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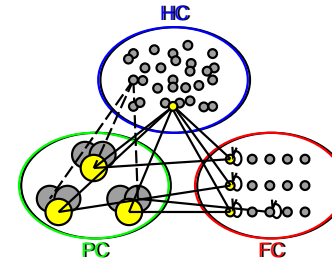
Prefrontal-Hippocampal Interactions: A Computational Perspective

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A Tripartite Cognitive Architecture



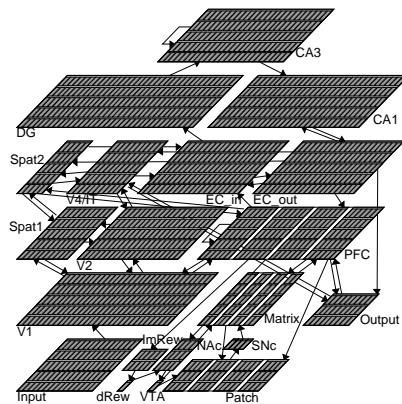
PC = Posterior cortex: graded, overlapping, slow learning of statistics in *weights* (*semantic*).
HC = Hippocampus: sparse (separated, conjunctive), rapid automatic learning in *wts* (*episodic*).
FC = Frontal cortex: robust maintenance, adaptive gating (BG), top-down control in isolated *acts* (*WM*).

Each area requires specializations for optimal performance of complementary set of functions (*avoiding tradeoffs*).

But same underlying mechanisms: neurons w/ synapses, etc just different *parameters* (continuum of function).

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A Tripartite Cognitive Architecture



Under construction; stick to principles for now..

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Broad Points

- Strong claim: it just has to be this way (computational necessity).
- Stronger claim: it is this way — lots of consistent data.
- Challenge: disprove it! (what are the difficult data?)

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Specific Points

- *Automatic & rapid* learning of conjunctions is key for dissociating HC from PC.
- Organization of PFC may be according to abstraction & temporal duration of maintenance.
- *Distractors* & *proactive interference* are key for dissociating FC from HC.

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Principled Distinctions from Computational Tradeoffs

McClelland, McNaughton & O'Reilly, 1995; O'Reilly & Rudy, 2001; Norman & O'Reilly, 2003

Goals:	Remember Specifics	Extract Generalities
Example:	Where is car parked?	Best parking strategy?

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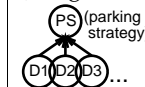
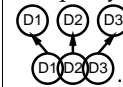
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Solution:

1. **Separate** reps (keep days separate) **Overlapping** reps (integrate over days)

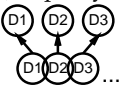
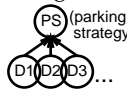


9 Principled Distinctions from Computational Tradeoffs

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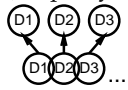
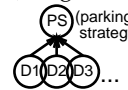
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2.	Fast learning (encode immediately)	Slow learning (integrate over days)

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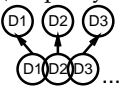
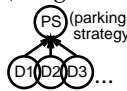
Solution:

1.	Separate reps (keep days separate) 	Overlapping reps (integrate over days) 
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3.	Learn automatically (encode everything)	Task-driven learning (extract relevant stuff)

11 Principled Distinctions from Computational Tradeoffs

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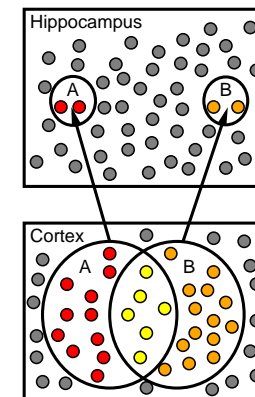
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These are incompatible, need two different systems:

System:	Hippocampus	Neocortex
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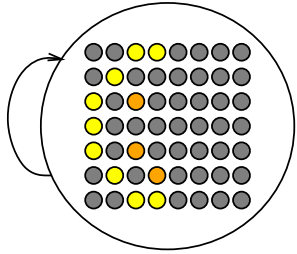
12 Hippocampal Sparseness → Separation, Conjunctions



(and makes fMRI of hippocampus so unreliable!?)

