- Memory = any persistent effect of experience (not just memorization of facts, events, names, etc.)
- Weights vs activations
- Gradual, integrative cortical learning and priming effects
- Rapid memorization: The hippocampus
- Active memory: prefrontal cortex

Memory: Weights vs Activations

Despite appearances, memory is not unitary.

(shoes; breakfast; sentence)

Memory: Weights vs Activations

Despite appearances, memory is not unitary. (shoes; breakfast; sentence)

Weights:

- Long-lasting.
- Requires re-activation.
- Wts in diff't brain systems store different types of memories!

Activations:

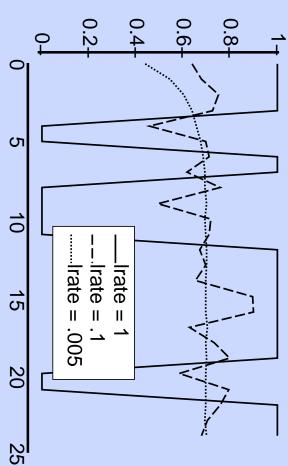
- Short-term.
- Already active, can influence processing.

Weight-based Memories

- Cortex does gradual, integrative learning
- Cortex can learn arbitrary input-output mappings given:
- multiple passes through the training set
- a relatively small learning rate

Weight-based Memories

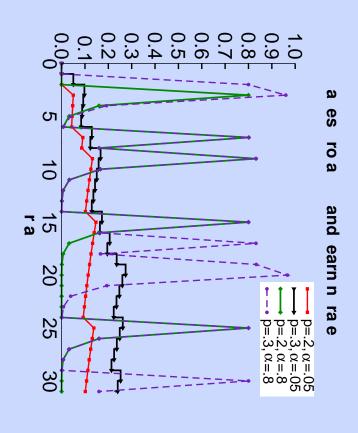
Rapid weight changes causes interference:



Two systems needed:

- Slow learning cortex.
- Rapid learning hippocampus (pattern sep avoids interference).

b. Slow vs Fast [Reinforcement] Learning

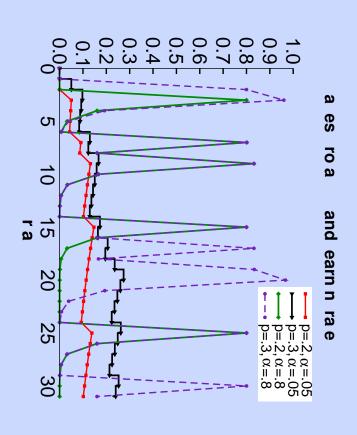


[Reinforcement] Learning must be slow to capture best actions that work on average.

But you also have to be able to sensitive to rapid changes in value (e.g., stock market).

Tradeoff solved by 2 systems: BG learns slowly, PFC relies on (flexible updating of) activation-based memory, and can override habitual choices

b. Slow vs Fast [Reinforcement] Learning



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Tradeoff solved by 2 systems:

override habitual choices. BG learns slowly, PFC relies on (flexible updating of) activation-based memory, and can

action-outcome learning, across species, methods. → lots of evidence for differential BG and PFC contributions to habitual and rapid

Memory: Rapid Learning, Interference, & The Hippocampus

- 1. AB-AC List Learning
- 2. The Hippocampus.

interference. Humans can rapidly learn overlapping associations without too much

window-reason Example: learn one set of paired associates (the A-B list):

interference. Humans can rapidly learn overlapping associations without too much

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... Then, learn overlapping set (the A-C list):

window-locomotive

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window-locomotive

bicycle-dishtowel

Then test on AB list:

window-?

Then test on AB list: window-? bicycle-?

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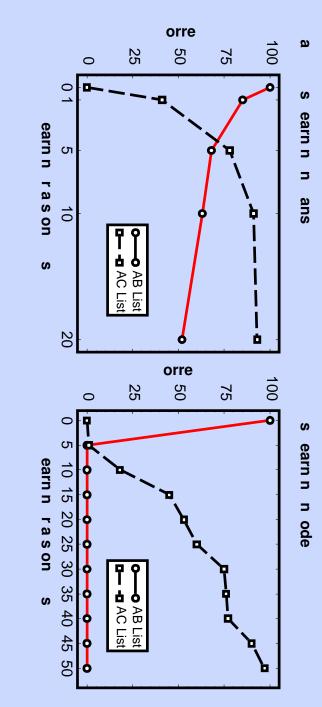
and on AC list:

window-?

Then test on AB list:

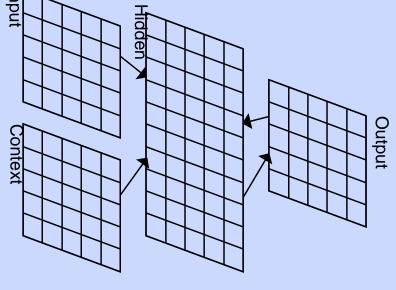
window-? bicycle-?

and on AC list: window-? bicycle-?



Standard network shows catastrophic interference (McCloskey & Cohen, 1989).

AB-AC Exploration

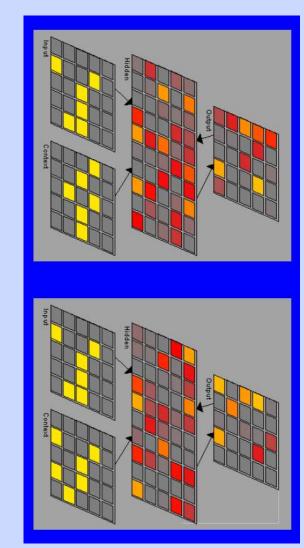


Input = A, Output = B,C

context pattern Context differentiates the lists: Each list is associated with a different

[ab_ac_interference.proj]

AB-AC Simulations: Summary



- There is overlap between the hidden units activated by an input pattern in the AC context. pattern ("window") in the AB context and units activated by that same
- This causes interference (changing weights for one changes weights for the other)
- Can this be fixed?

How can we reduce overlap between hidden units activated by patterns in the AB and AC contexts?

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- How can we reduce overlap between hidden units activated by patterns in the AB and AC contexts?
- → Lower the number of units that are activated → increase inhibition (increase g_i)..

But still need *different* units to be active for AB and AC inputs...

- units "pay more attention" to it → Increase relative weight scale of the context layer so that hidden
- will "like" both the AB and AC version of a pattern → Also increase initial weight *variance*: Lowers the odds that a unit

- Note that even with all these changes, interference gets only slightly
- Also network learns much slower than people do...

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- This speeds up learning, but makes interference worse!
- Also, by changing all these parameters, cortex can no longer generalize (requires overlapping distributed representations)
- → Trade-off: Must need another brain system!

Memory is not unitary.

- 1. Weights versus activations.
- 2. Specialized neural systems: computational tradeoffs.

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Abandon neural network models?

