QUANTIFYING ECONOMY IN NETWORKS

PRECISION CONVERGENCE
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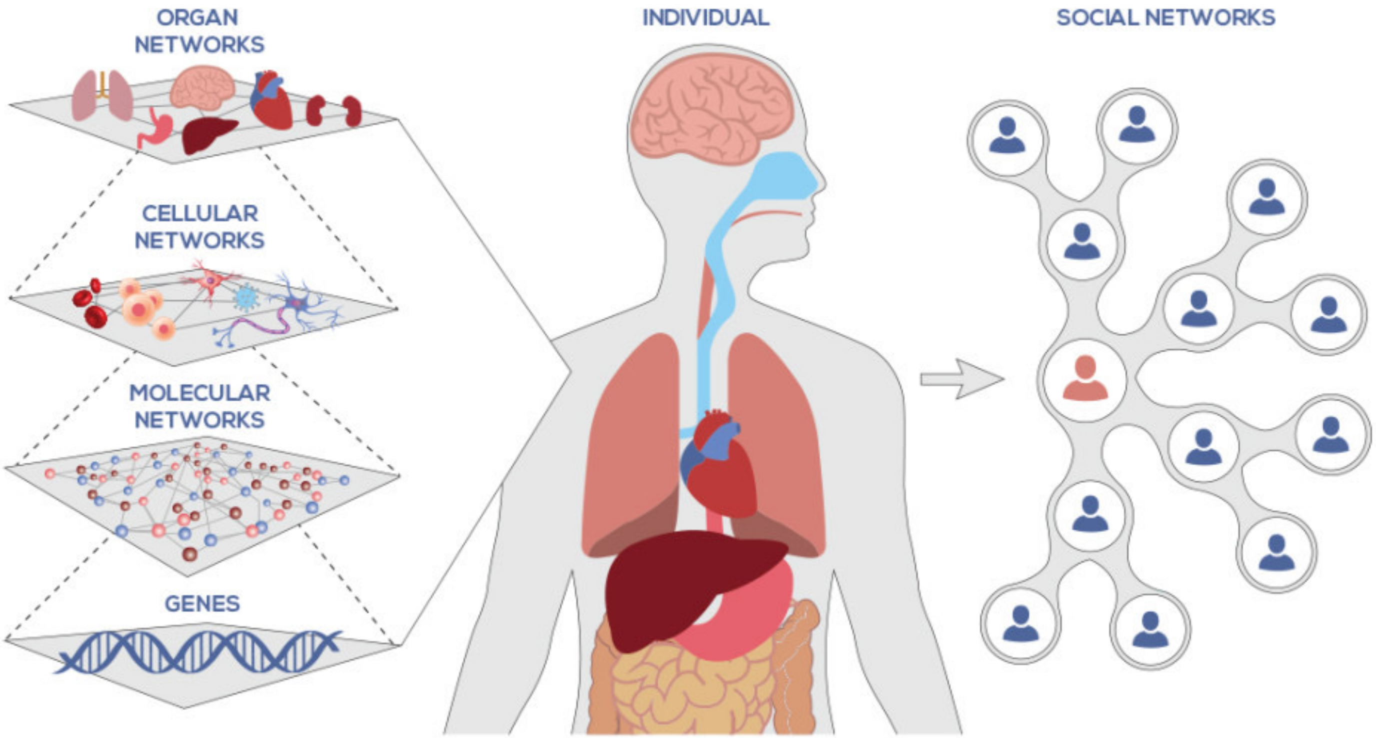
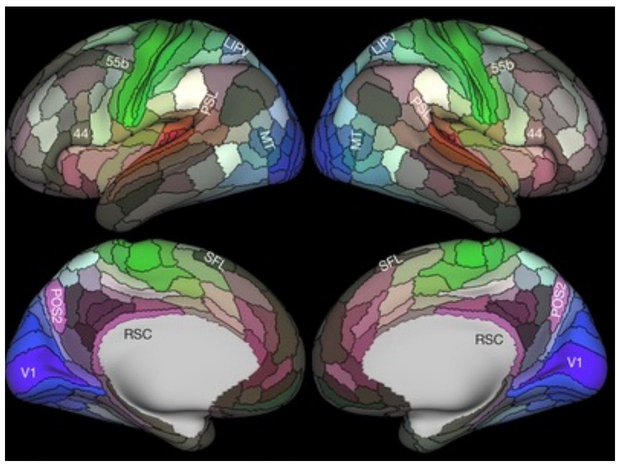
Biological systems are organized as networks

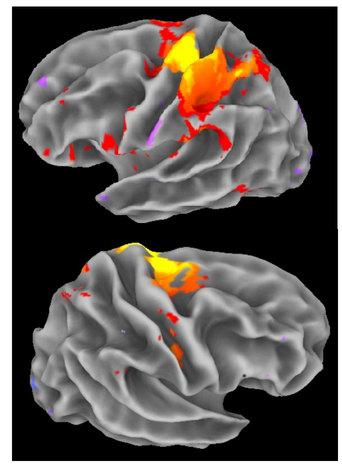
The function of many biological systems is made possible by a network along which items of interest (e.g., nutrients, goods, or information) can be routed.



The brain is a networked biological system

The human brain is a notable example. It is comprised of regions that perform specific functions and engage in particular computations.



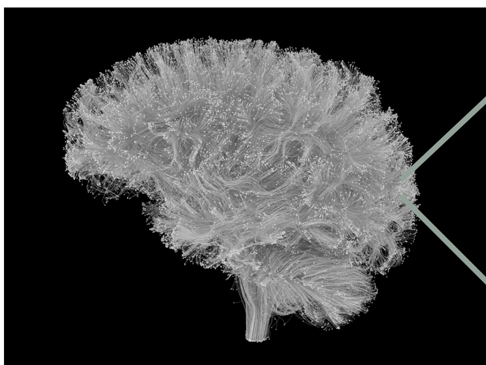


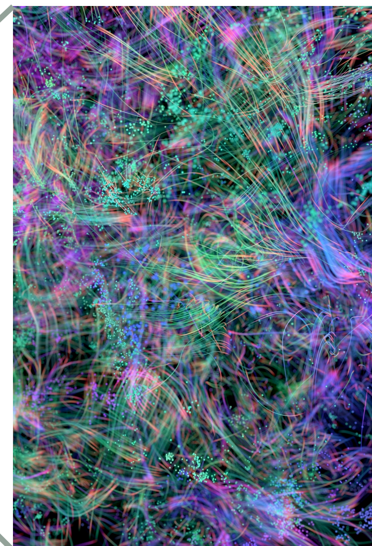
Motion
Vision
Audition
Object recognition
Attention
Decision-making
Emotion processing
Language
Cognitive control