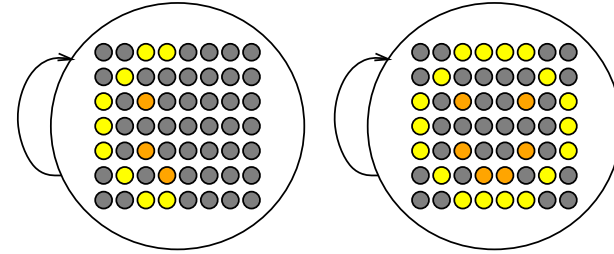
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Recall: Pattern Completion



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Recall: Pattern Completion



Hippocampal conjunctive representations support *pattern completion* — partial cues retrieve whole memory.

Need to bind elements together for cue to reactivate whole.

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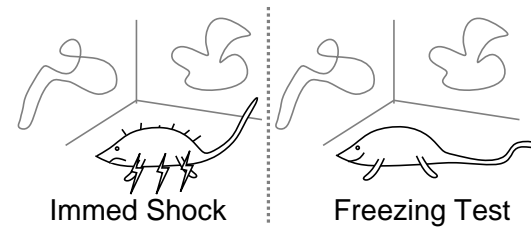
Testing the Theory: Rapid Incidental Conjunctive Memory in Rats

Fear conditioning preexposure paradigm:

- Uniquely illustrates all 3 properties of hippocampal memories.
- Provides the best animal model of human episodic memory!

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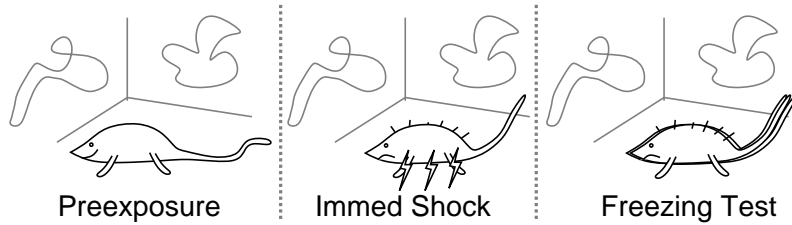
Immediate Shock Effect (Fanselow)



Shocking immediately in context produces no freezing at test!

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Eliminating Immediate Shock Effect



Preexposure to context eliminates immediate shock effect.

Interpretation:

- Preexposure: **incidental binding** of features in **hippocampus**.
- Shock: **conjunctive** rep. is **pattern completed**, assoc w/ shock.
- Test: shock/fear is **pattern completed** from cues at test.

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Conditioning to a Memory

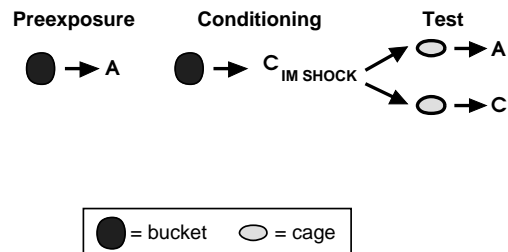
Can we trigger pattern completion to activate a memory of a context, *even when that context isn't physically present?*

1. At Shock: The **hippocampus** can **pattern complete** a memory of a context that is not present, given a retrieval cue.
2. Then, fear conditioning can occur *to that memory*, instead of to the context that is actually present.

This would provide strong evidence for hippocampal "episodic" recall in animals.

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Conditioning to a Memory: Experimental Paradigm



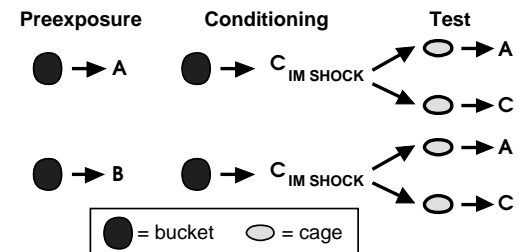
Preexposure leads to **conjunction** of bucket and context A.

Bucket can trigger **pattern completion** of A at shock (in C).