Hippo To the Rescue

Two specialized, complementary systems resolve fundamental tradeoff:

pattern-separated representations! The hippocampus can learn rapidly without interference by using sparse,

structure & regularities, semantic knowledge. Meanwhile, cortex slowly learns overlapping representations of similarity

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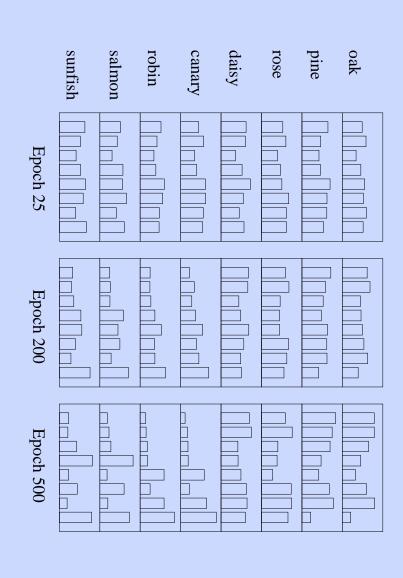
structure & regularities, semantic knowledge. Meanwhile, cortex slowly learns overlapping representations of similarity

e.g. "one small step for man" 9/11, etc

Complementary Learning Systems

Neocortex	Hippocampus	System:
two different systems:	These are incompatible, need two different systems:	Thes
(extract relevant stuff)	(encode everything)	
Task-driven learning	Learn automatically	3.
(integrate over days)	(encode immediately)	
Slow learning	Fast learning	2.
01 02 03	(中)	
PS (parking strategy)	₽ ₽	
(integrate over days)	(keep days separate)	
Overlapping reps	Separate reps	1.
• • 3	Solution:	
Accumulate experience	Avoid interference	Need to:
Best parking strategy?	:: Where is car parked?	Example:
Extract Generalities	Remember Specifics	Goals:

Systematic Overlap Develops by Slowly Integrating over Experience



Amnesics show:

spared implicit memory, skill learning (without recall)

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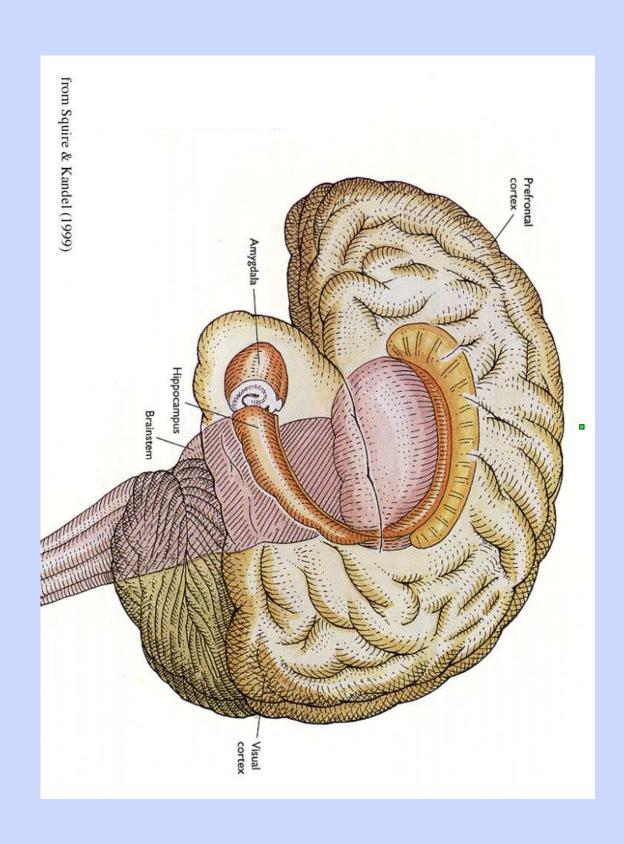
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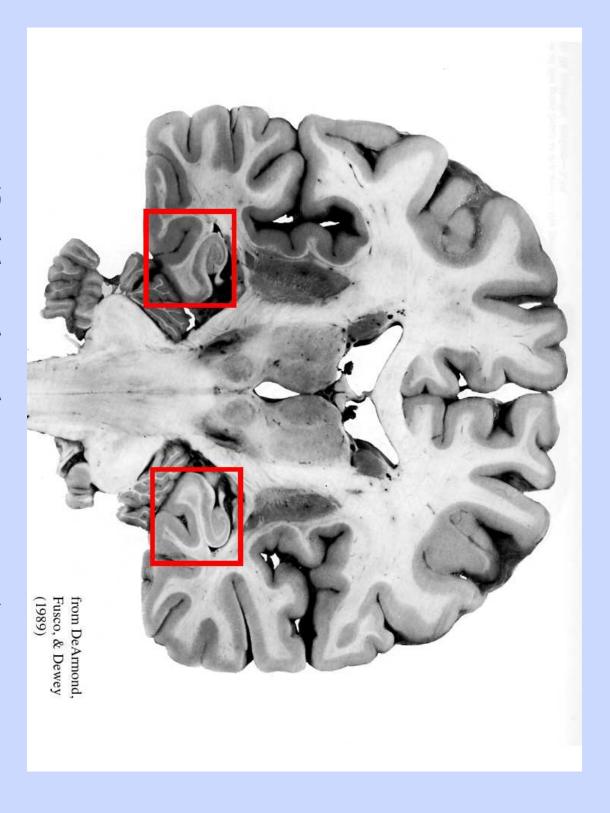
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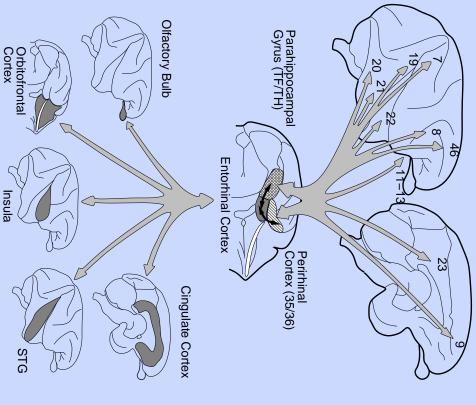
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- remote memories spared but recent ones completely forgotten sleep, etc "Consolidation": reactivation of memories across multiple contexts,





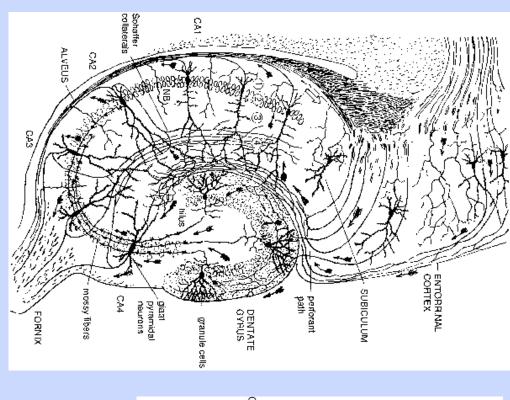
(Greek: hippo=horse, kampos=sea monster).

