Integrators"
Michale Fee

Eigenvalues govern properties of integration

$$\tau_n \frac{dc_1}{dt} = -c_1 + \lambda_1 c_1 + burst\ input$$

Between bursts: $\boxed{\dfrac{dc}{dt} = kc, \quad \text{where} \quad k = \dfrac{\lambda - 1}{\tau_n}}$

$\lambda = 1$: Perfect integrator

$$c(t) \sim constant$$

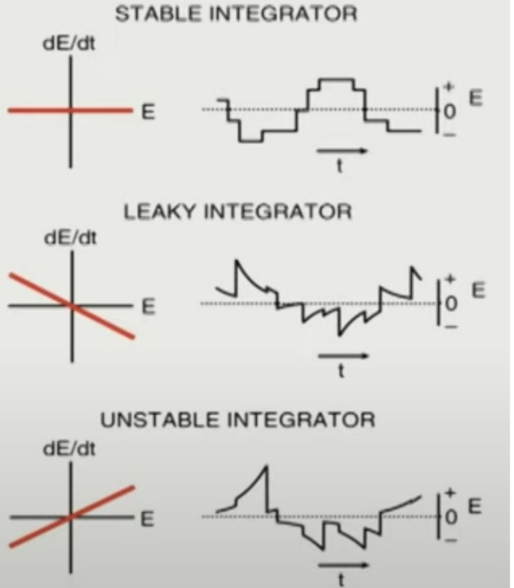
$\lambda < 1$: Leaky integrator

$$c(t) \sim e^{-|k|t}$$

$$\tau_{leak} = \frac{1}{|k|} = \frac{\tau_n}{1-\lambda}$$

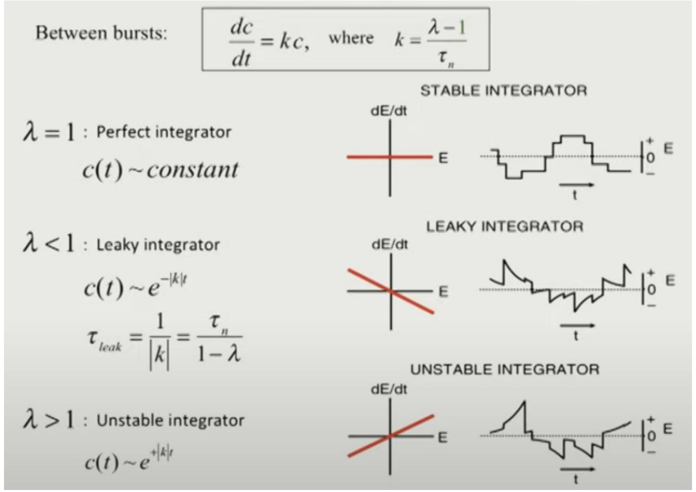
$\lambda > 1$: Unstable integrator

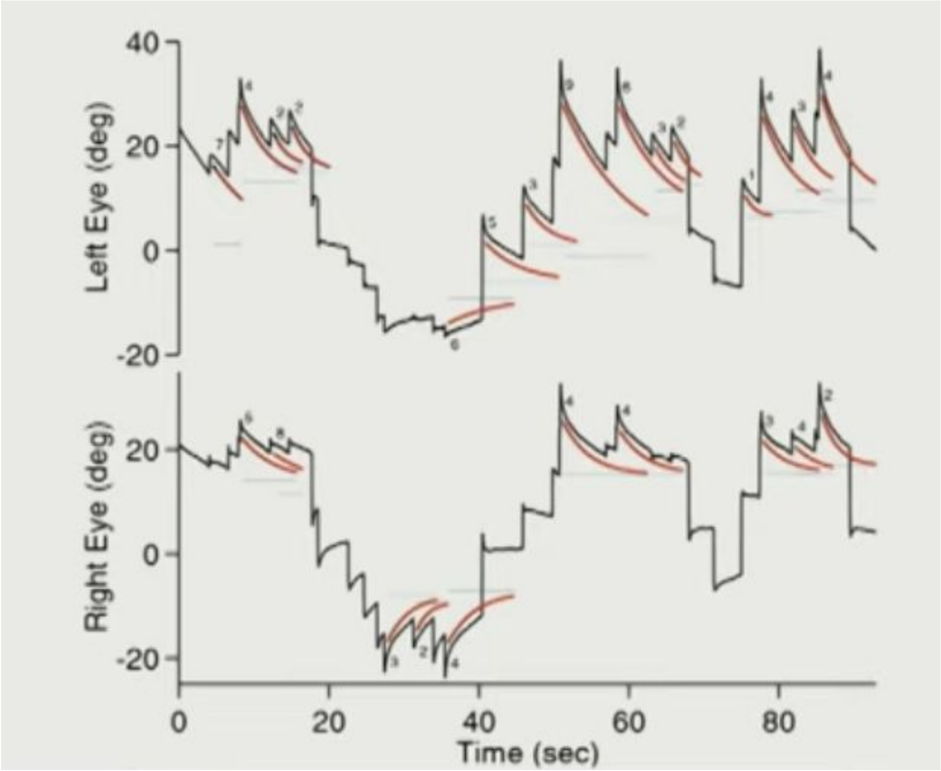
$$c(t) \sim e^{+|k|t}$$



“Neural Integrators” Michale Fee

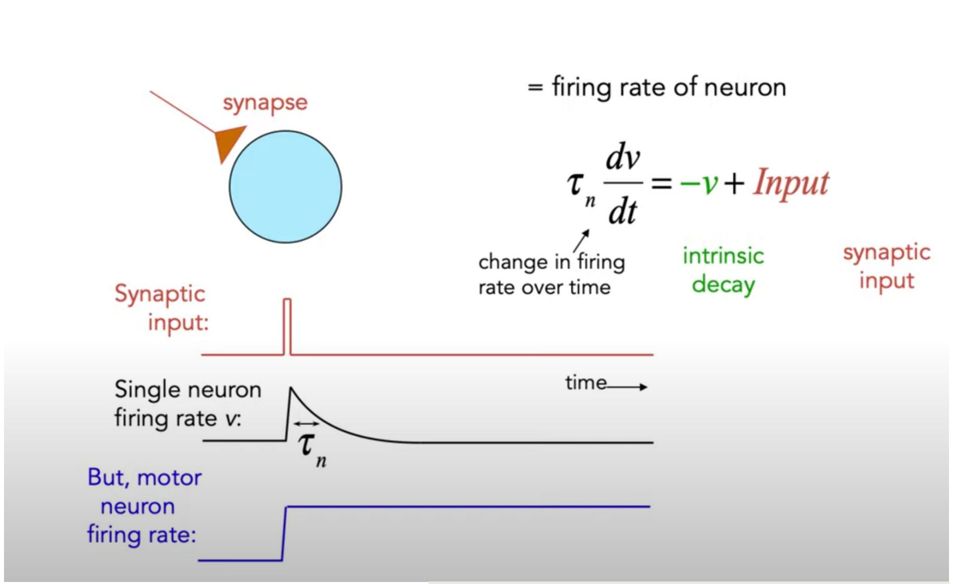
Anesthesia modulates feedback
And therefore the effective time constant of computation





"Neural Integrators" Michale Fee

Timescale of integration extended by recurrent connectivity



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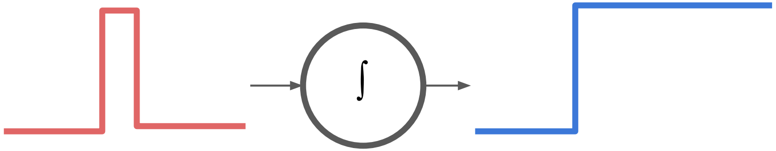
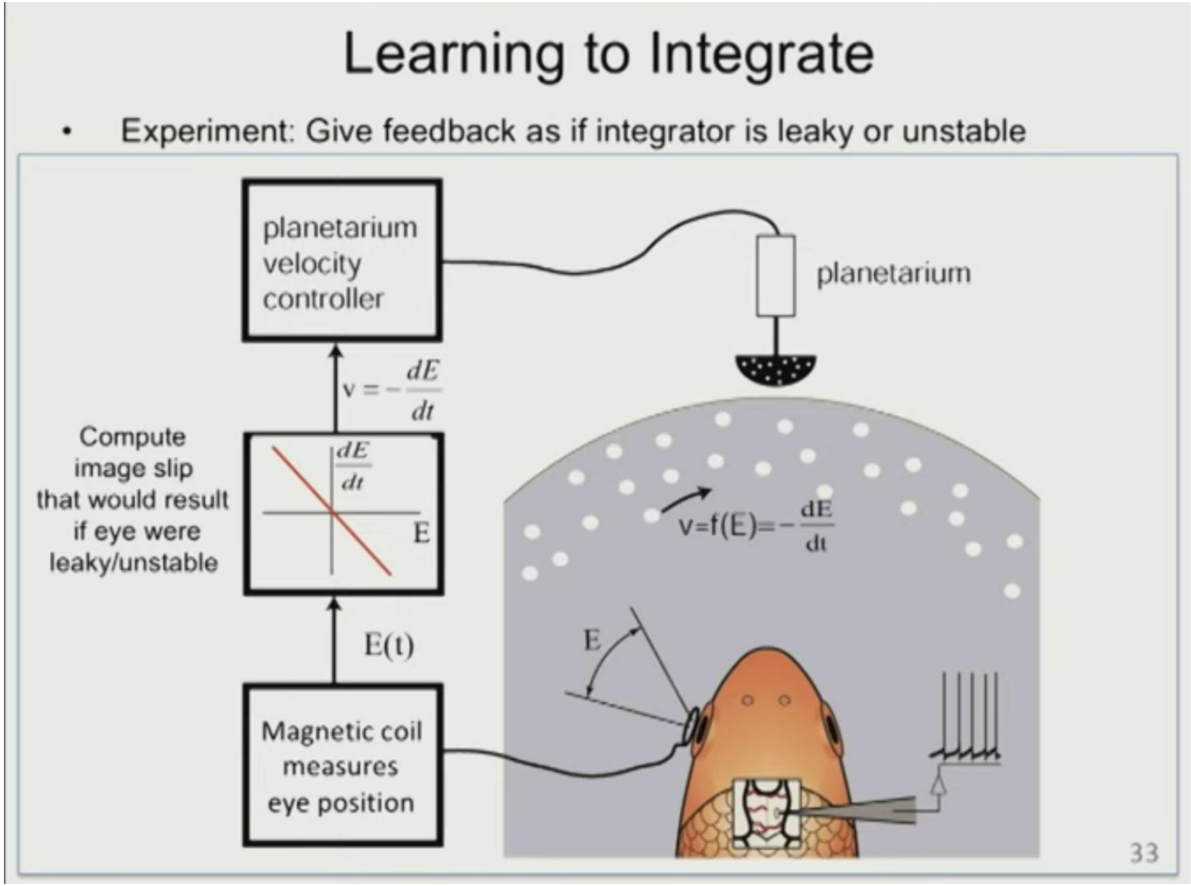