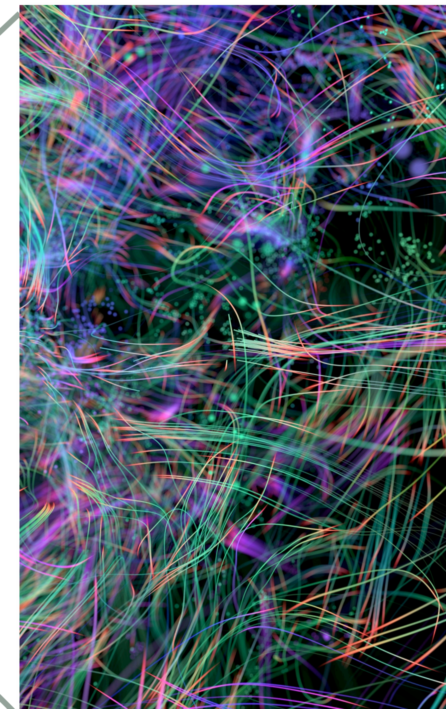
In humans, these functions and computations are typically studied using non-invasive imaging techniques such as magnetic resonance imaging (MRI).

Regions are interconnected in a network

Brain regions are interconnected by large white matter tracts. Each tract is a bundle of neuronal axons along which information-bearing electrical signals can propagate.

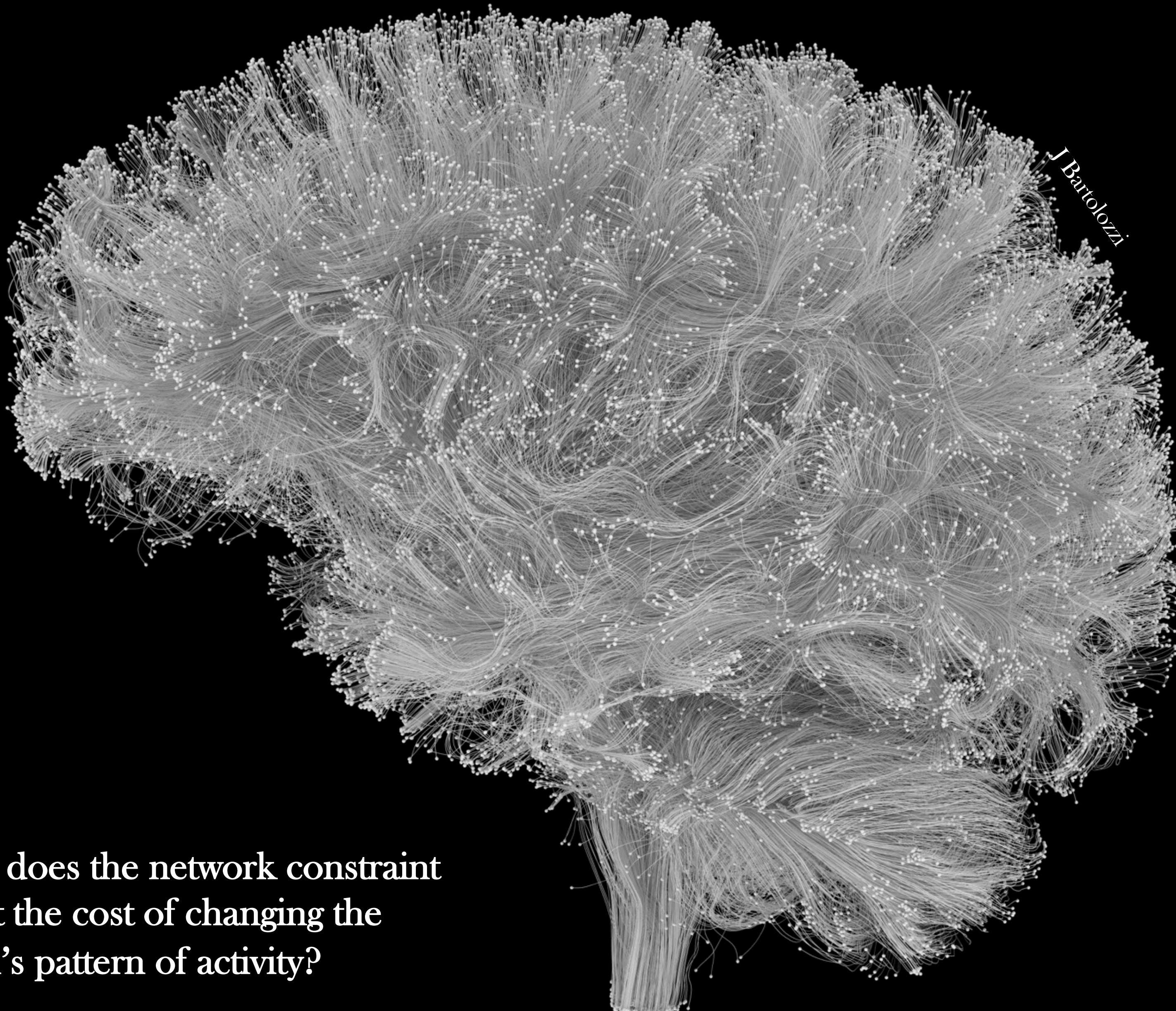






The tracts evince a pattern of connectivity that constrains the passage of information.

Network defines an activity cost



How does the network constraint affect the cost of changing the brain's pattern of activity?

Quantifying economy in networks

OUTLINE:

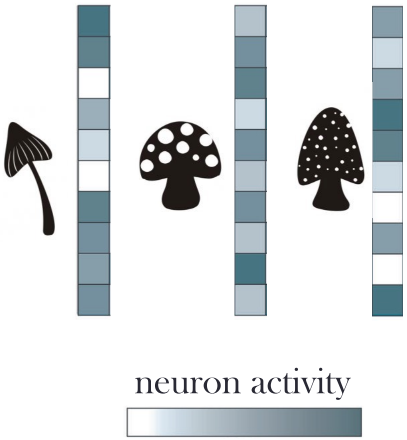
I. The notion of network economy and the energy of state transitions