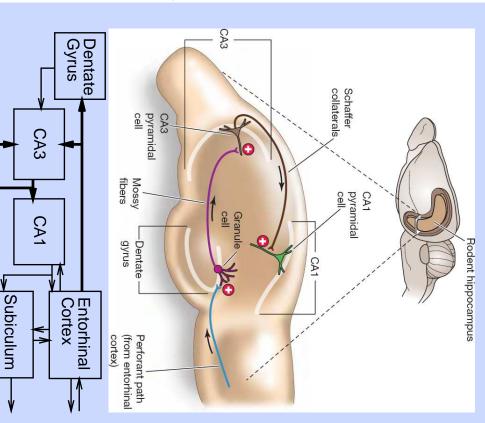
Hippo = King-of-the-Cortex



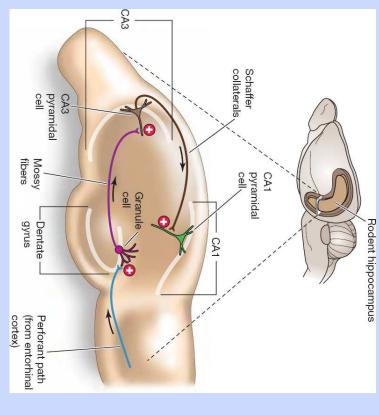
memory Hippo binds together multiple cortical representations into one coherent

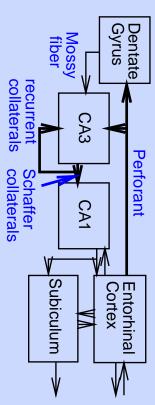
Hippocampal Anatomy



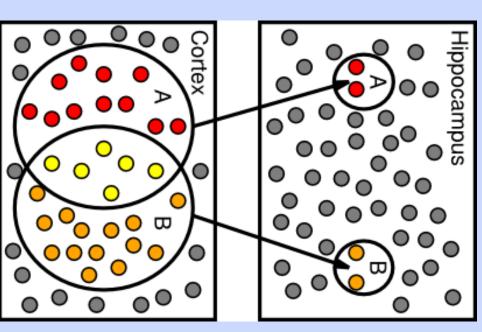


Hippocampal Anatomy





Pattern Separation & Conjunctions



Explaining Pattern Separation

inputs? How does the hippocampus assign distinct representations to similar

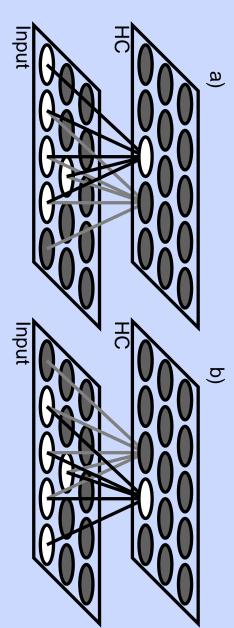
Explaining Pattern Separation

inputs? How does the hippocampus assign distinct representations to similar

- Partial connectivity: units are specialized for responding to a particular set of input features
- Sparse activity: fierce inhibitory competition
- Units only survive this competition if they receive a very large amount of excitatory input
- Units only fire if all features they detect are present in the input
- → Units represent *conjunctions* of features

Pattern Separation & Conjunctions: Space and episodes

Pattern Separation & Conjunctions: Space and episodes



- Here each HC unit connected to 5 inputs; k = 1
- Changing one input unit causes a different HC unit to win!

Sparse Activity

9.4	384	2.5	250,000	CA1
5.0	240	2.5	160,000	CA3
1.0	625	0.5	1,000,00	DG
25.0	144	7.0	200,000	EC
Pct Act	Units	Pct Act	Neurons	Area
Model	M	ıt	Rat	

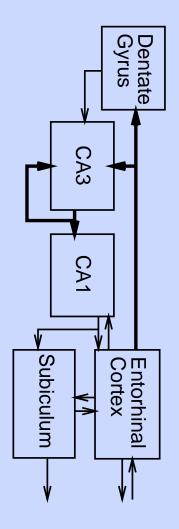
Sparse Activity CA3 CS CA1 CS CA1 CS Entorhinal Cortex Subiculum Fine them The them The

College friend example: "This one time, at this one party..."

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which reinstates original EC pattern... Pattern completion in CA3 activates corresponding CA1 rep,

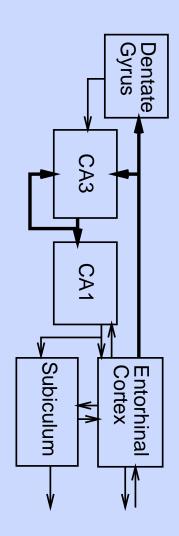
 \rightarrow "You told me this already!".



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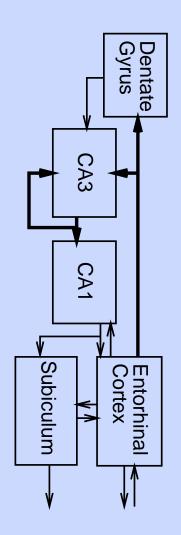


separate, or instead complete to an existing memory? How does your hippo 'know' whether to store new memory and keep it

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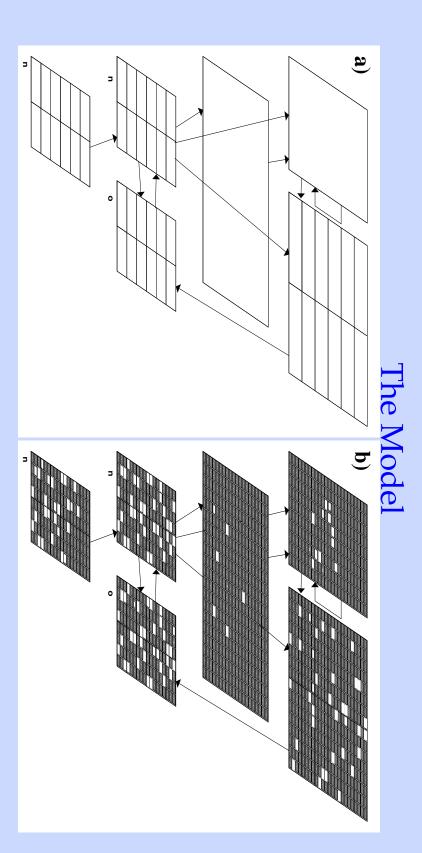
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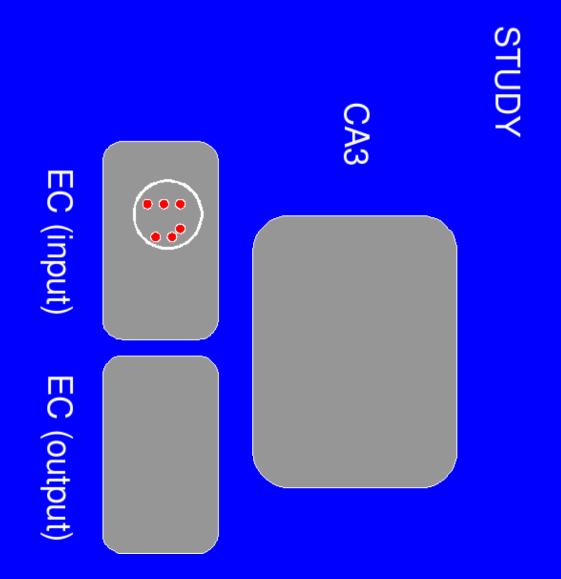
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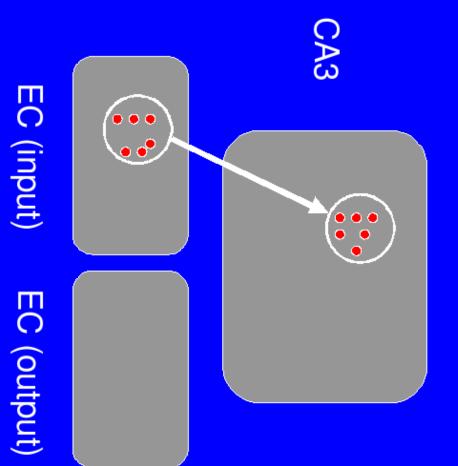
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complet while LTD supports pat sep; O'Reilly & McLelland '94). ightarrow hippo designed to minimize this tradeoff (LTP in CA3 supports pat