$$\tau_n \frac{dc_1}{dt} = -c_1 + \lambda_1 c_1 + burst\ input$$

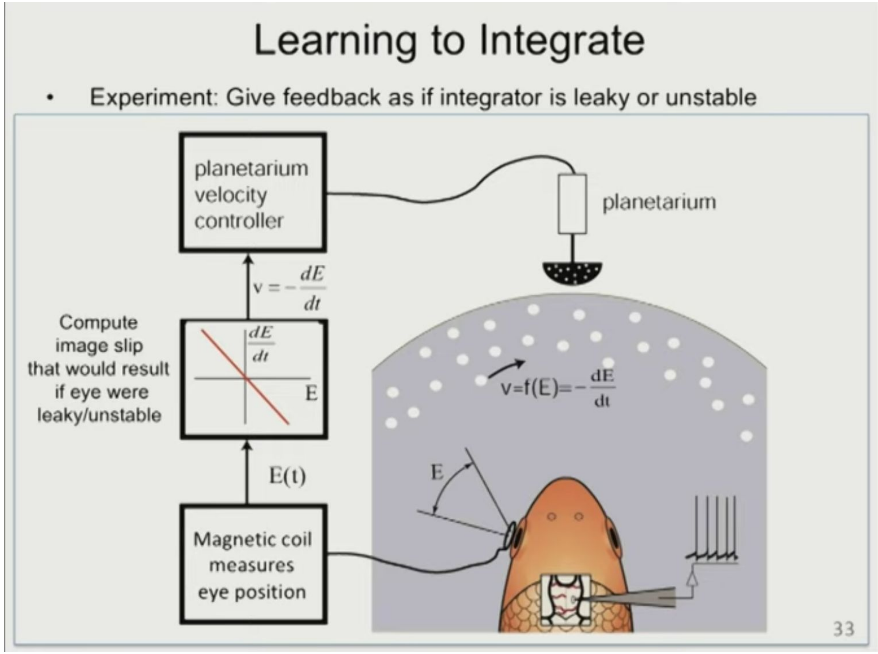
"Neural Integrators"
Michale Fee

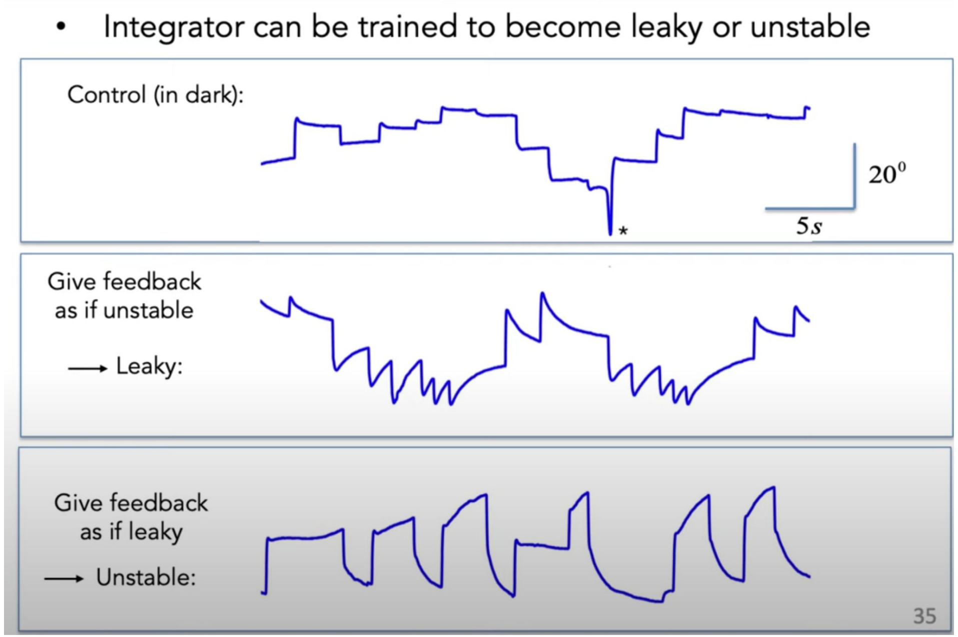
VR-modified sensory feedback induces changes in integration



"Plasticity and tuning by visual feedback of the stability of a neural integrator" (2004) Major et al.

VR-modified sensory feedback induces changes in integration





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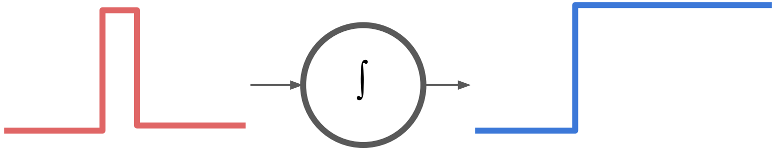
Intermediate summary

- **Goldfish do integrals!**
  - They implement them with network feedback
  - Properties governed by eigenvalues
- Sensory feedback “robustifies” integrator



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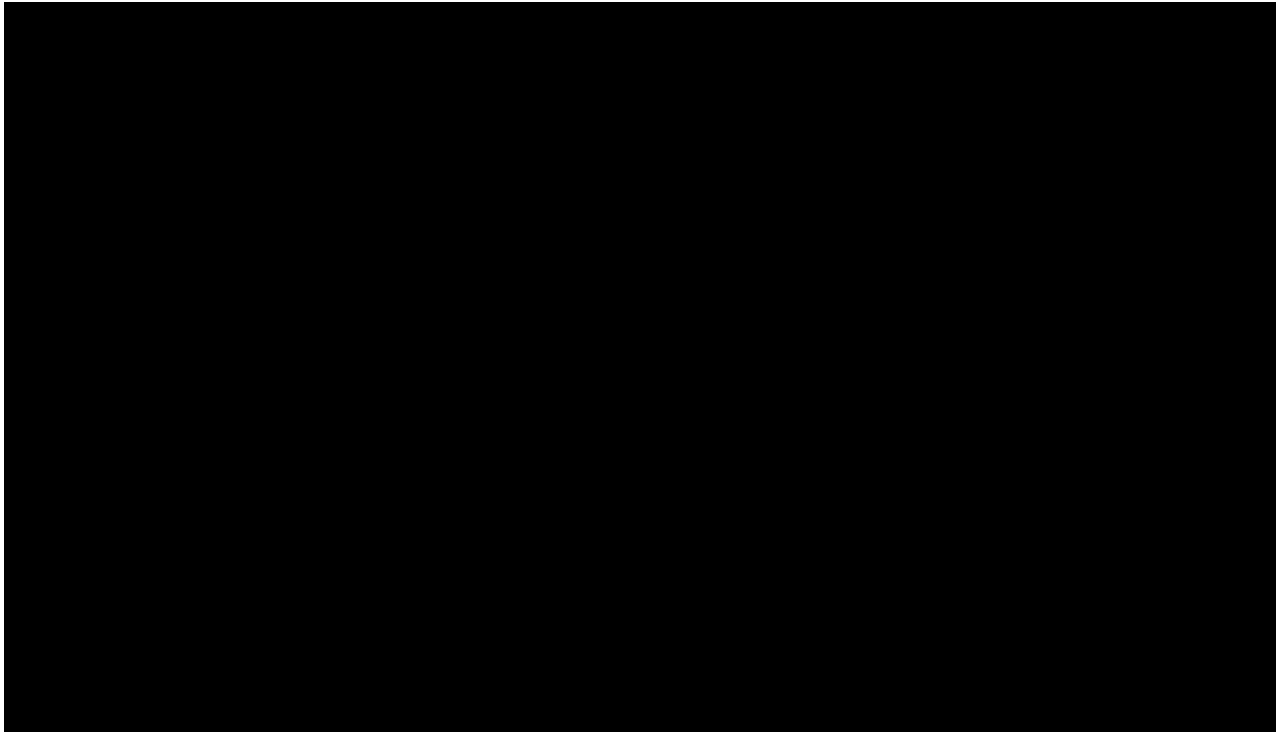
“Neural Integrators”
Michale Fee

Decision Making

Problem: **Random dot motion task**



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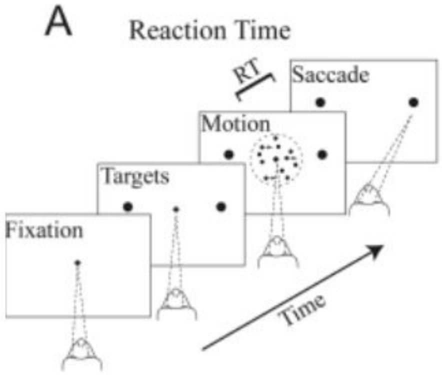
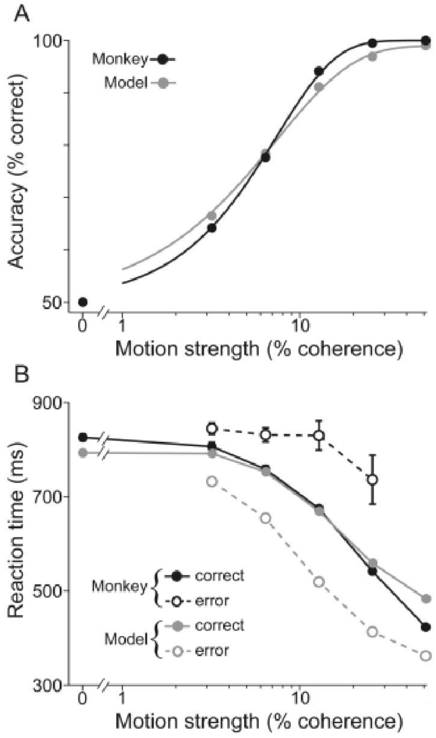




"[A Role for Neural Integrators in Perceptual Decision Making](#)"
(2003) Mazurek et al.