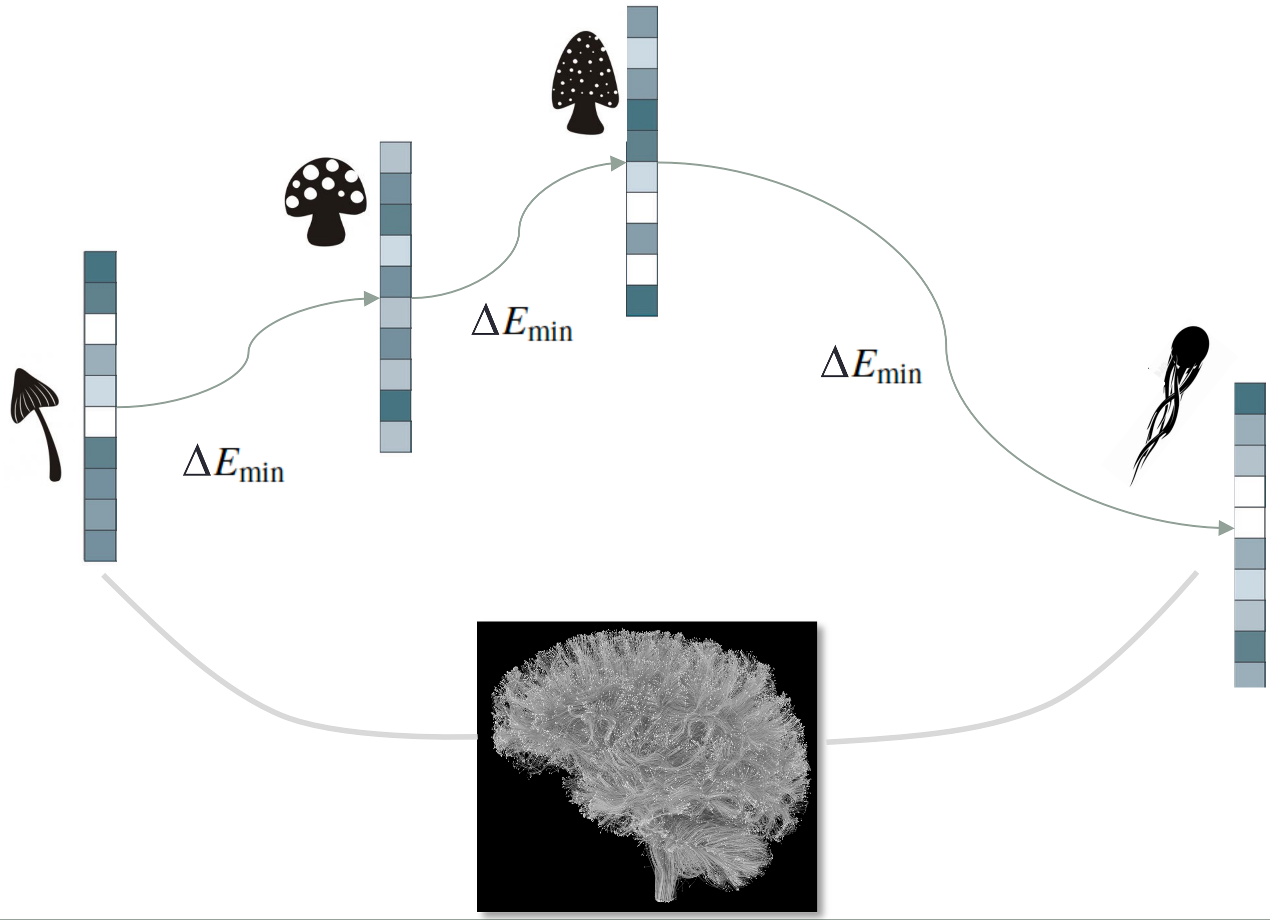
II. Primer on network control theory to quantify energy costs

III. How network economy can inform how we think about cognitive effort

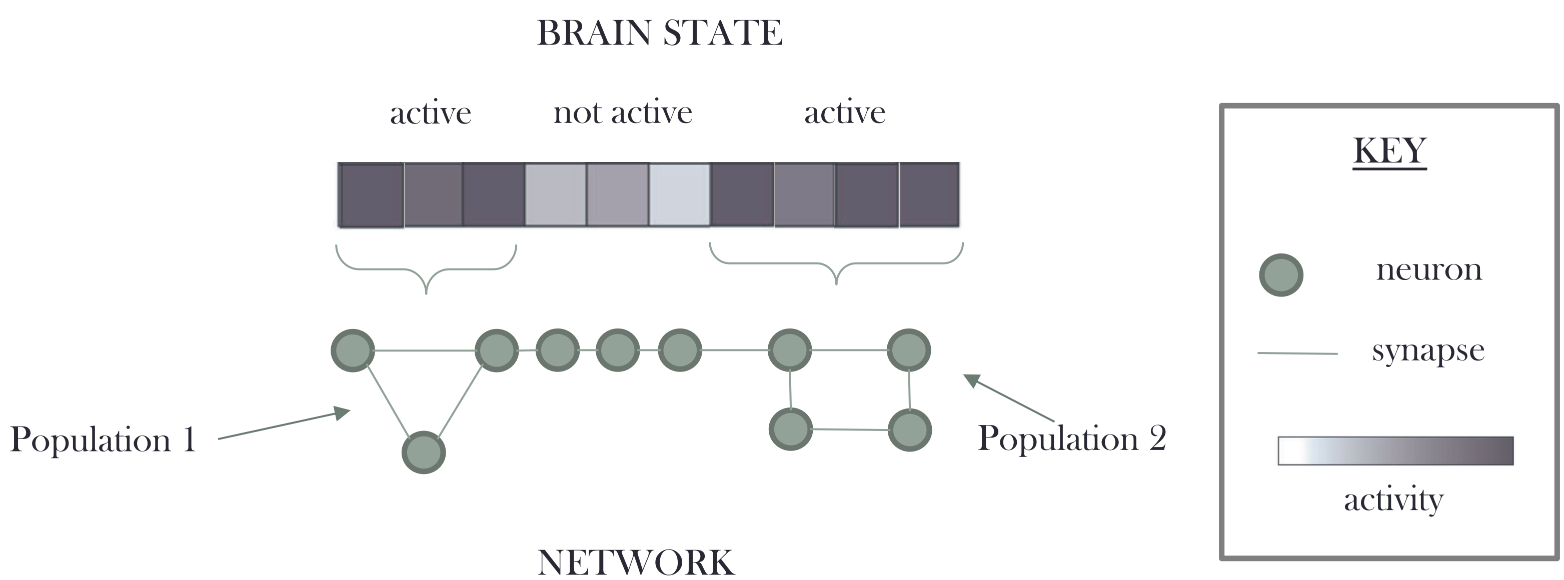
The network control model in pictures

Brain states
representing objects,
events, experiences,
and concepts.