STUDY

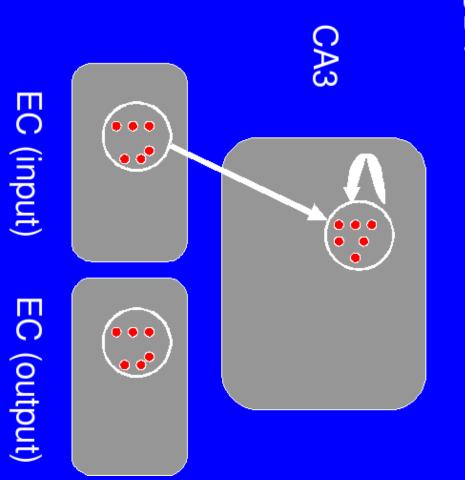


STUDY CA3

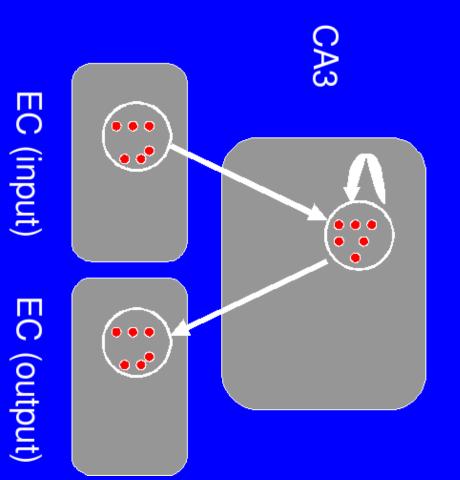
EC (input)

EC (output)

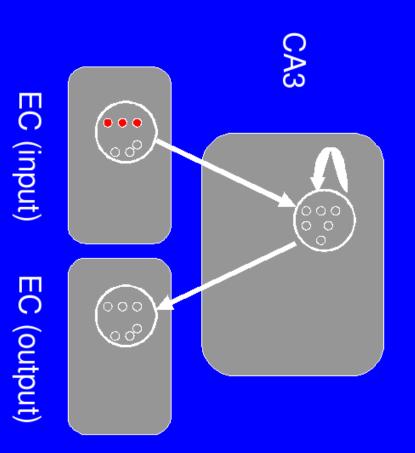
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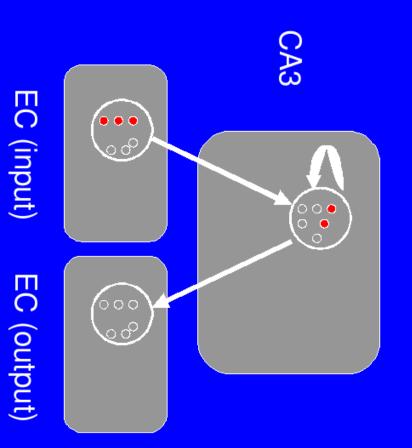
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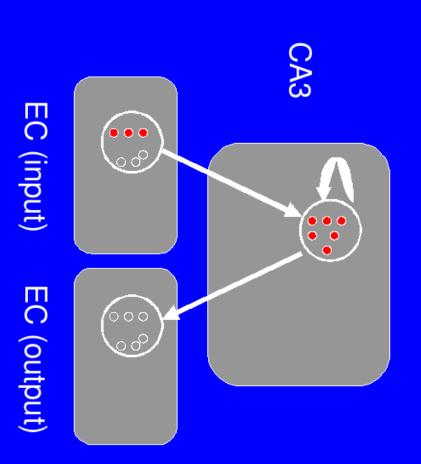
TEST