Solution: **A bayesian decision approach - Drift diffusion**

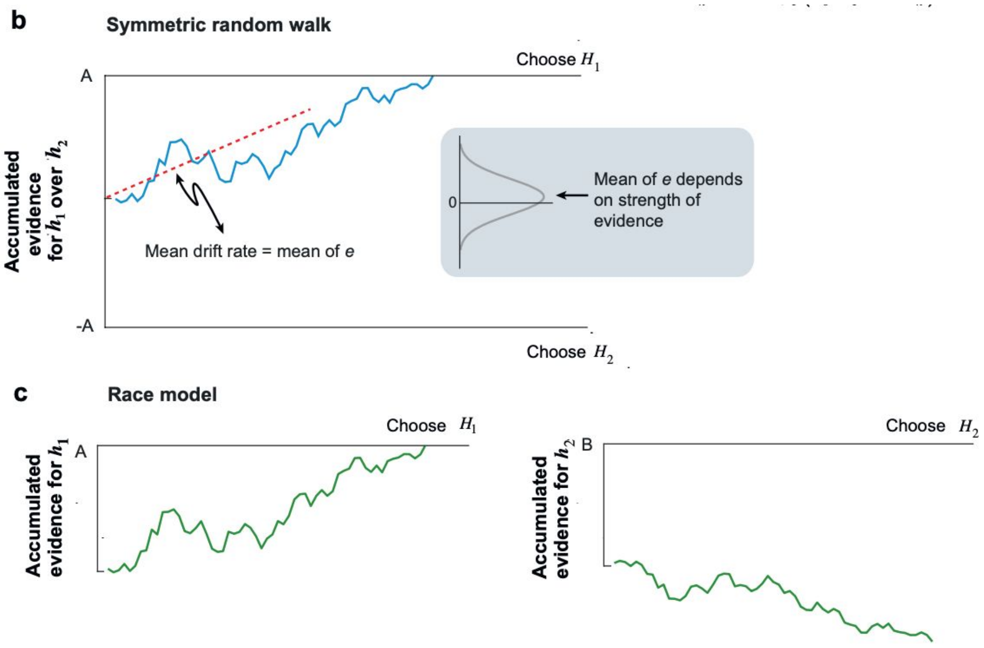
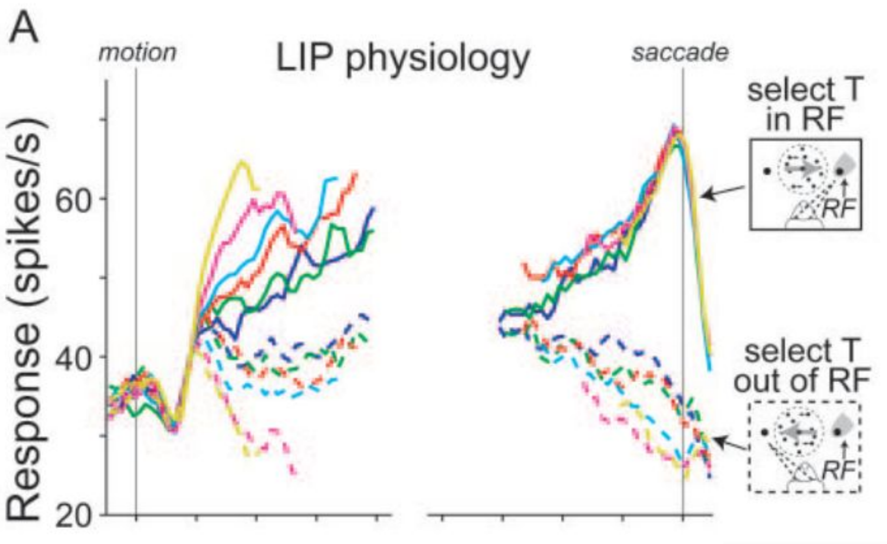
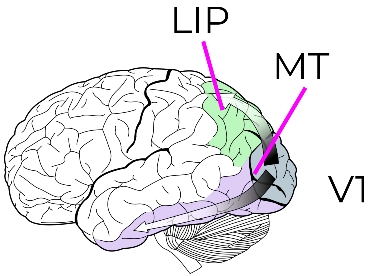


Figure 2

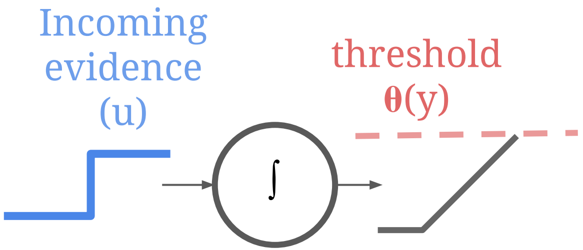
“The Neural Basis of Decision Making” (2007) Gold & Shadlen
“Perceptual decision making: drift-diffusion model is equivalent to a Bayesian model” (2014) Bitzer

Neural Solution: Integrate evidence!





"Response of Neurons in the Lateral Intraparietal Area during a Combined Visual Discrimination Reaction Time Task" (2002)
Roitman & Shadlen



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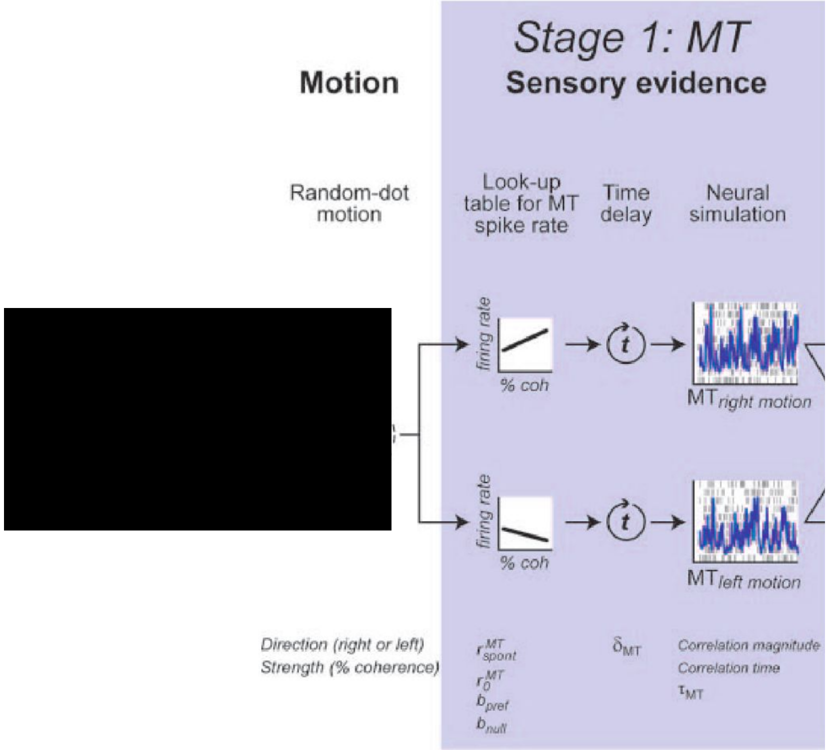

"A Role for Neural Integrators in Perceptual Decision Making" (2003) Mazurek et al.

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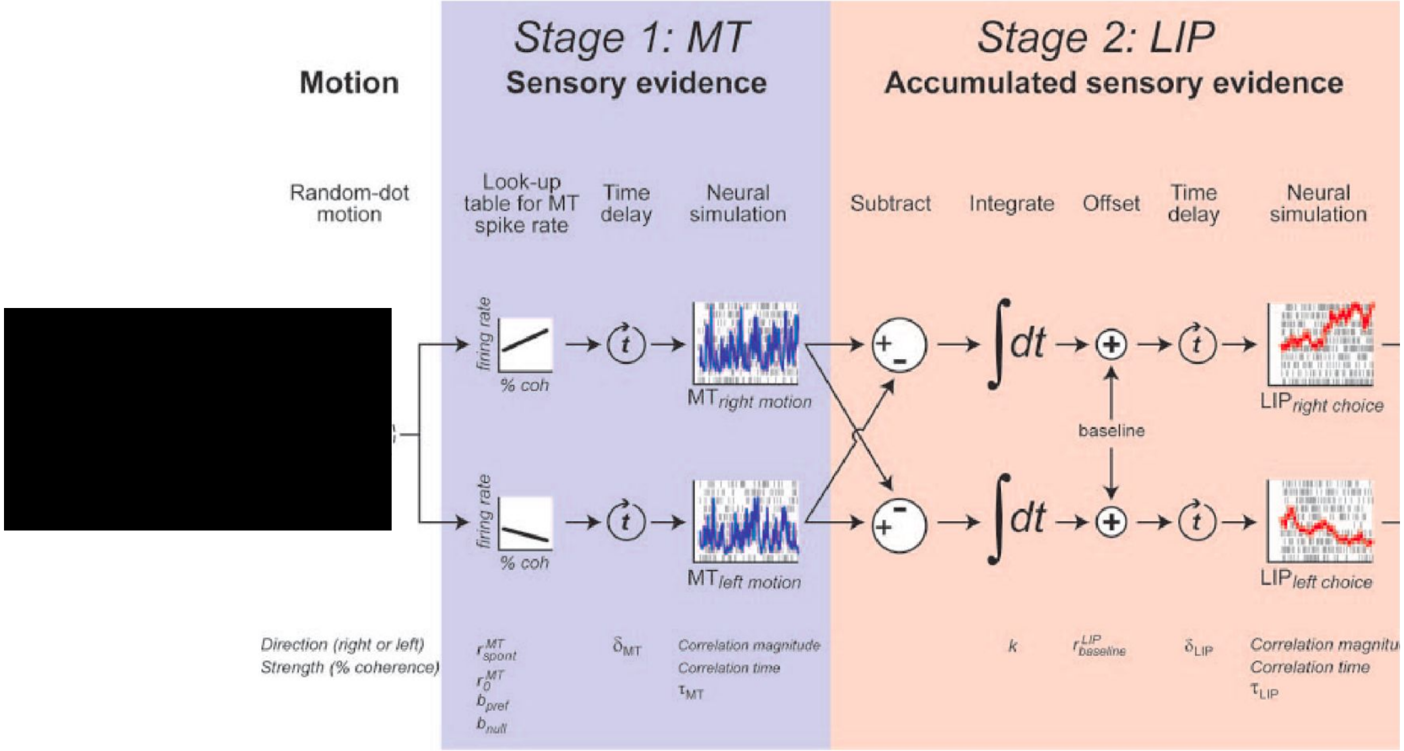