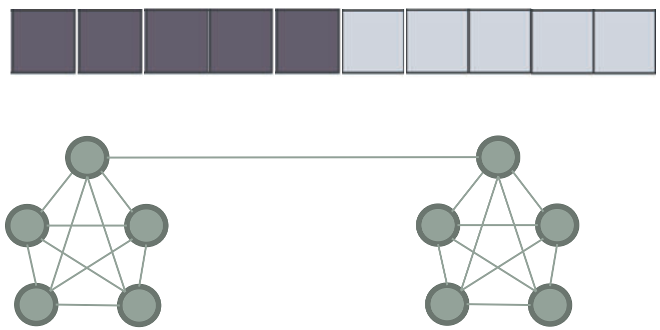
Network constraints on state transitions



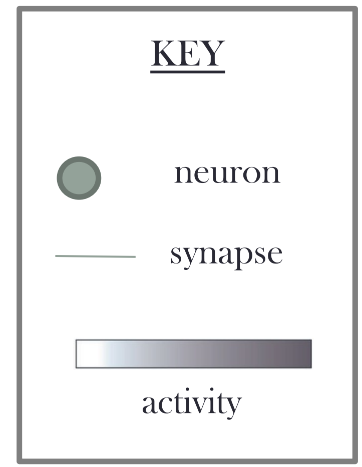
Active neurons spread activity to other neurons around them. Having an active population is easy if the neurons in that population are connected.

Networks make certain states easy or difficult

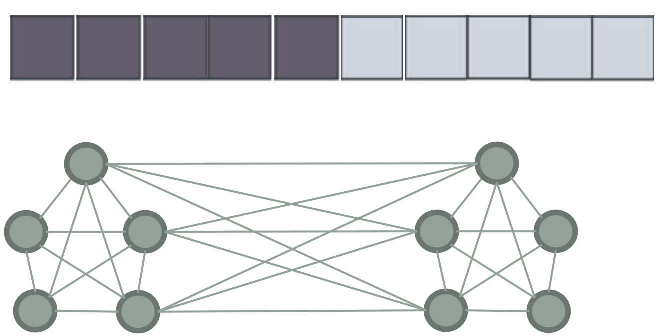
EASY



The density and the topology of the network differentially constrain the difficulty of state transitions.



DIFFICULT



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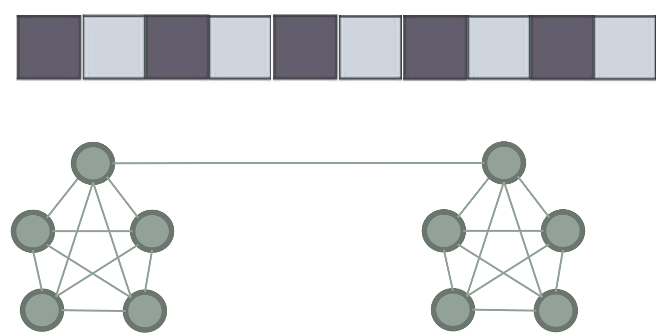
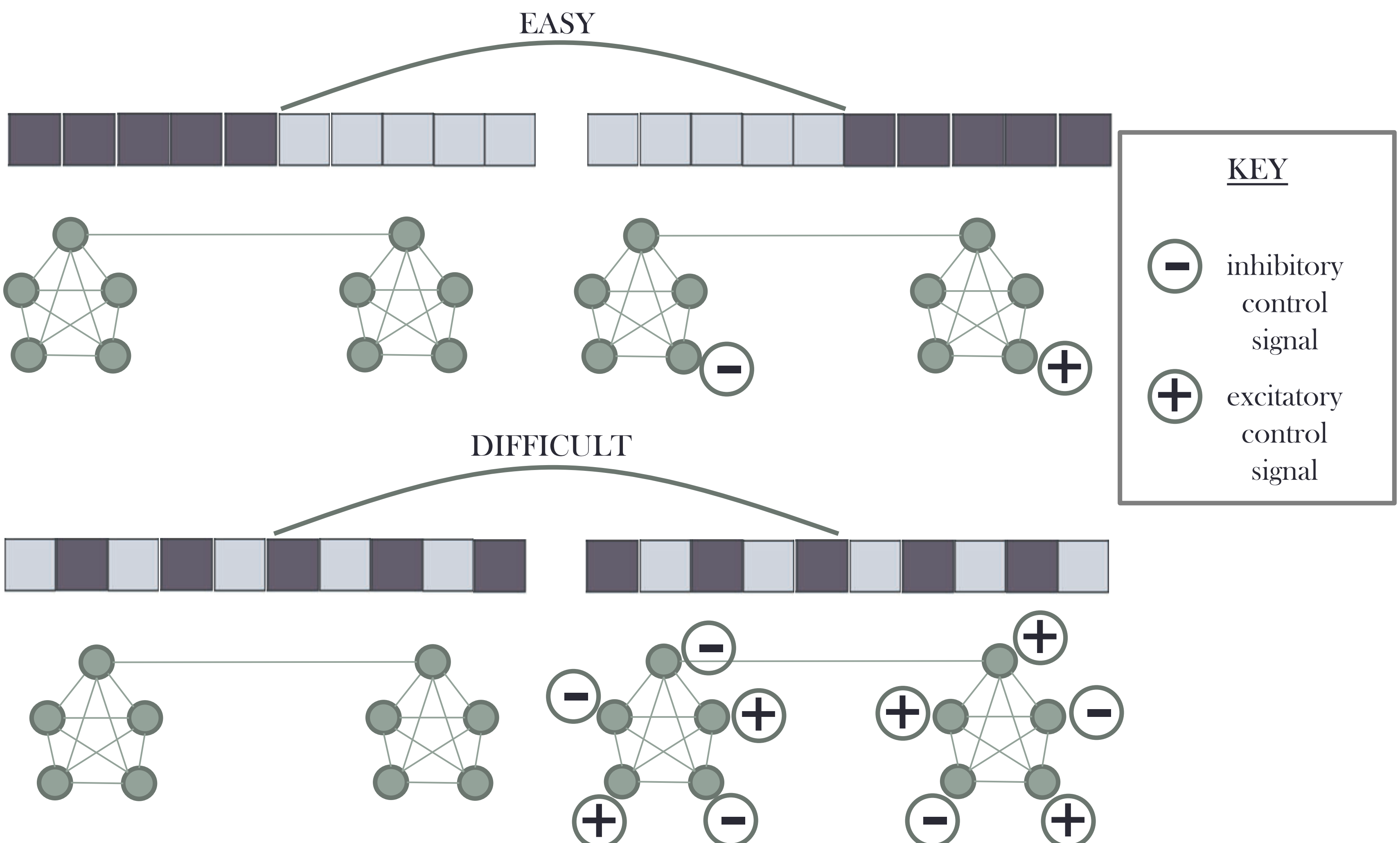
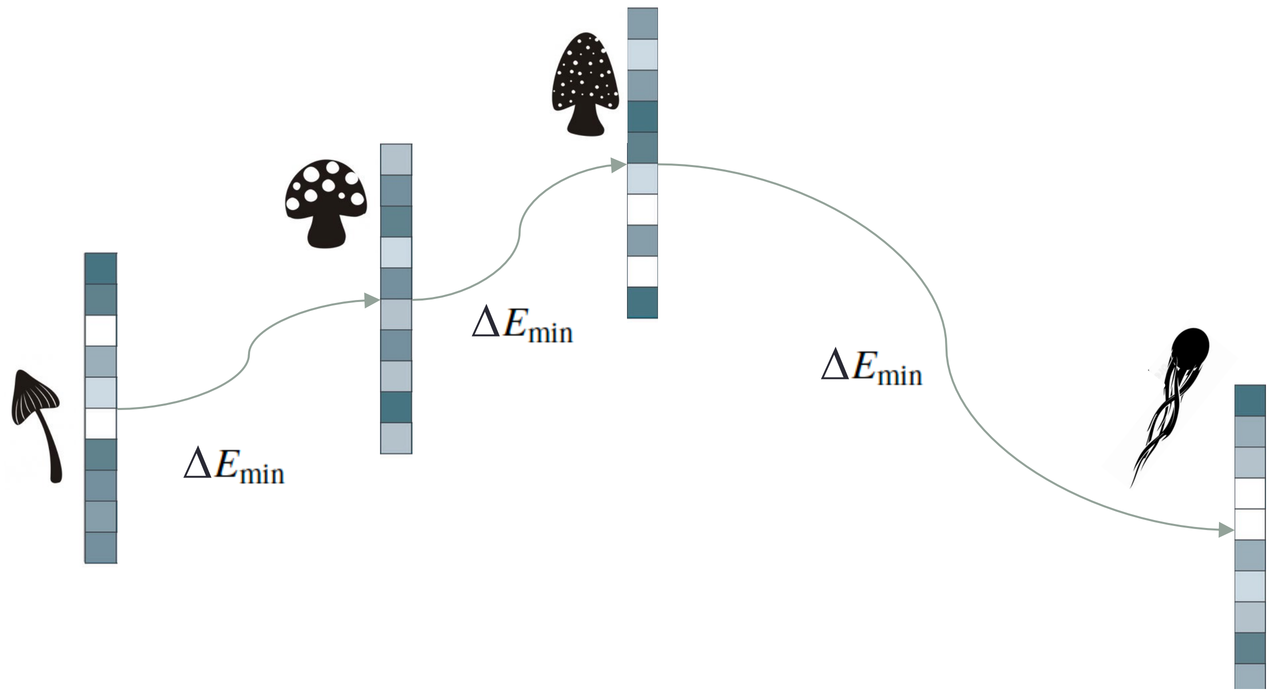