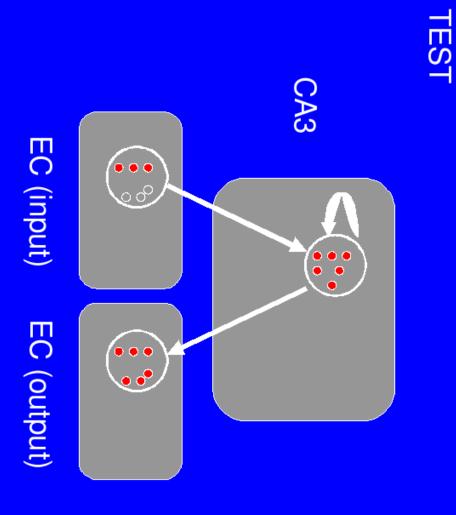


TEST



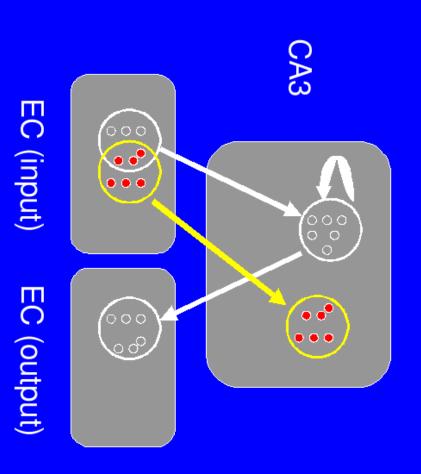
TEST



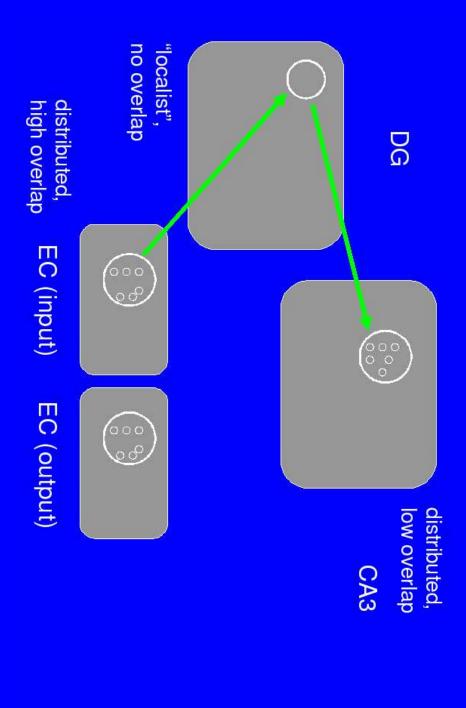


Pattern Separation

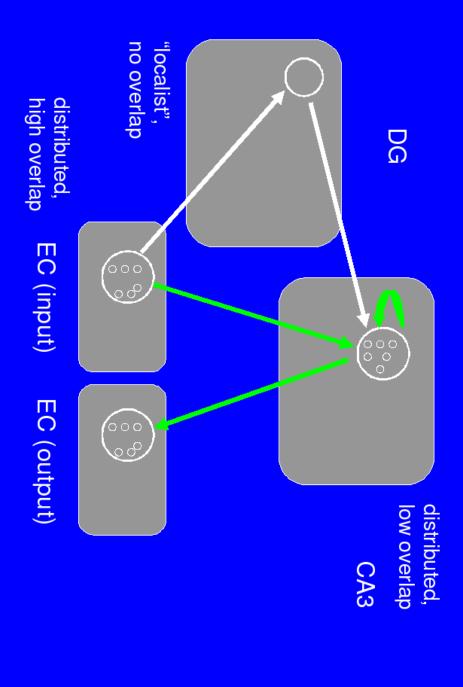
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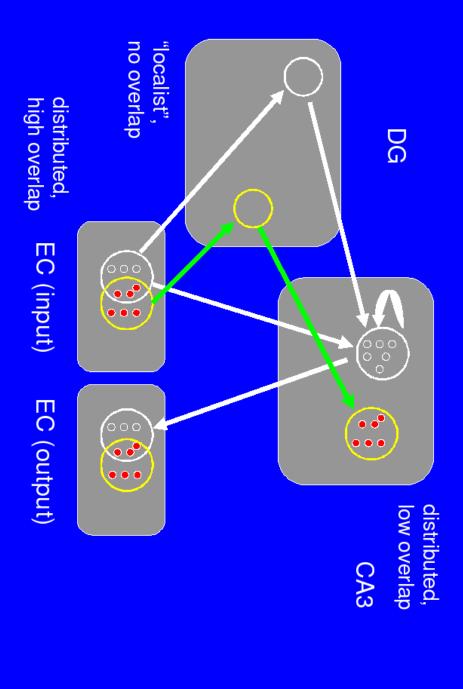


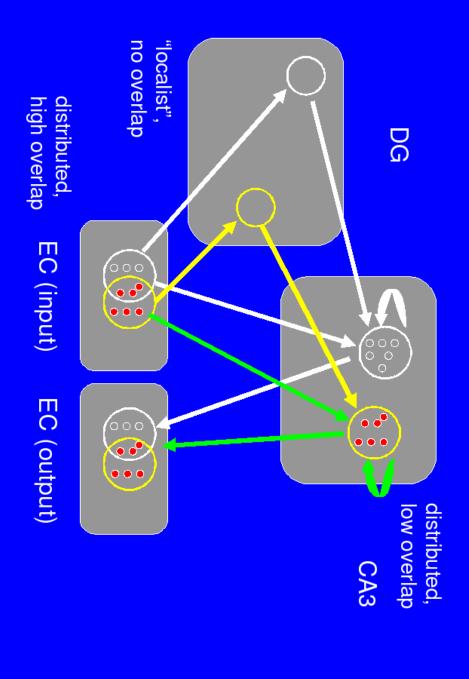
DG = Pattern Separation Turbocharger

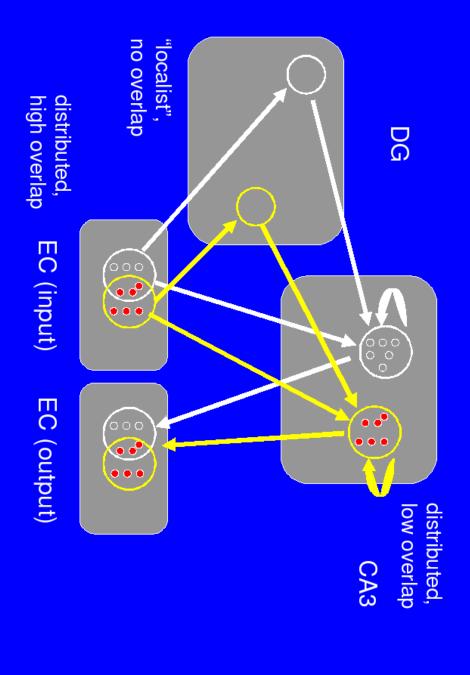


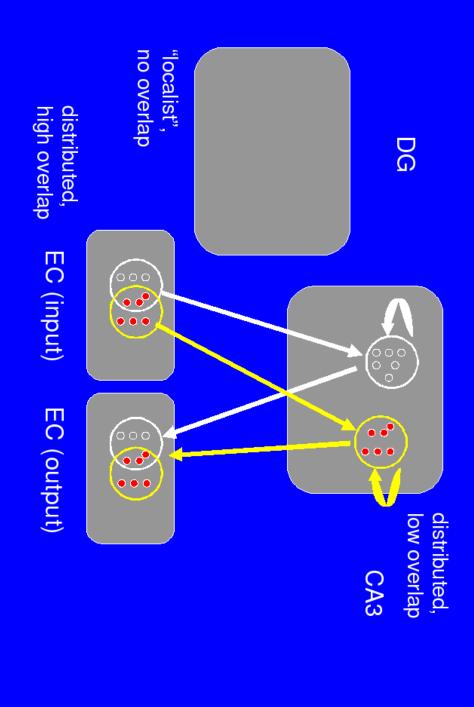
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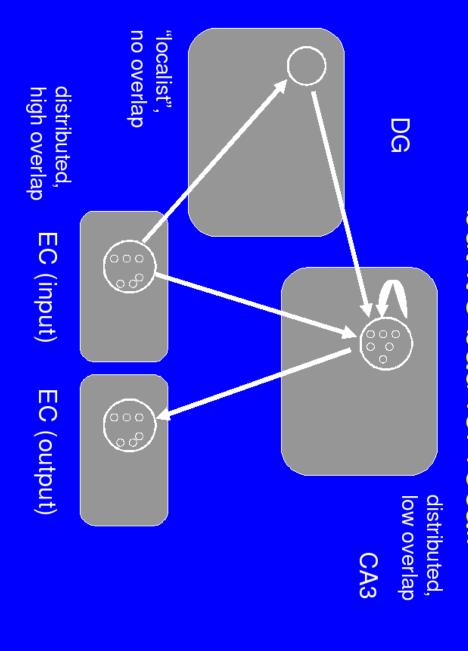