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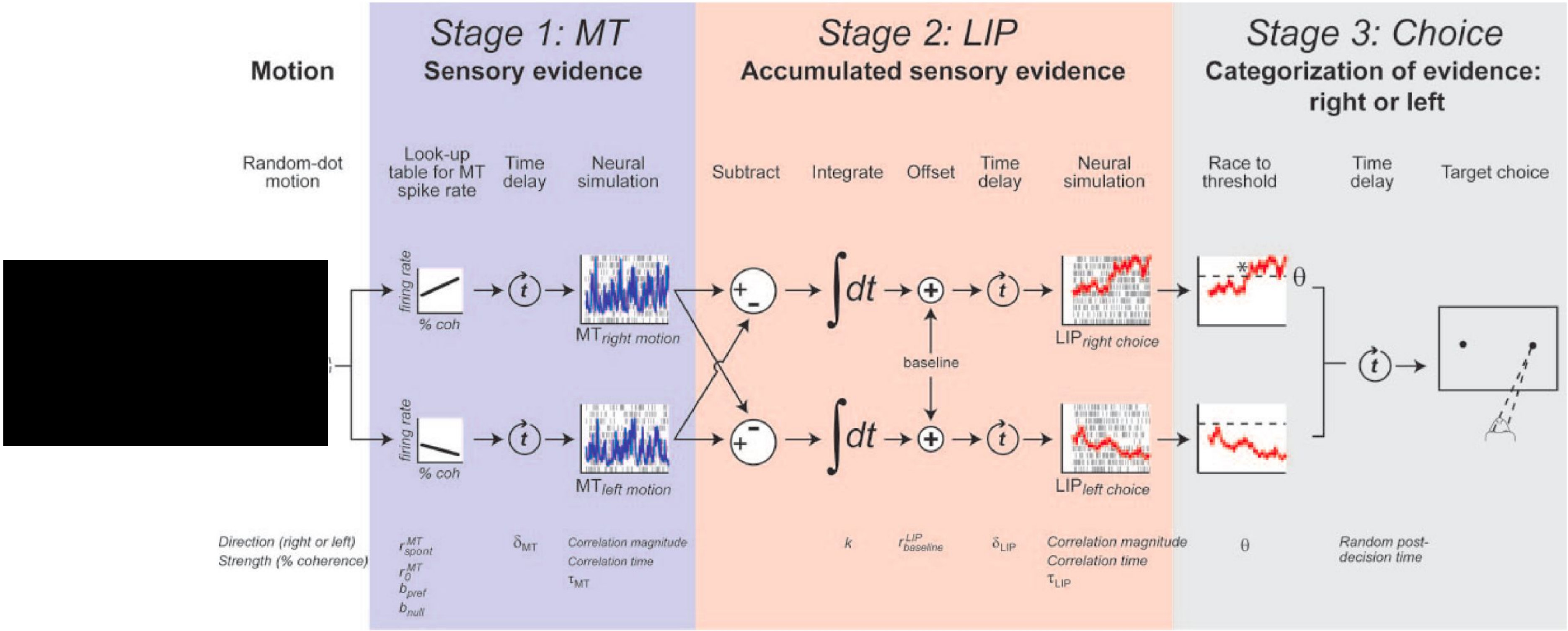
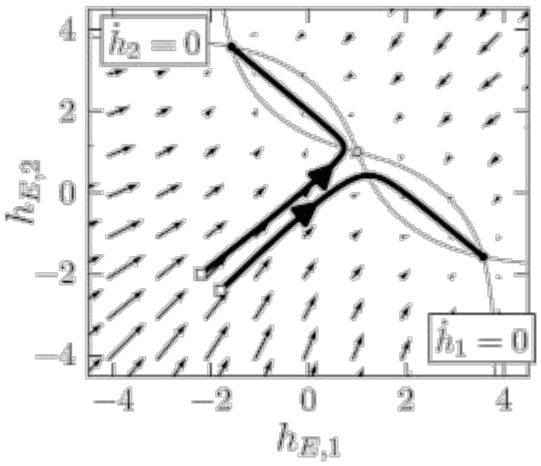
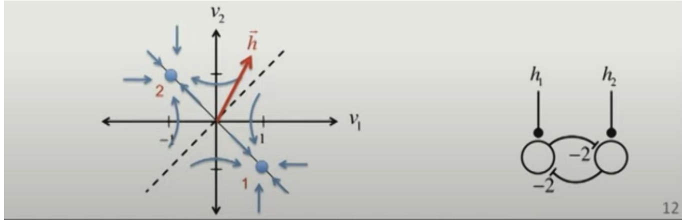


"A Role for Neural Integrators in Perceptual Decision Making"
(2003) Mazurek et al.

A winner-takes-all "force field"

Although not discussed in detail here, an alternate model of the dynamics of decision making involves reciprocal inhibition to allow one dimension to "win" over the other given small changes in inputs



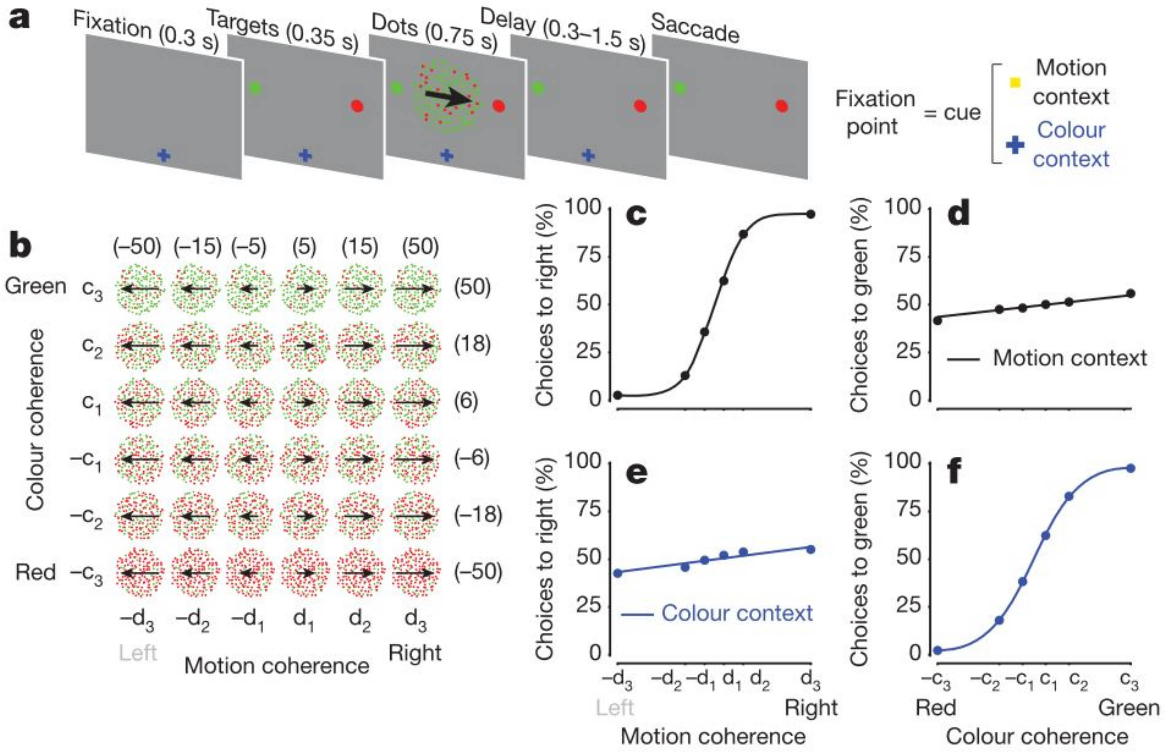


see "Neuronal Dynamics 16.3 Dynamics of decision making" Gerstner et al. for a textbook walkthrough and

"Neurobiological Models of Two-Choice Decision Making Can Be Reduced to a One-Dimensional Nonlinear Diffusion Equation" (2008) Roxin & Ledberg

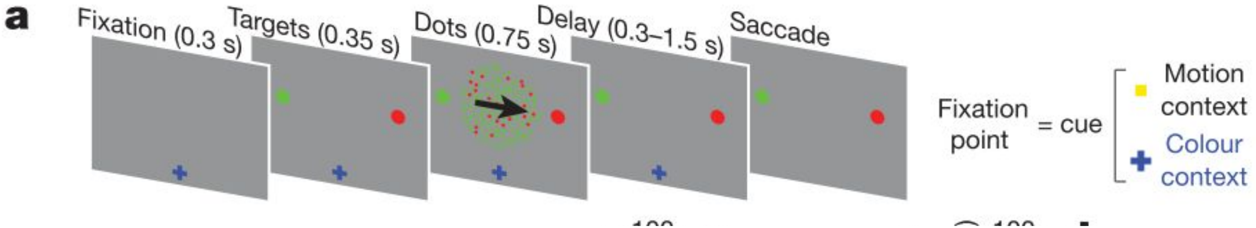
Animation here: http://jackterwilliger.com/attractor-networks/

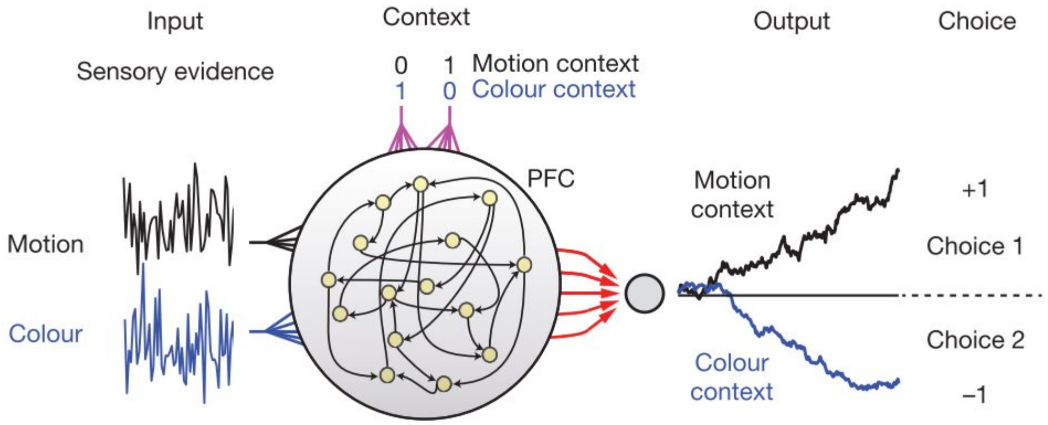
Context-dependent decision-making



"Context-dependent computation by recurrent dynamics in prefrontal cortex" (2013) Mante et al.

How do multiple types of information get integrated?





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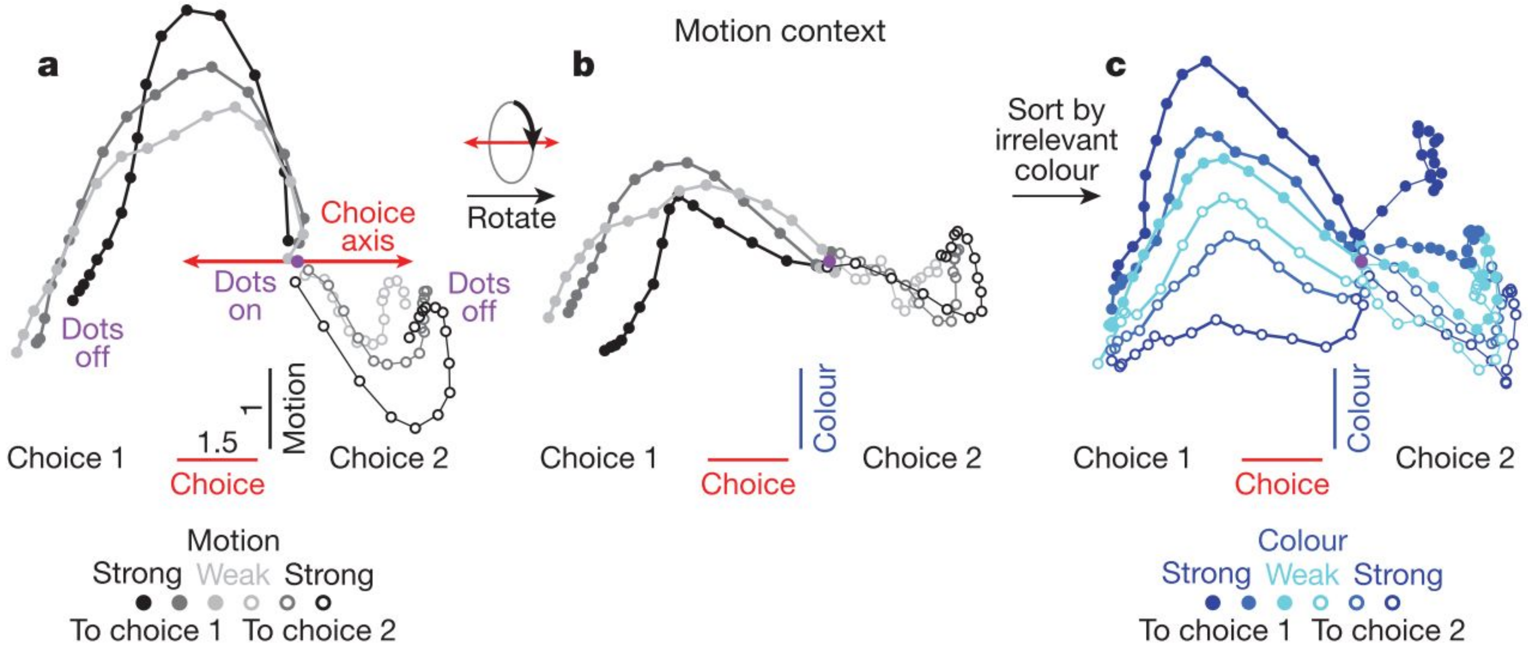
Trajectories of neural activity get rotated depending on task-context