Networks make certain state *transitions* easy or difficult



Each state change has an associated energy cost



The network architecture of neural systems constrains which transitions are easy (small $\Delta E_{\min}$) versus which transitions are hard (large $\Delta E_{\min}$).

Because each transition has an energy cost, we can assess whether some brains (or regions) are <u>wired for more economical transitions</u> than others.

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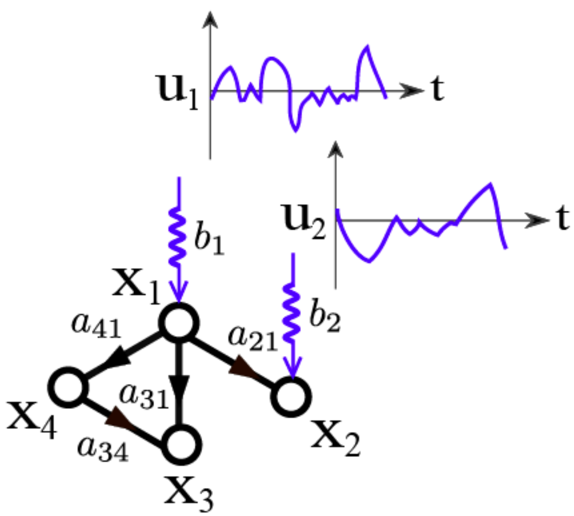
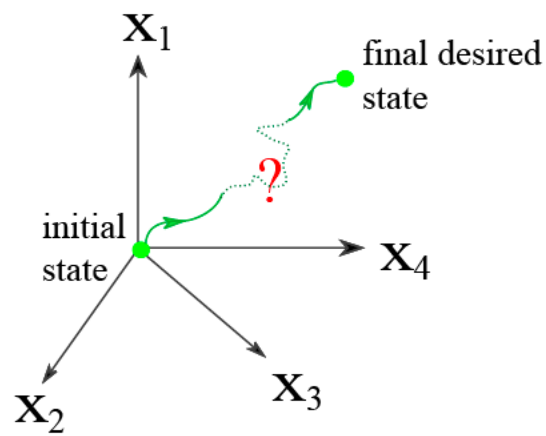
The network control model

One such model that has proven particularly promising is the network control model, which draws upon and extends theoretical work in systems engineering.





Network control theory is a mathematical framework that determines which perturbations can drive the whole system to a desired state. It is typically applied to the study of the power grid, mechanical systems, air traffic control systems, & robotics.

Figure from Liu *et al.* Nature 2011

A network control model for the brain

The model stipulates how activity flows along structural connections.

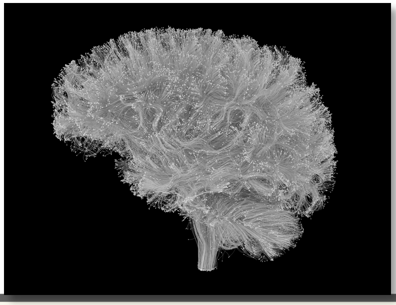
Number of regions being controlled

$$x(t+1) = Ax(t) + B_{\mathcal{K}} u_{\mathcal{K}}(t)$$

State of brain regions over time

Weighted adjacency matrix

Control energy



Choosing a model of dynamics

complexity

- Linear, time-invariant models

$$\frac{d}{dt}\mathbf{x}(t) = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t)$$
$$\mathbf{y}(t) = \mathbf{C}\mathbf{x}(t).$$

- Simple
- Extensively machinery
- First approximation for nonlinear dynamics

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- Nonlinear models

$$\frac{d}{dt}\mathbf{x}(t) = f(\mathbf{x}(t), \mathbf{u}(t), t)$$
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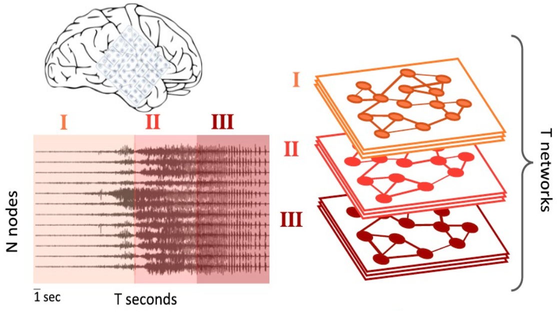
- Effective connectivity provides time-dependent networks
- Useful for context-dependent dynamics & control