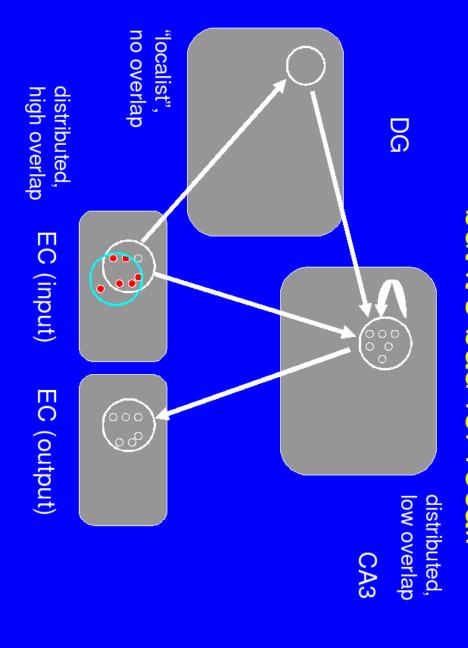




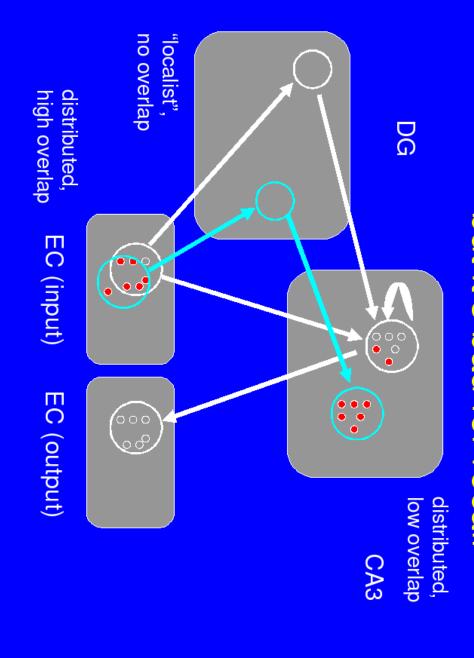
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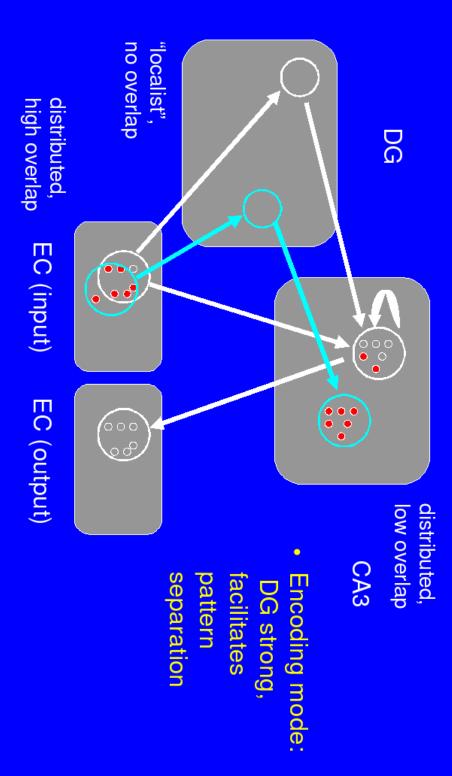
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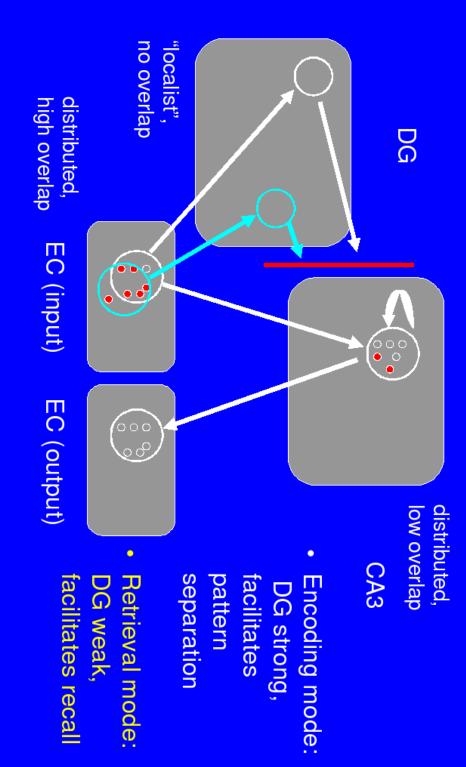
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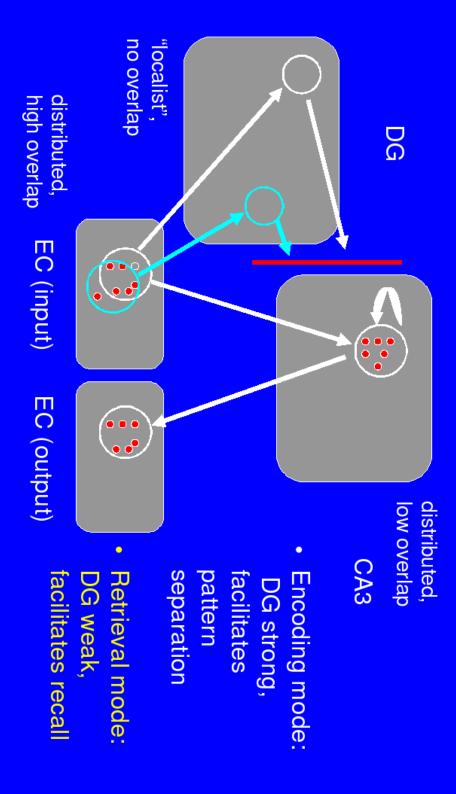
Possible Solution: Two Modes



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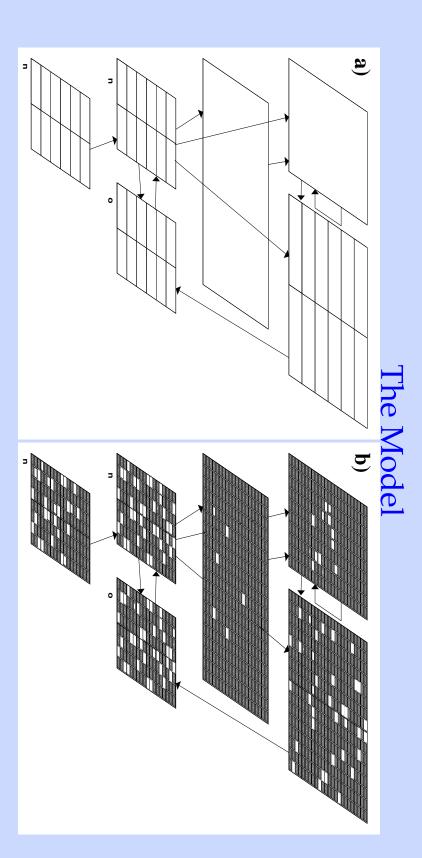


Possible Solution: Two Modes



Hippocampus: Summary

- CA3 stores sparse, pattern-separated representations of cortical input patterns
- Recurrent self projections in CA3 facilitate recall (pattern completion)
- Dentate Gyrus (DG) acts as a removable pattern separation turbocharger
- DG uses super-sparse representations, helps increase pat separation at encoding
- DG "steps aside" at retrieval
- Evidence for two modes: theta cycle (eg. Hasselmo et al, 2002); neuromodulatory control over rel DG effect on CA3



memory (not directly evident in experiments before) Model makes clear predictions about how different regions contribute to

Many of these have been subsequently confirmed!