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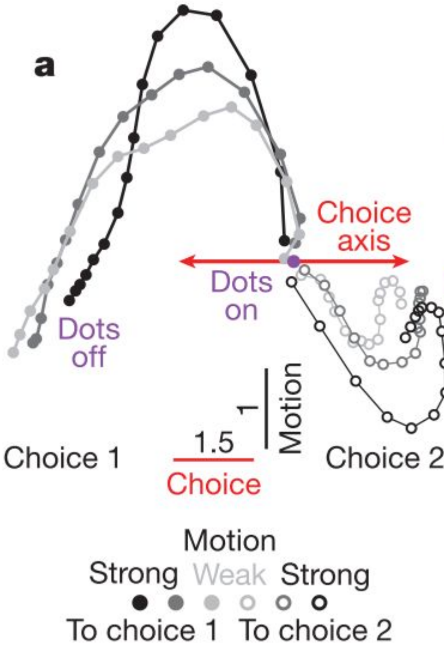
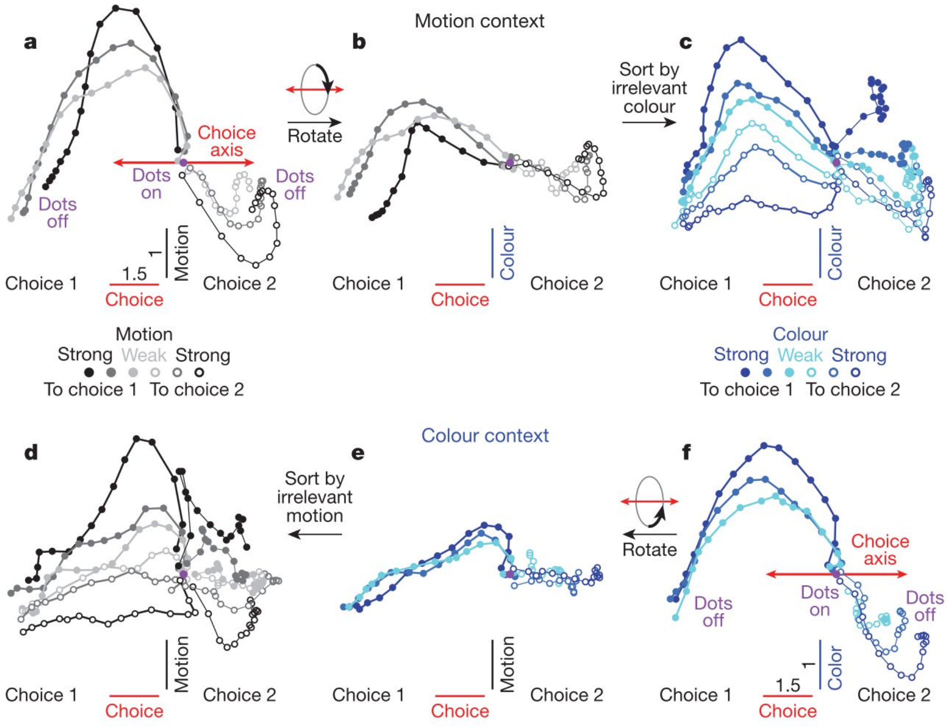


Neural trajectories projected onto 3D:

- *Choice*
- *Motion strength*
- *Color strength*

“Context-dependent computation by recurrent dynamics in prefrontal cortex” (2013) Mante et al.

Trajectories of neural activity get rotated depending on task-context



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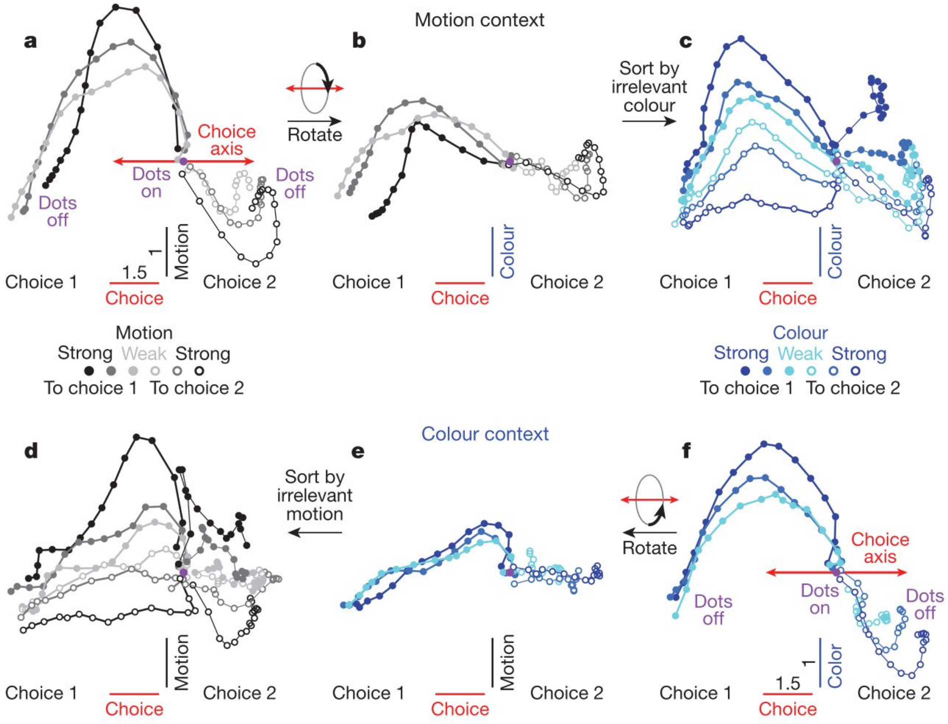
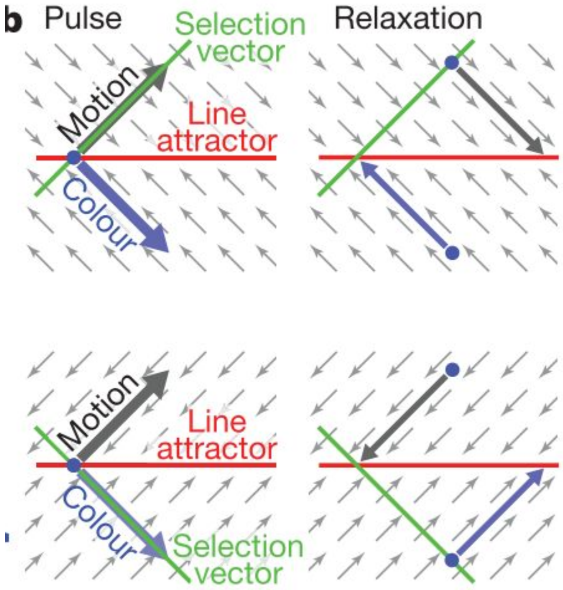
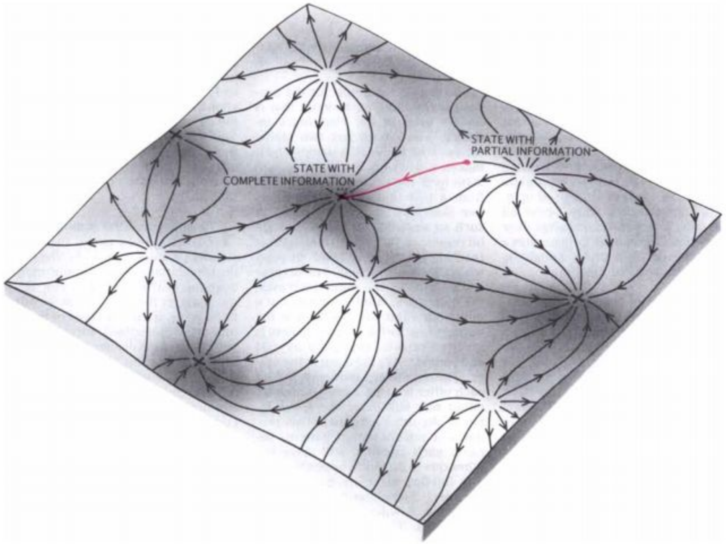




“Context-dependent computation by recurrent dynamics in prefrontal cortex” (2013) Mante et al.