Intact rat should associate shock with memory of A *not* C!

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Conditioning to a Memory: Experimental Paradigm

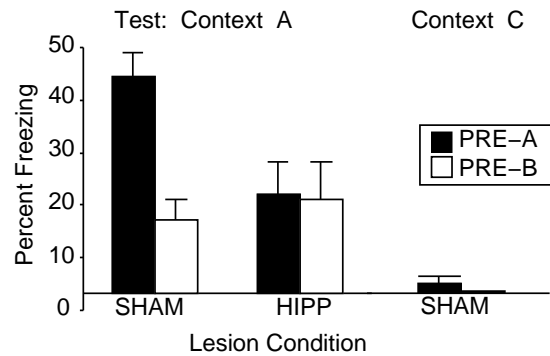


Alternate preexposure environment B serves as a control.

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Conditioning to a Memory: Rat Data

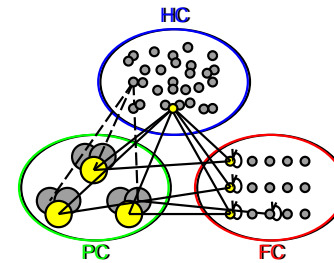
Rudy, Barrientos & O'Reilly, 2002



Note: Standard contextual fear conditioning not HC dependent!

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A Tripartite Cognitive Architecture: HC vs. PC



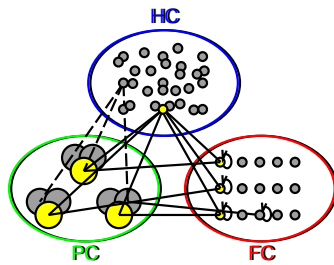
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Rapid & Automatic (incidental): key for *dissociating* HC from PC (PC can more slowly learn conjunctive representations if needed).

Watch out for automatic encoding during retrieval! (Stark)

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A Tripartite Cognitive Architecture: HC vs. PC



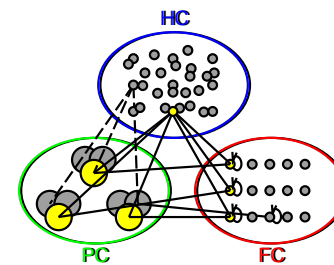
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Caveats: HC is also sensitive to task demands, attention, top-down input from PFC, etc (can be, but is not always, automatic).

PC can learn automatically (priming, familiarity) too: but not *novel conjunctions*.

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A Tripartite Cognitive Architecture: HC vs. PC



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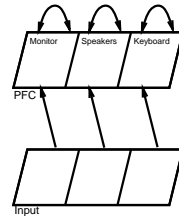
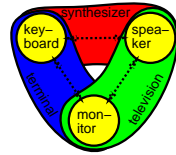
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Tradeoffs for Robust Maintenance in the PFC

Tradeoff: overlapping, interconnected reps = spreading activation, inferences, *semantics*.

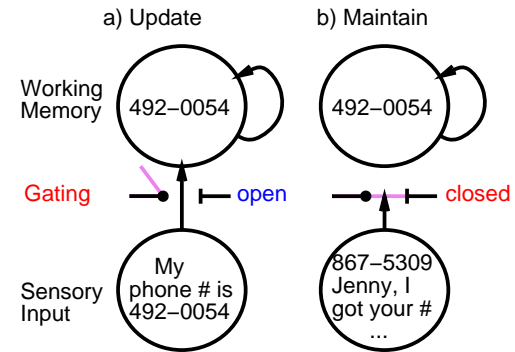
But spreading activation in *WM* w/out external input = loose memory

Solution = *isolated* representations in PFC:
(e.g., stripes; Levitt et al, 1993)
& *intrinsic bistability* (up/down states)



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Tradeoffs for Robust Maintenance in the PFC