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framework, ranging from Hebb to Marr to Nadel, McNaughton, O'Reilly...) (note that model itself is incremental synthesis of many ideas in a coherent

phenomena in rats and humans. It has been applied to explain many different learning and memory

(change environment ever so slightly see new populations of correlated act) Pattern separation in Rat DG (Leutgeb et al, 2007, Science)

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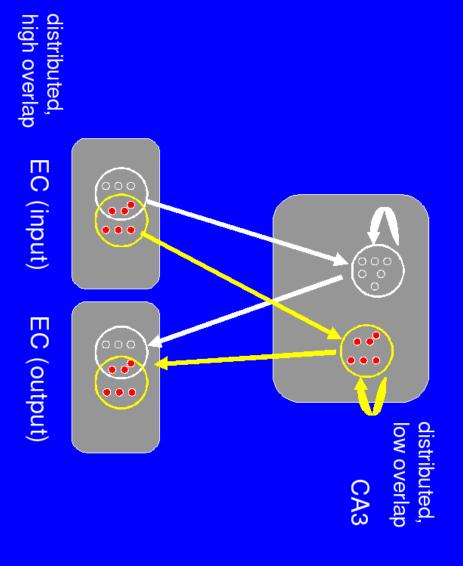
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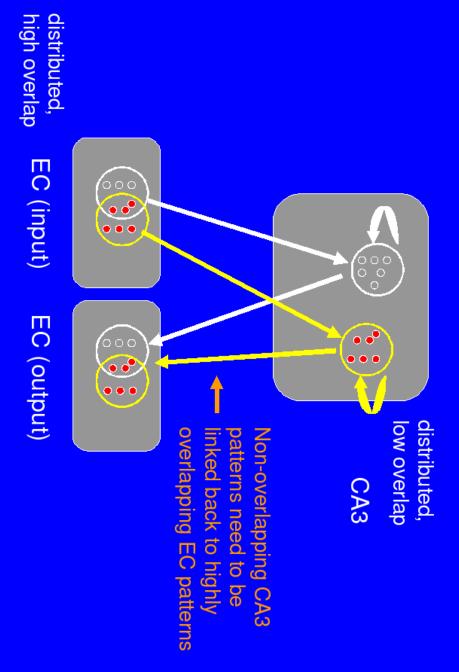
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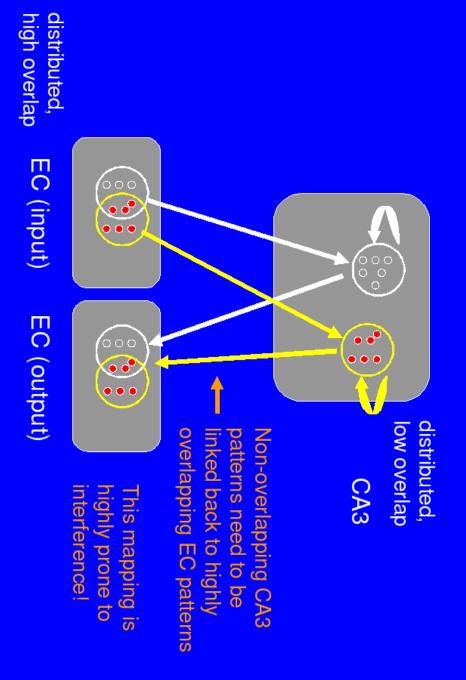
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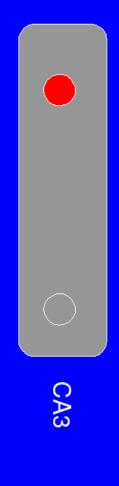
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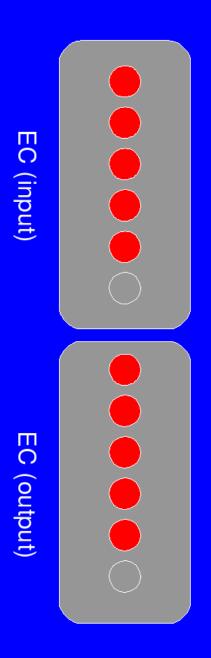
et al '11 Nature (discriminate between items with overlapping contexts) Neurogenesis in DG supports behavioral pat sep Clellan et al '09, Science; Nahay