Hopfield Networks: Categorical Memory



“Collective Computation in Neuronlike Circuits” (1987) Tank & Hopfield

Recall, recognition, and partial information

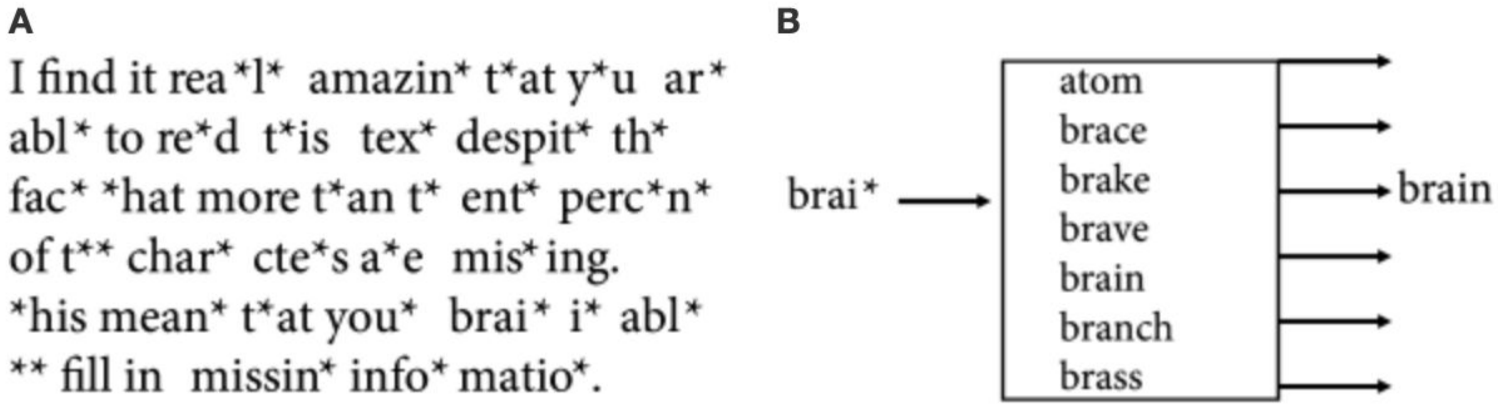
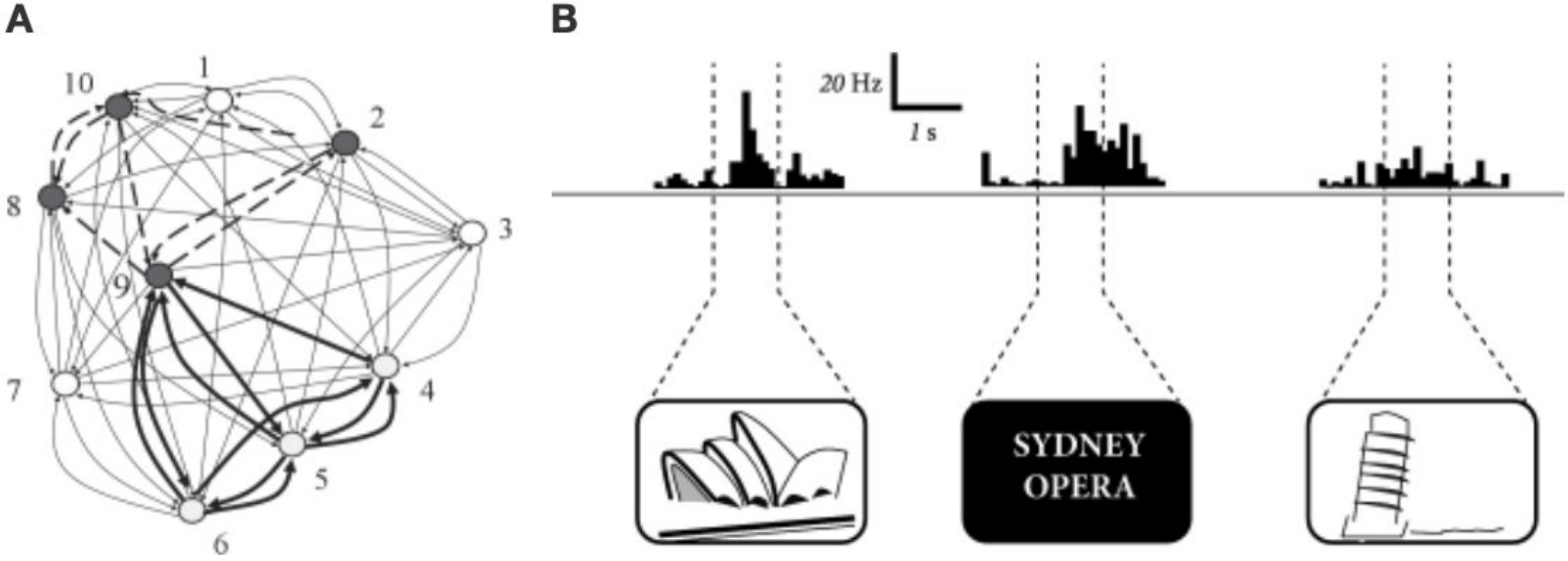


Fig. 17.1: Memory recall cued by partial information. **A**. Read it!. **B**. Schematic view of the recall process. Your brain has memorized a list of words. Based on partial information and the context, your brain is able to complete the missing characters.

Neuronal Dynamics - Ch.17 Memory & Attractor Dynamics Gerstner et al.

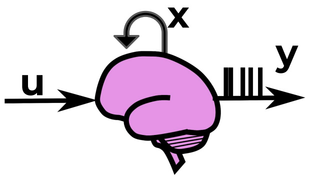
Evidence that memories are stored in networks

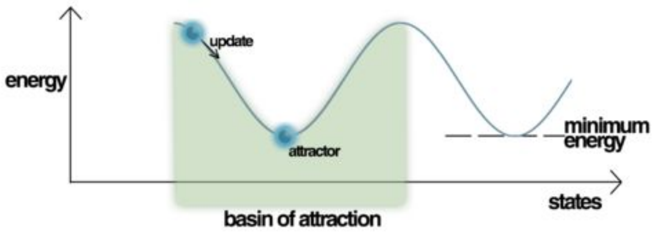


"*Invariant visual representation by single neurons in the human brain*" (2005) Quiroga et al.

"physicists love the idea that math they already know might explain how the brain works"
- Geoff Hinton

Hopfield networks - an early solution



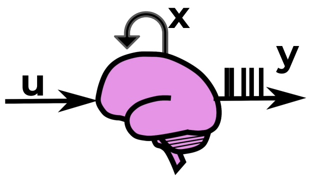


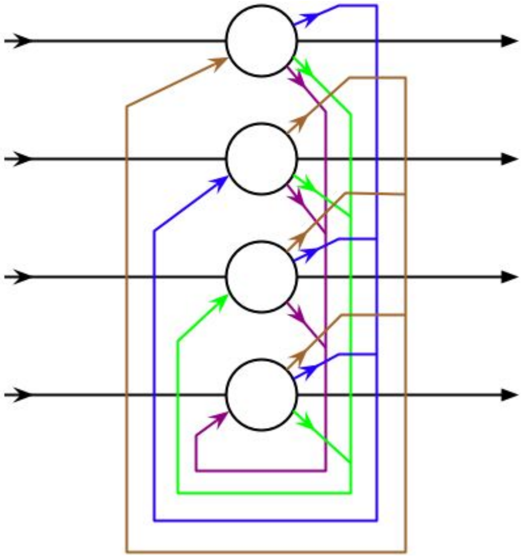
- In general nonlinear networks are very hard to analyze
- **Hopfield's insight:** network can implement memory by minimizing an energy function
  - (if connection weights are symmetric)
- Advantages
  - Content-addressable memory
  - Robust to "hardware damage"
- Drove a resurgence of interest in studying ANNs
- (inefficient memory storage - see E.Gardner)

"Hopfield Nets" Geoff Hinton
(great lecture from a giant in artificial neural networks)

"Memory as settling onto faces of a crystal"
- idea which may have inspired the
"memory as minima of a landscape" idea
"Principles of literary criticism" (1924) Richards

Hopfield networks - an early solution





- Binary "on-off" neurons (McCulloch-Pitts 1943)
  - Weighted inputs
  - Threshold output
- Recurrent connections
  - (no self-connection)
- State of the network is the collection of activity of the nodes
- Two phases of operation:
  - Learn
  - Settle

$$V_i^{t+1} = sign(\sum_j W_{ij} \cdot V_i)$$

$$\Delta W_{ij} = V_i V_j$$

Recognition - Content-Addressable Memory

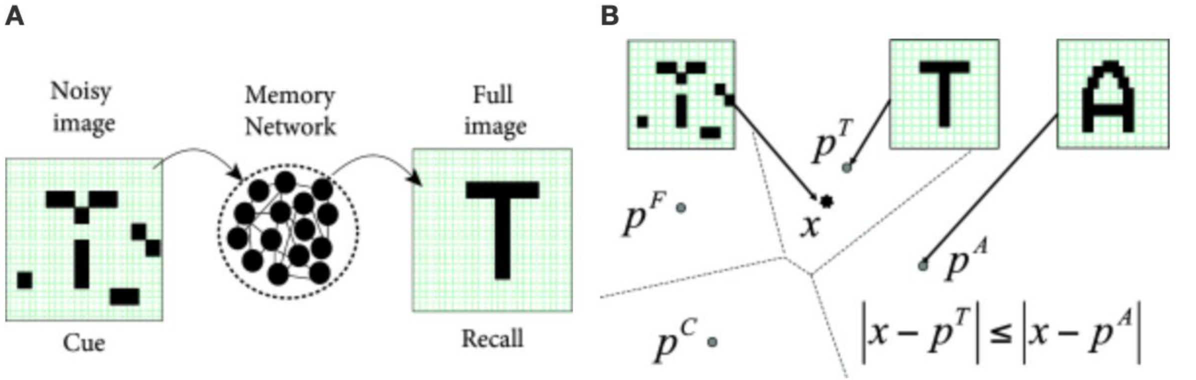


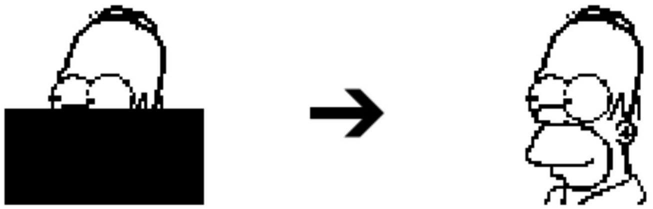
Fig. 17.2: Recall and recognition as search for nearest prototype. **A**. A letter ‘T’ in a noisy image (left) serves as a cue in order to recall a noise-free prototype letter ‘T’ from the memory embedded in a neural network. **B**. Recognition of the input x (black star, representing a noisy ‘T’) can be interpreted as an algorithm that searches for the nearest prototype p^α such that $|x - p^\alpha| \leq |x - p^\mu|$ for all μ, and p^μ denotes all possible prototypes (gray circles). The dashed lines are the sets of points with equal distance to two different prototypes.

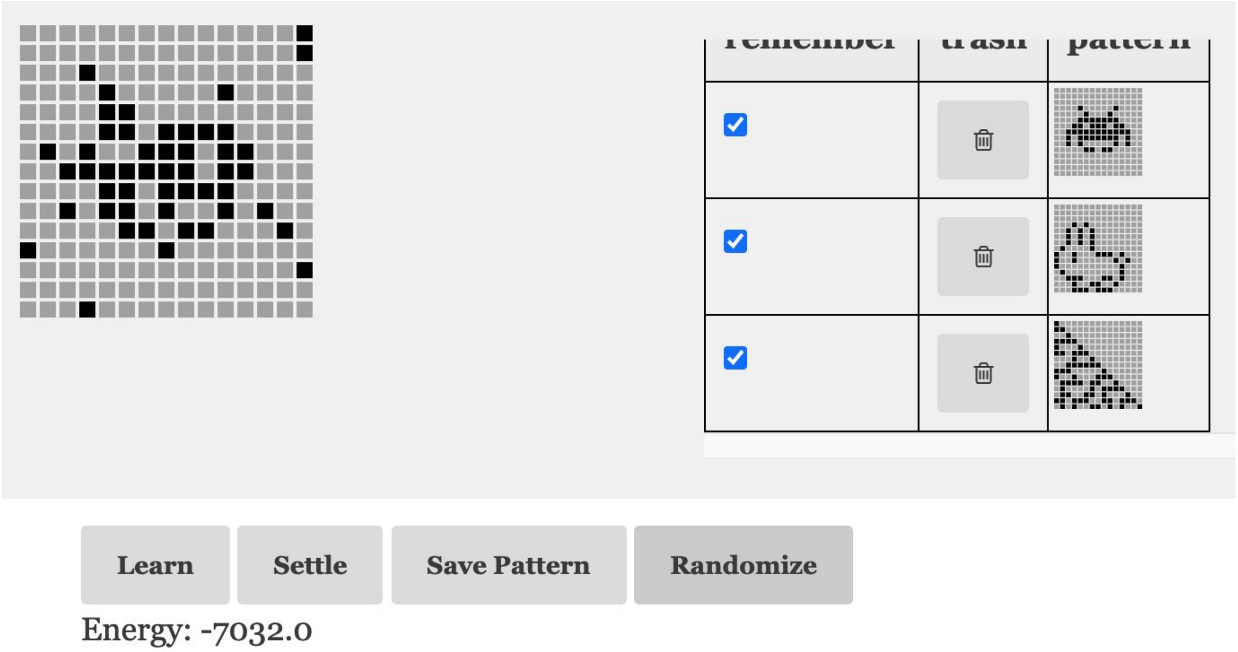
Neuronal Dynamics - Ch.17 Memory & Attractor Dynamics Gerstner et al.