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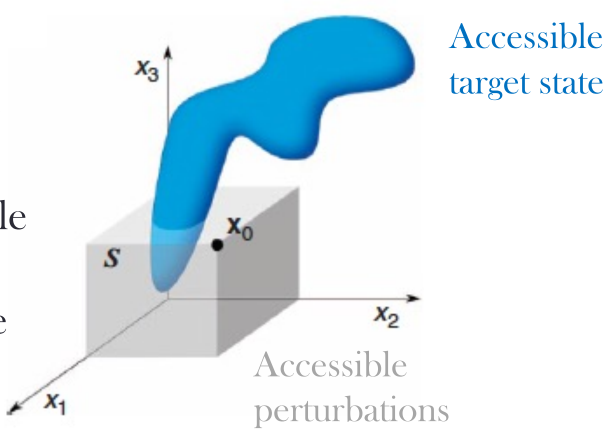
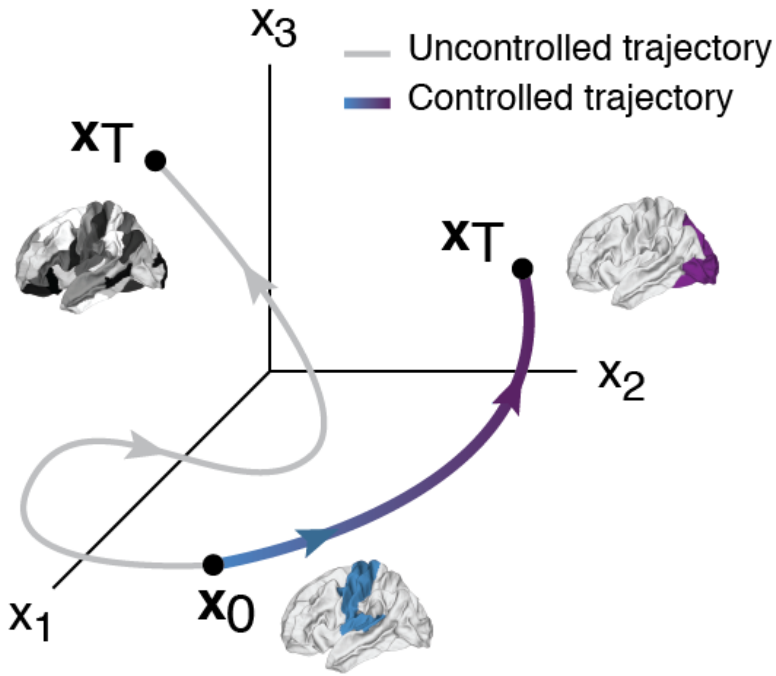
- Useful for scenarios inaccessible sectors of state space



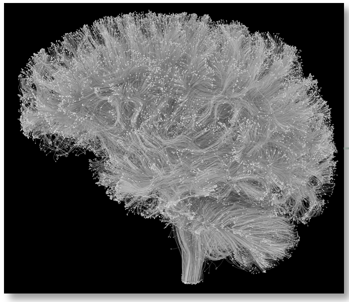
Outputs of NCT

- **Impulse response:** a system's output when presented with a brief input signal.
- **Controlled response:** the system's response to some controlling input u(t) from some initial state x_0.
- **Controllability:** A system is controllable if there is a control input that brings our system from any initial state to any final state in finite time.
- **Minimum energy control:** Designing the control input u(t) to minimize the control energy E (and possibly other factors) to drive the desired response.

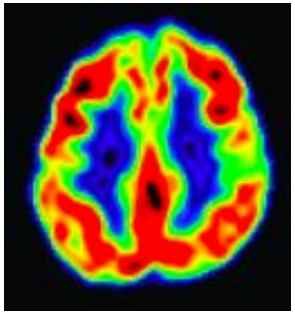


What kind of energy *is* control energy?

control energy



glucose metabolism



Xiaosong He decided to use temporal lobe epilepsy as a lesion model in which to evaluate the relationship between control energy and glucose metabolism.

- FDG-PET imaging marked glucose metabolism
- Individual-specific diffusion imaging was used to estimate regional control energy

➢ Control energy is strongly correlated with glucose metabolism.

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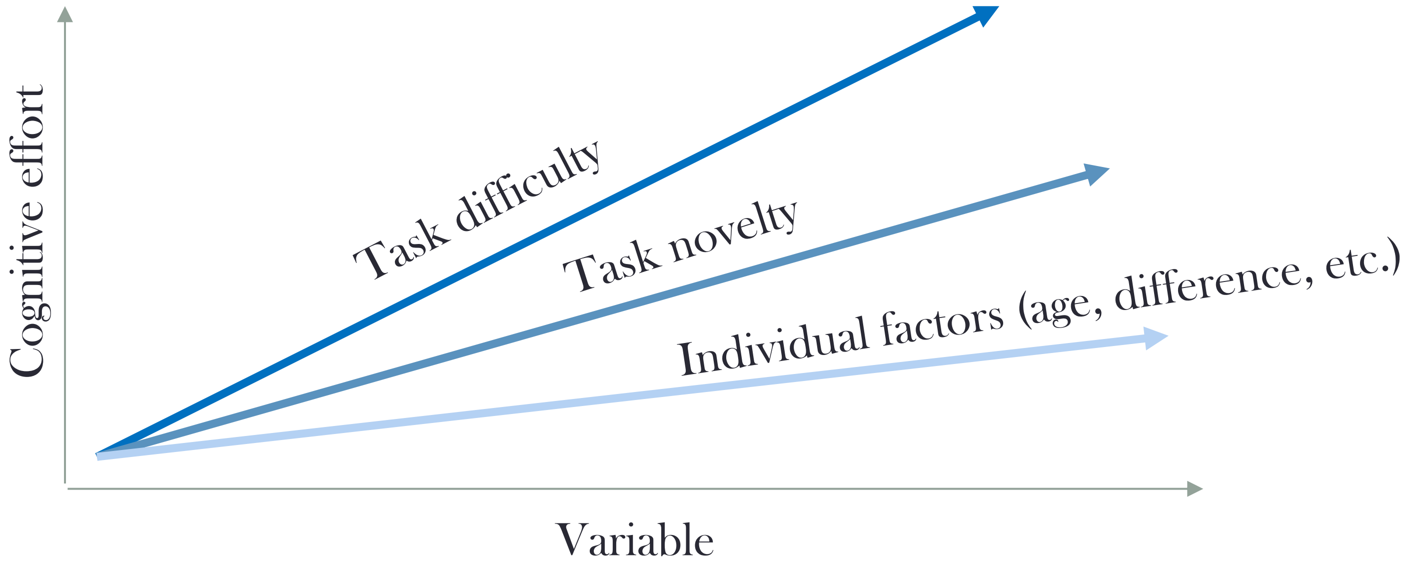
Cognitive Effort

– The engaged proportion of limited-capacity central processing.