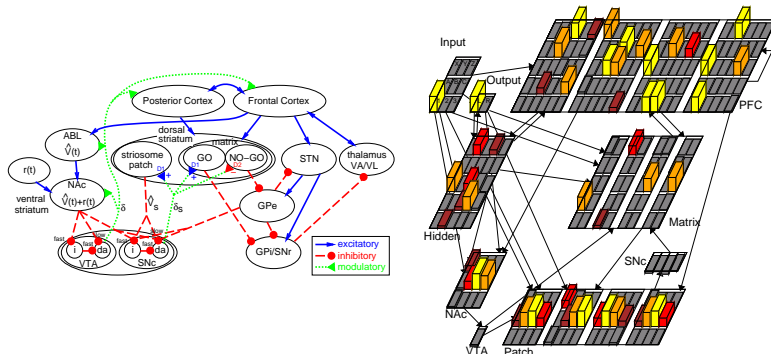


Adaptive gating required for having *both* rapid updating and robust maintenance (O'Reilly, Braver & Cohen, 1999).

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The Basal Ganglia Support Adaptive Gating

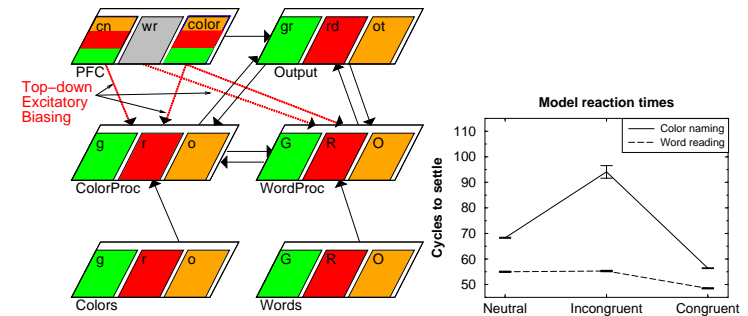
Frank, Loughry & O'Reilly, 2001; O'Reilly, submitted



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Top-Down Excitatory Biasing: Not Inhibition

Cohen, Dunbar & McClelland, 1990; Herd, Banich & O'Reilly, submitted; c.f. Petrides, 1994

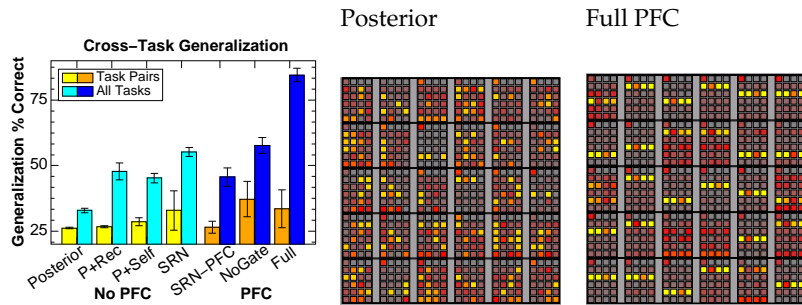


Robustly maintained PFC reps bias task-appropriate processing in posterior cortex, hippocampus (e.g., Stroop task).

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PFC Specializations → Rule-Like Abstract Reps

Rougier, Noelle, Braver, Cohen & O'Reilly, in prep



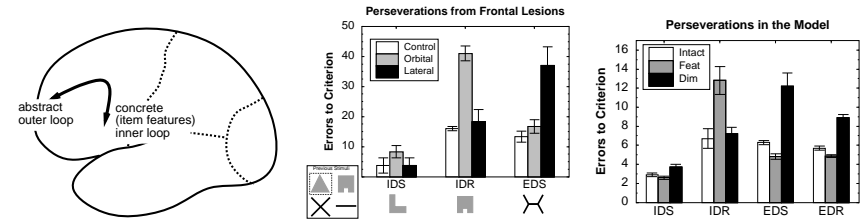
Rule = One stim dimension relevant at a time = one row.

Abstraction derives from sustained maintenance over trials!