Hopfield network demo

Enter your own images

Watch the network recall them





Demos & discussion:

http://jackterwilliger.com/attractor-networks/

https://ml-jku.github.io/hopfield-layers/

Navigation

Dynamics for **navigation**

desert ants

5288 Neurobiology: Müller and Wehner

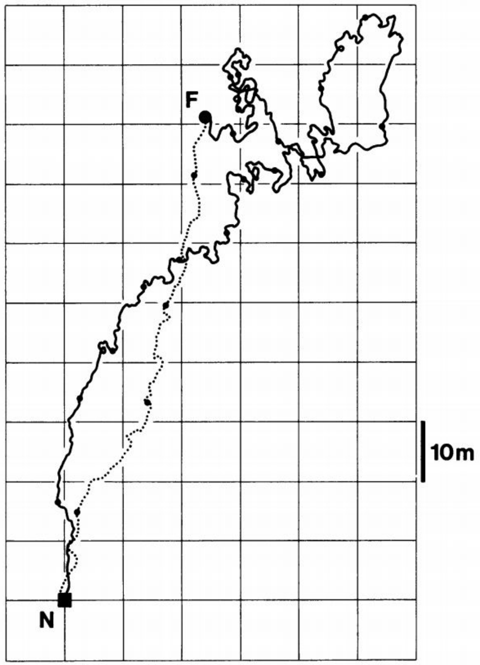


FIG. 1. Foraging trip of an individual ant, *Cataglyphis fortis*. Outbound and inbound trajectories are depicted by solid and stippled lines, respectively. *N*, nest; *F*, location of food item found by the searching ant. The length of the outbound path is 354.5 m; the maximal distance from the nest is 113.2 m. Time marks (small filled circles) are given every 60 s.

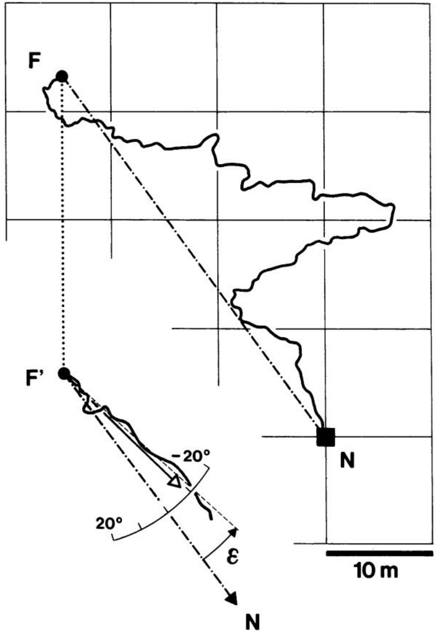


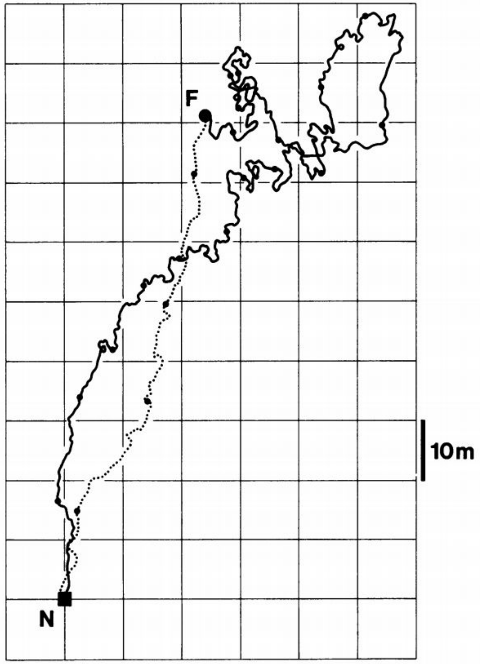
FIG. 4. Natural foraging path of an ant. *N*, nest; *F*, location where the ant found a food item. In the experiment, the ant was displaced from *F* to *F'*. After release, its homing direction was recorded (see *Inset*). Black arrow, direction of the nest; white arrow, ant's homing direction as computed from Eq. 3; ε, error angle by which the ant's trajectory deviates from the true home direction (*N*).

"Path integration in desert ants" (1988) Muller & Wehner

Dynamics for **navigation**

desert ants

5288 Neurobiology: Müller and Wehner



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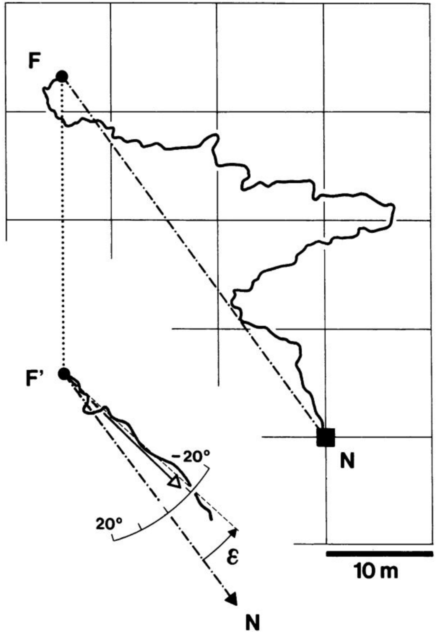

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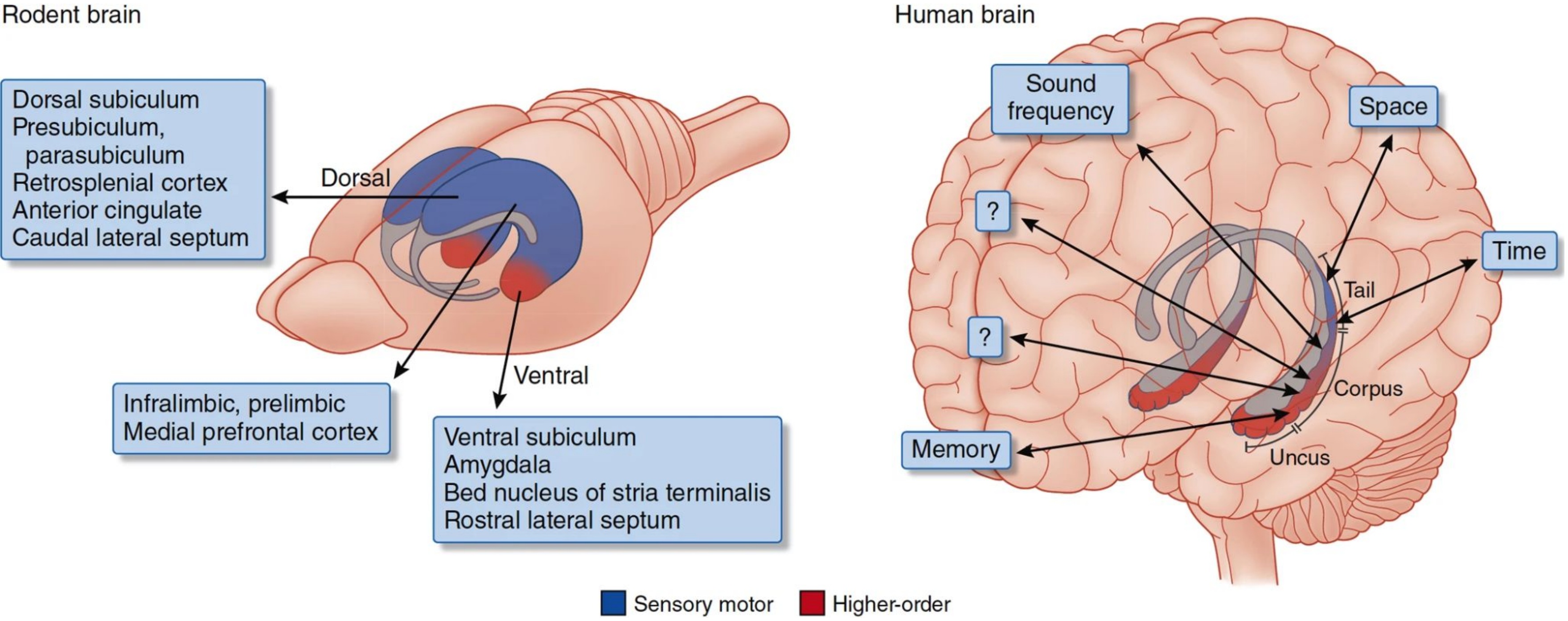
Hippocampus



"Viewpoints: how the hippocampus contributes to memory, navigation and cognition" (2017) Lisman et al.

Place cells & grid cells

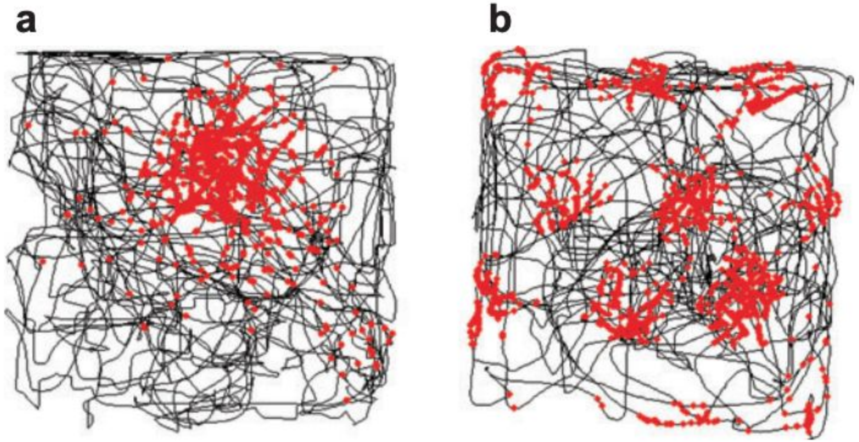
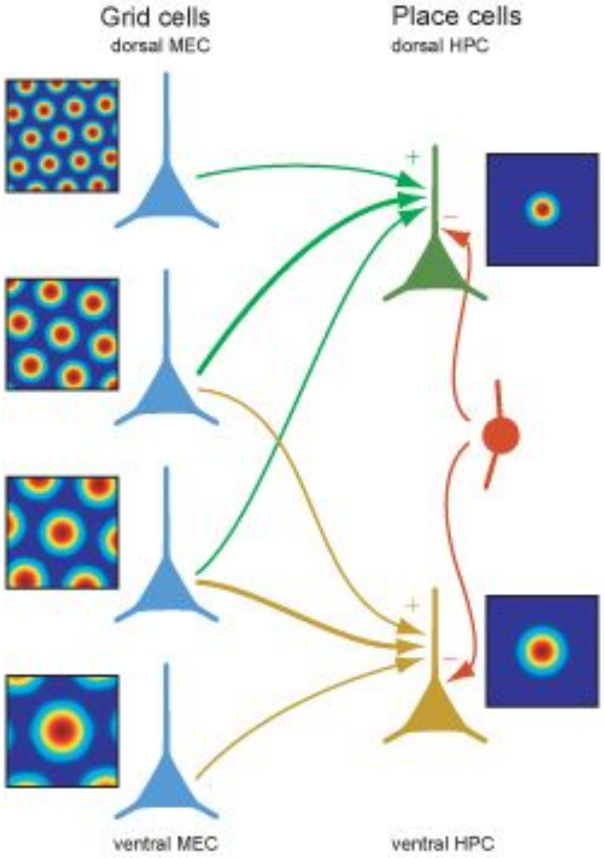