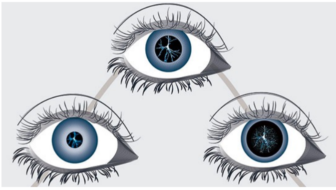


Not identical with difficulty, motivation, attention, or cognitive control.

Measuring cognitive effort

A few common measurements include:

1. Self-report. Ask the participant: How effortful did that feel?



2. Autonomic Response. Measure physiologic markers of autonomic arousal.

3. Activation. More activation for same behavioral output = more cognitive effort.

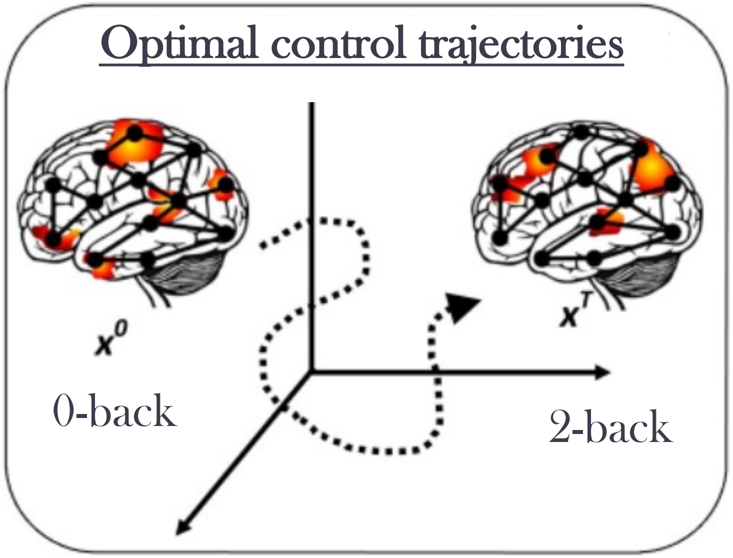
4. Dynamical Complexity. More dynamical complexity suggests greater cognitive effort.

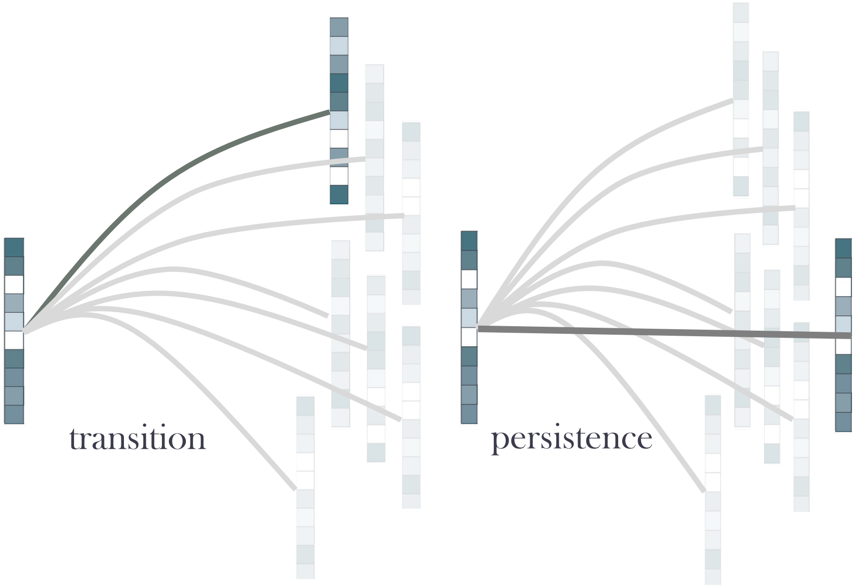
Alternative: Cost of orchestrating complex activity dynamics on a network, operationalized by network control theory (& specifically control energy).

Westbrook & Braver. Cogn Affect Behav Neurosci. 2015

Estimating network energetics of cognitive effort

How much control energy is required to transition from an attention state to a working memory state? How much energy is required to persistently hold a state?

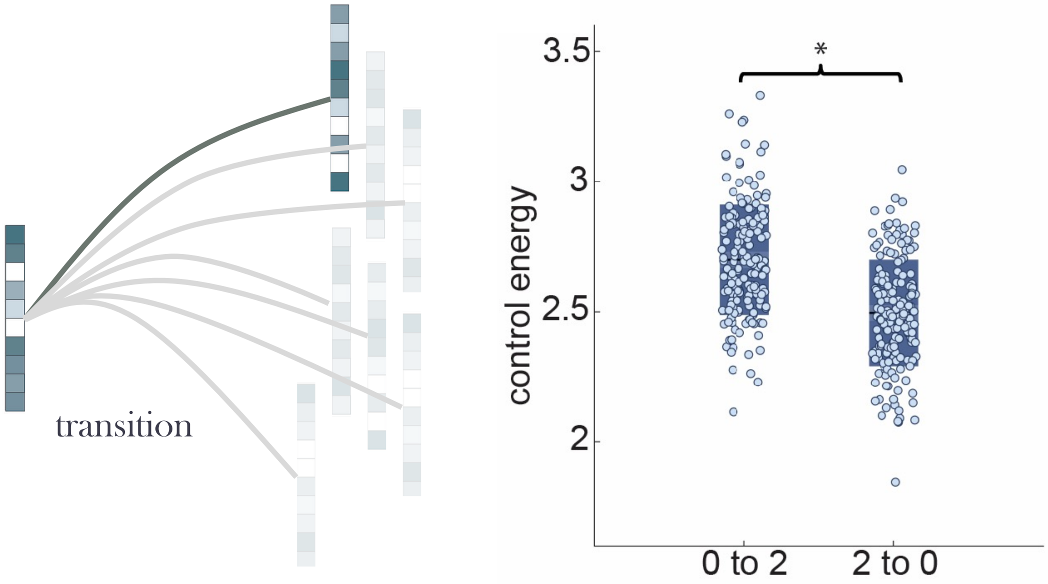




Precise control of state transitions and state persistence is required for optimal performance, including task accuracy and speed.