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Anterior-Posterior/Inferior Gradient of Abstraction

O'Reilly, Noelle, Braver & Cohen, 2002



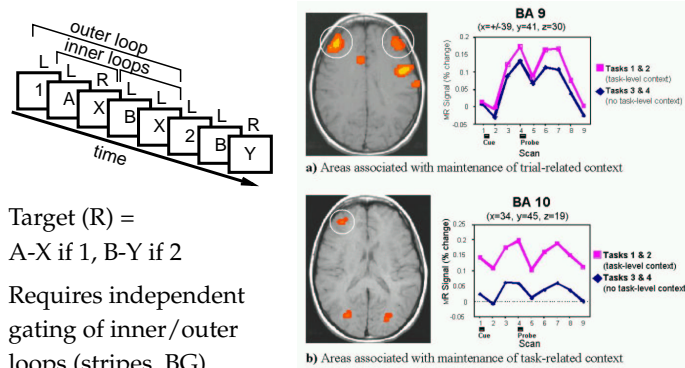
Intra-dim switching deficits = PFC feature reps lesion (inferior).

Extra-dimensional = PFC abstract dimensional reps lesion (dorsal).

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Inner-Loop/Outer-Loop Gradient

O'Reilly, submitted; c.f., Koehhlin et al, 99; Christoff & Gabrieli, 00; Braver & Bongiolatti, 02



Target (R) =

A-X if 1, B-Y if 2

Requires independent gating of inner/outer loops (stripes, BG)

Outer-loop = longer maintenance = more abstract!

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Application

Rugg:

Outer loop = correct/incorrect = abstract task

Inner loop = item-specific "monitoring" = concrete.

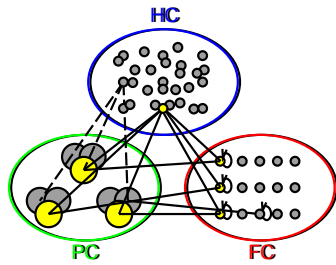
Petrides:

Outer loop = multiple item maintenance = dorsal

Inner loop = single item maintenance = ventral.

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A Tripartite Cognitive Architecture



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Strong claim: it just has to be this way!

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Interactions!

PFC top-down biasing can support encoding in **hippocampus** (lots of examples; nobody disagrees with this).

Hippocampal rapid, automatic encoding can support **working memory**-like short-term memory (Cohen & O'Reilly, 1996; O'Reilly, Braver & Cohen, 1999). (also non-controversial)

What are the challenging examples?

- Sustained WM-like activity in hippocampus.
- When can HC *not* support WM?

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Sustained Activity in Hippocampus (Ranganath, Suzuki, Reber)

Strong constraint: Hippocampus does not have neural specializations required for *robust* maintenance.

But many posterior areas can exhibit “residual” activity, and “reflect” sustained input (top-down biasing) from PFC (consistent with fMRI data; test with lesions?)

→ Need *distractors* during delay period to test robust maintenance (ala Miller, Desimone, et al).

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Neural Specializations in Entorhinal Cortex

- Intrinsic bistability (Egorov et al, 2002).
- Projections from basal ganglia?

Maybe EC has some of the specializations to do more robust active maintenance?

Useful for integrating stimulus information over an episode?

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When Can HC Not Support WM?

Weight-based learning is subject to effects of *proactive interference* (even with hippocampal patterns separation).

So, unique vs. repeated use of stimuli within a task is a way to selectively disable HC contributions to WM function.

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Interpretation of Reber

- Stimuli require novel conjunctive representations HC.
- PI builds up due to similarity of stimuli.
- Higher HC act on bad trials due to greater PI.

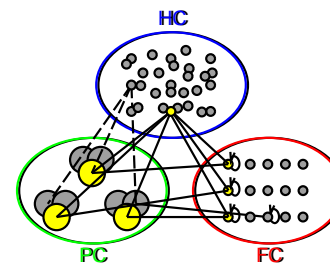
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Conclusions: Specific Points

- *Automatic & rapid* learning of novel conjunctions is key for dissociating HC from PC.
- Organization of PFC may be according to abstraction & temporal duration of maintenance.
- *Distractors* & *proactive interference* are key for dissociating FC from HC.

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A Tripartite Cognitive Architecture: Conclusions



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Computational models of entire system are just being developed.

Should provide more subtle predictions to test!