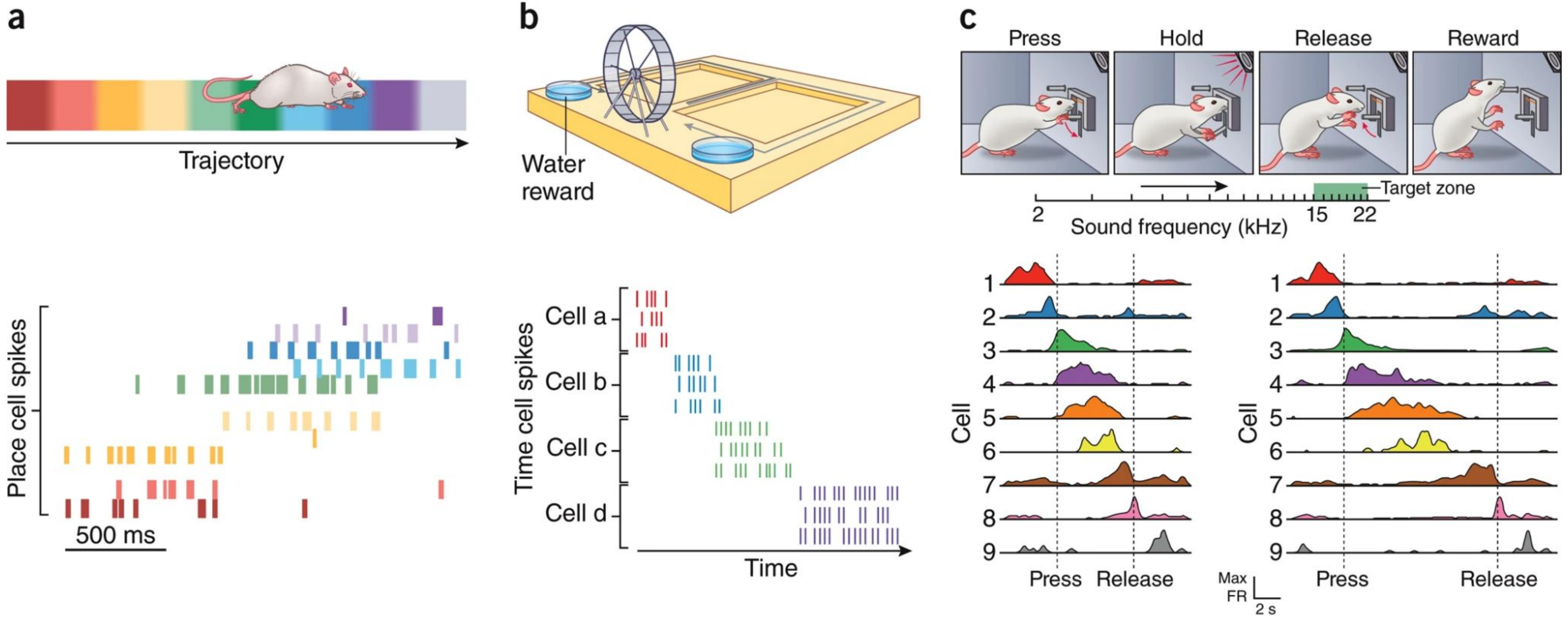
Figure 1

Place cell in the hippocampus (*a*) and grid cell in the medial entorhinal cortex (MEC) (*b*). Spike locations (*red*) are superimposed on the animal's trajectory in the recording enclosure (*black*). Whereas most place cells have a single firing location, the firing fields of a grid cell form a periodic triangular matrix tiling the entire environment available to the animal.



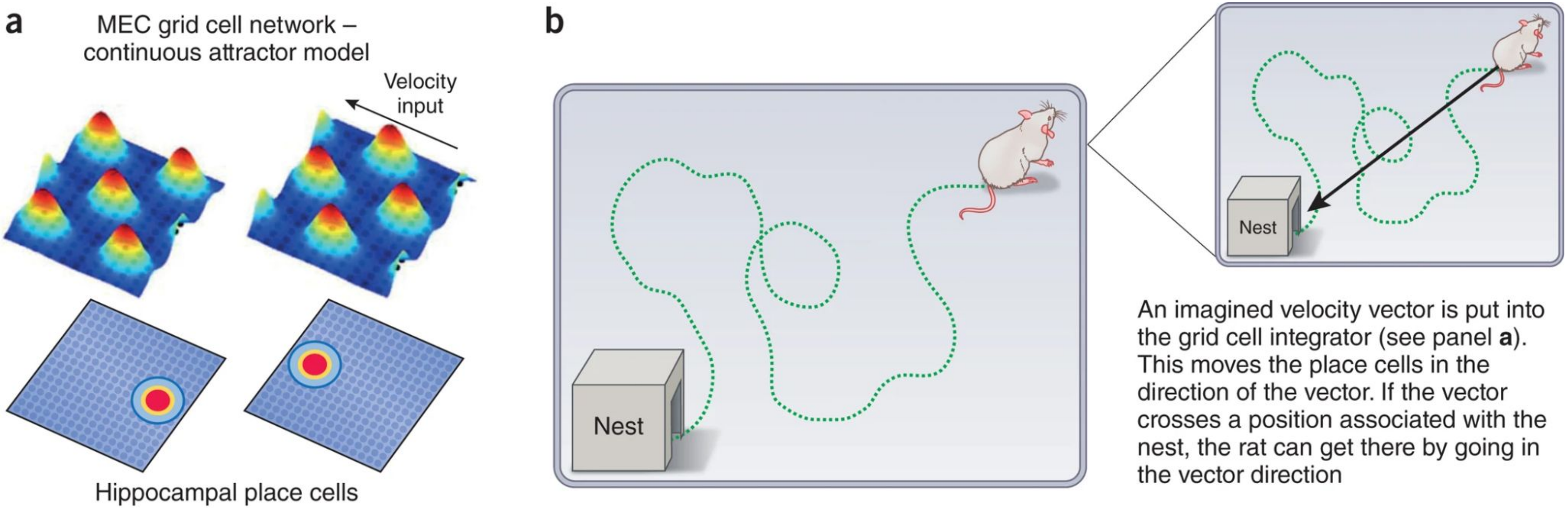
"Viewpoints: how the hippocampus contributes to memory, navigation and cognition"(2017) Lisman et al.
"What do grid cells contribute to place cell firing?" (2014) Bush et al.

Hippocampal pyramidal neurons provide organized responses to spatial stimuli, nonspatial stimuli, and time.



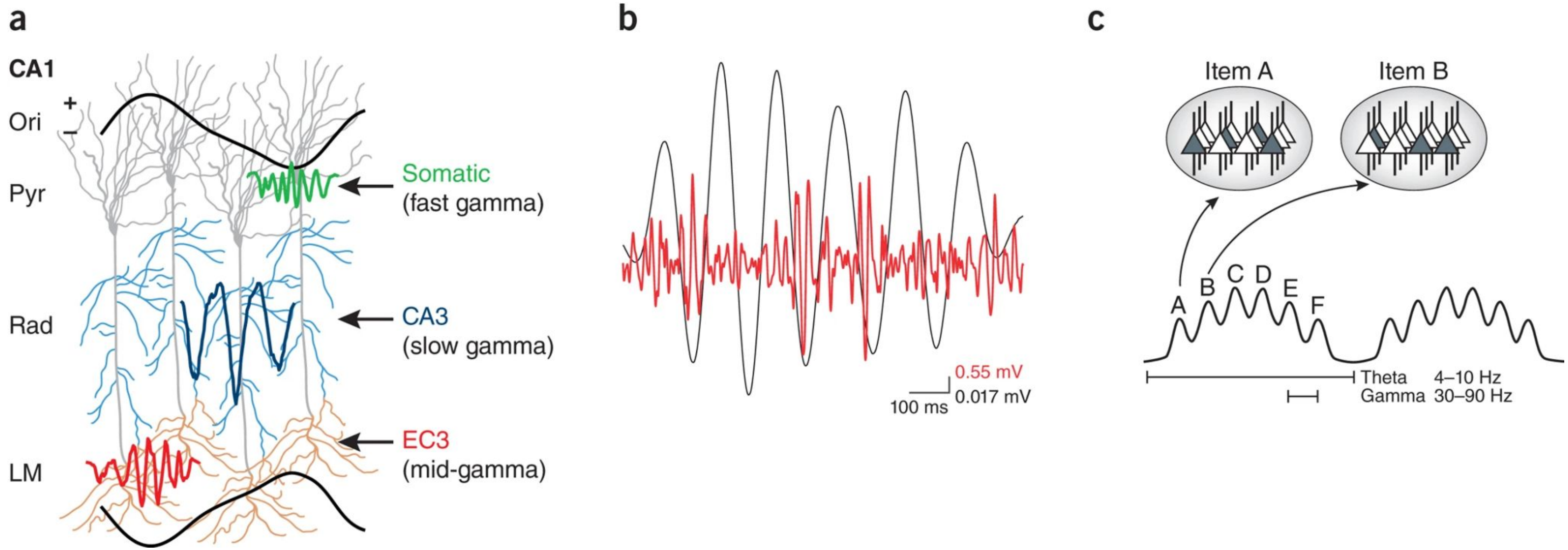
"Viewpoints: how the hippocampus contributes to memory, navigation and cognition" (2017) Lisman et al.

Implementation of direction through a continuous attractor



"Viewpoints: how the hippocampus contributes to memory, navigation and cognition" (2017) Lisman et al.

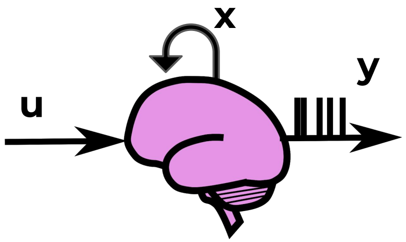
Theta & Gamma Oscillations in Navigation



“Viewpoints: how the hippocampus contributes to memory, navigation and cognition” (2017) Lisman et al.
"Theta phase precession in hippocampal neuronal populations and the compression of temporal sequences" (1996) Skaggs.

Takeaway for today's lecture

- **Memory** is integration
  - **Dynamical systems can integrate**
- **Decision making** is integration + a threshold
- Attractor networks implement memory & decision making
- **Navigation** (and other tasks)
  - Require integration + feedback
  - Feedback robustifies integration



$$\text{Memory} = \int \text{input } dt$$

$$\text{Decision} = \boldsymbol{\theta}\left(\int \text{input } dt\right)$$