Transitioning to the working memory state

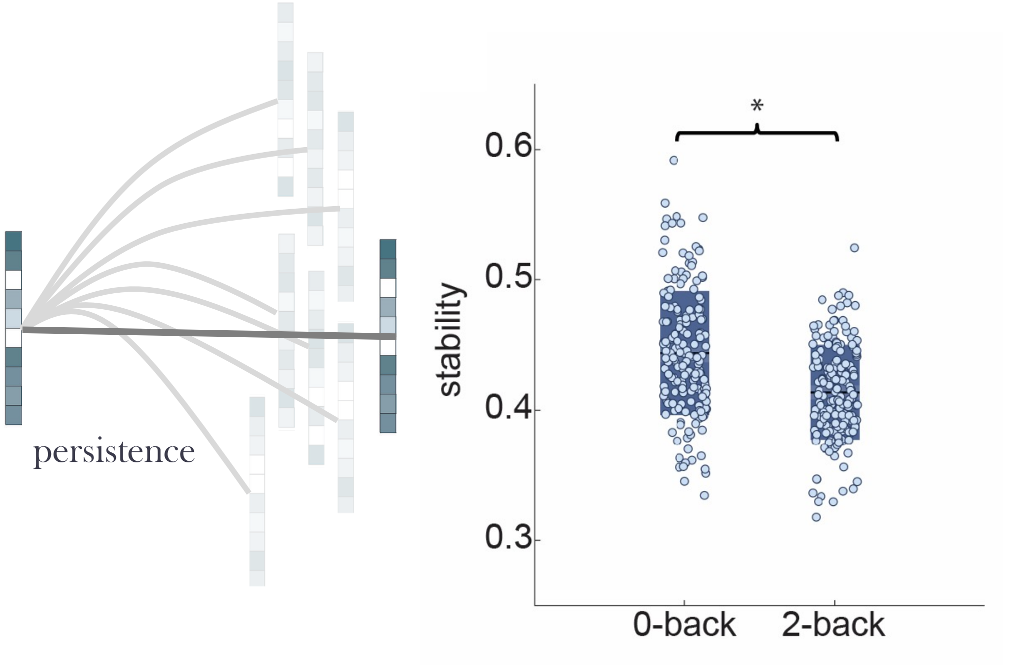
How much control energy is required to transition from 0-back (attention; low cognitive load) to 2-back (working memory; high cognitive load)? vs. from 2-back to 0-back?



Transitioning into a cognitively more demanding state required more control energy than the opposite transition.

Persisting in a high-load working memory state

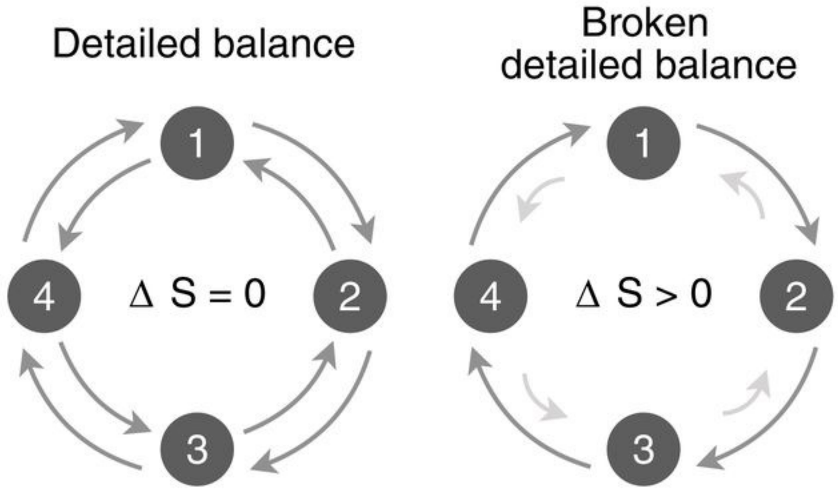
How much control energy is required to persist in a 2-back (high cognitive load) state?



The cognitively more demanding 2-back state was less stable than the attention (0-back) state. Greater stability of the 2-back state was associated with higher task accuracy.

How might structurally-constrained activity flow help us to understand the brain's non-equilibrium nature?

To perform biological functions, systems diverge from equilibrium.



They break detailed balance (exhibit net fluxes of transitions between states), thereby producing entropy in their environment.

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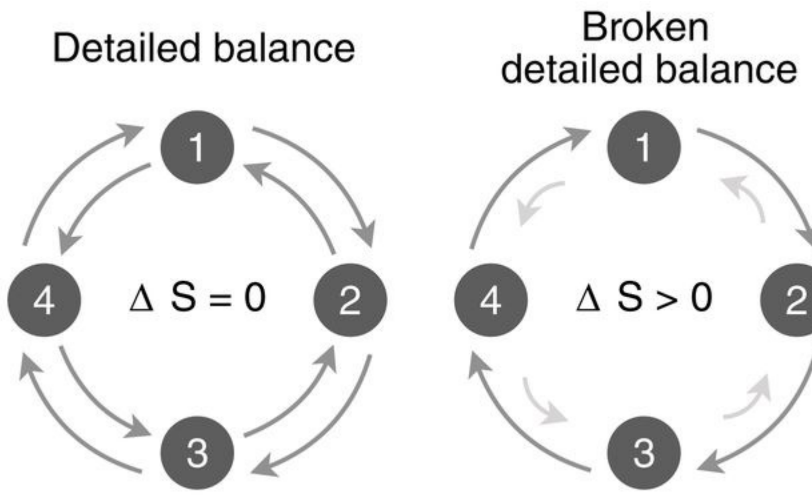

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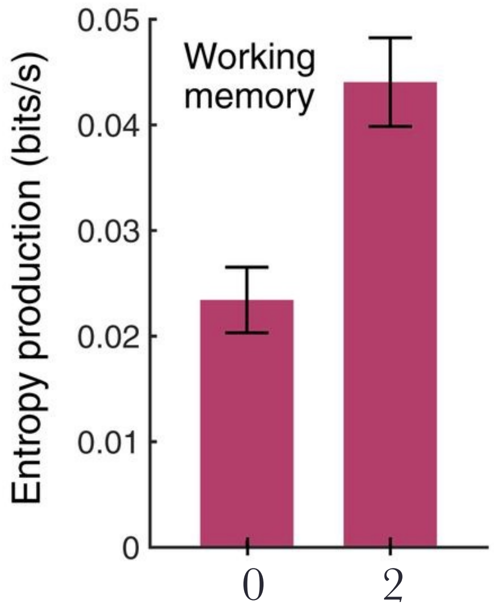

More cognitively effortful tasks display more broken detailed balance and produce greater entropy then less cognitively effortful tasks.

Summary

- The brain's structural network constrains the flow of activity, thereby influencing the types of computations and functions that can be performed.

- Network control theory models those constraints and provides an estimate of the energy required for brain state transitions.
  - Control energy can depend on context
  - Control energy is correlated with metabolic energy.

- Cognitive effort can be studied using notions of control energy.
  - Greater control energy is required for transitions to more cognitively demanding states.

- **Quantifying economy.** By estimating transition costs, we can assess which brains (or regions) are wired for more economical transitions, and in what contexts.

Thanks!