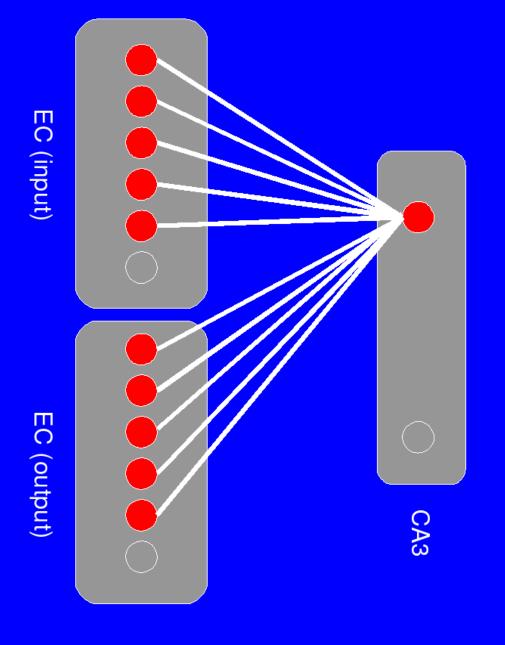


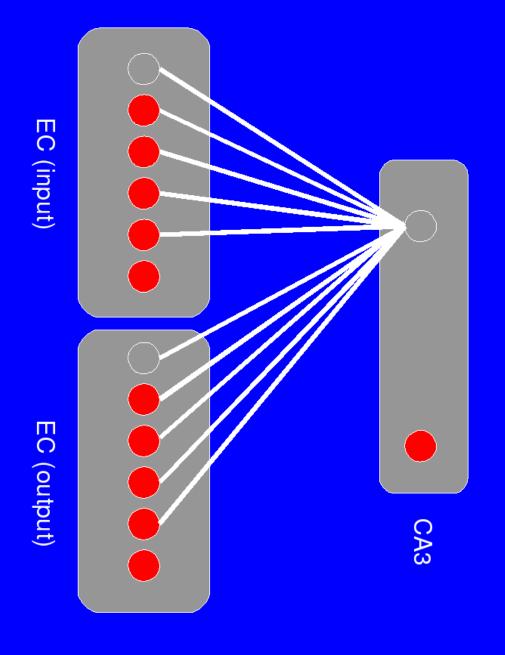


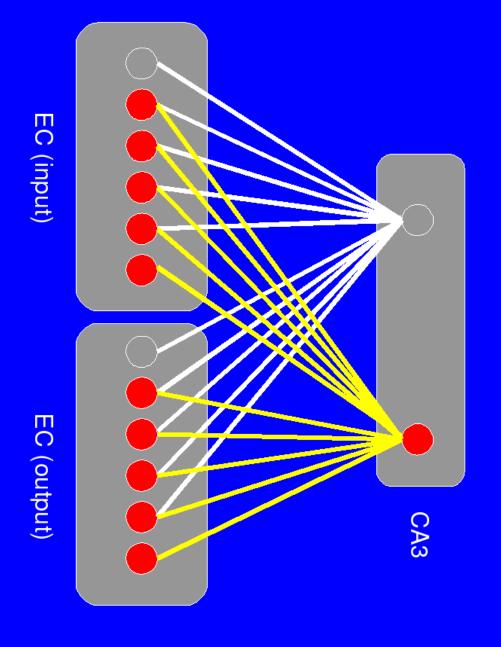


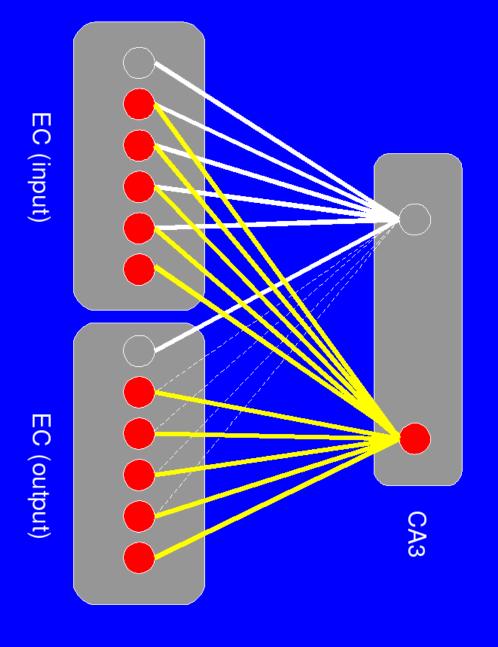


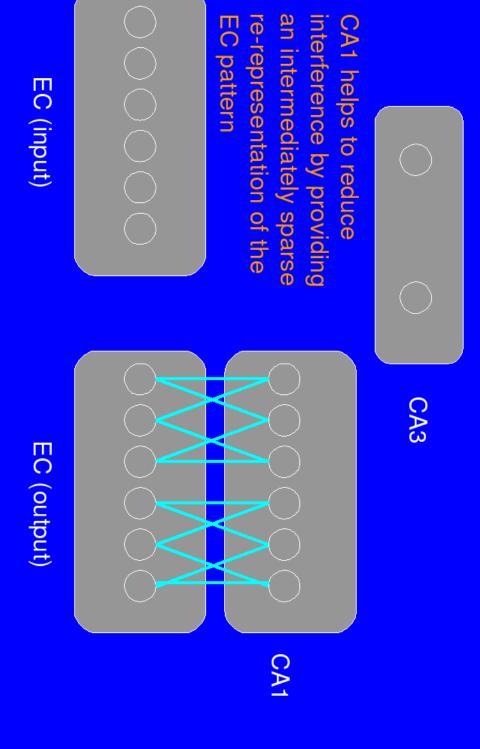


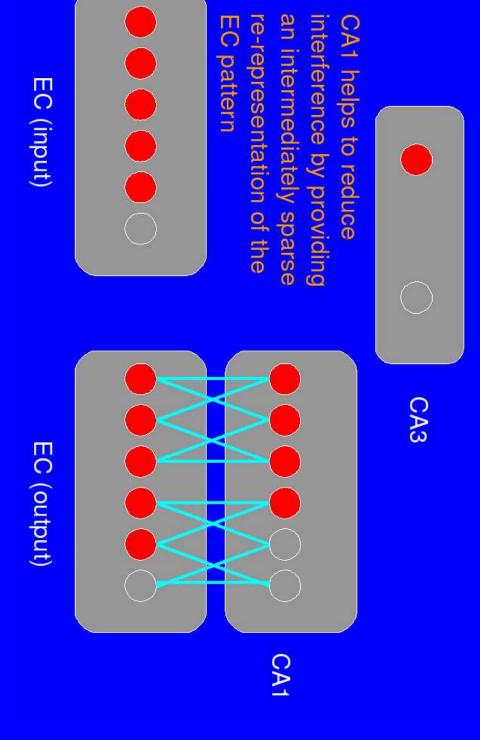


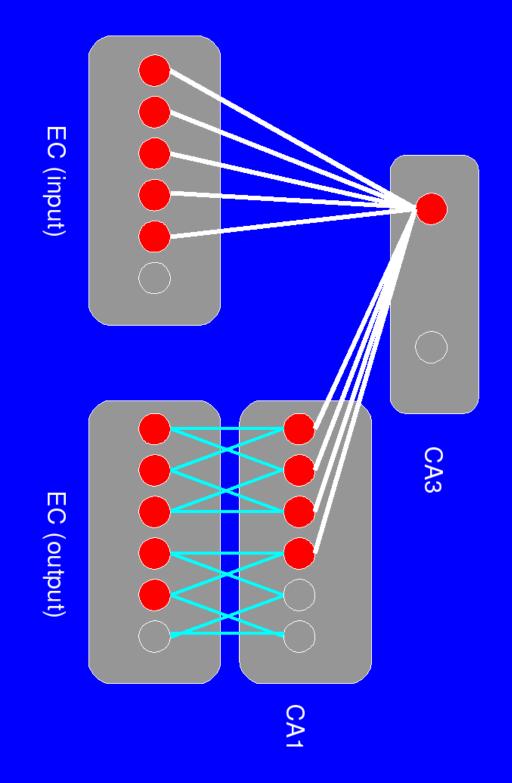


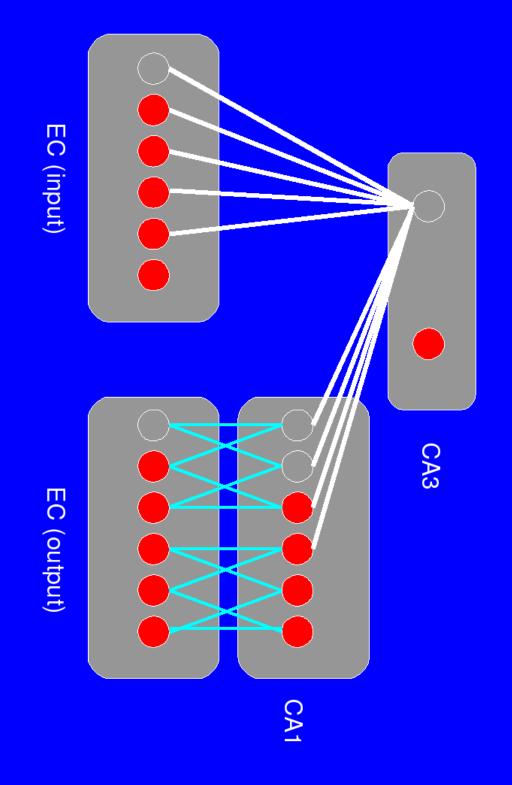


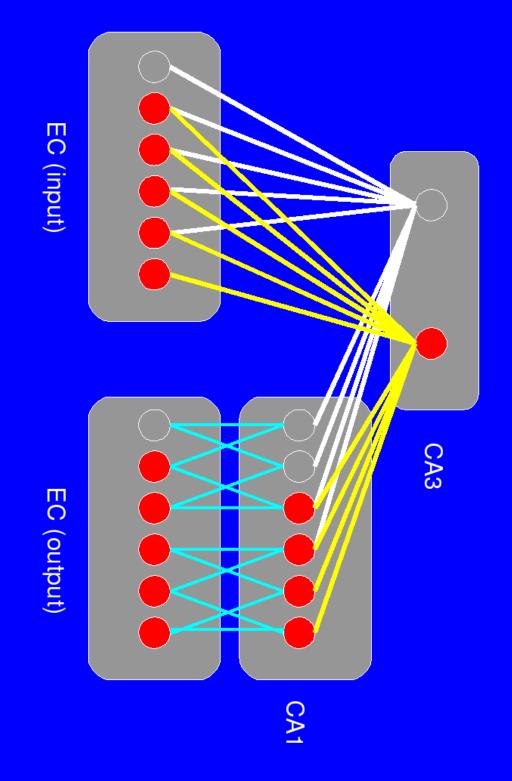


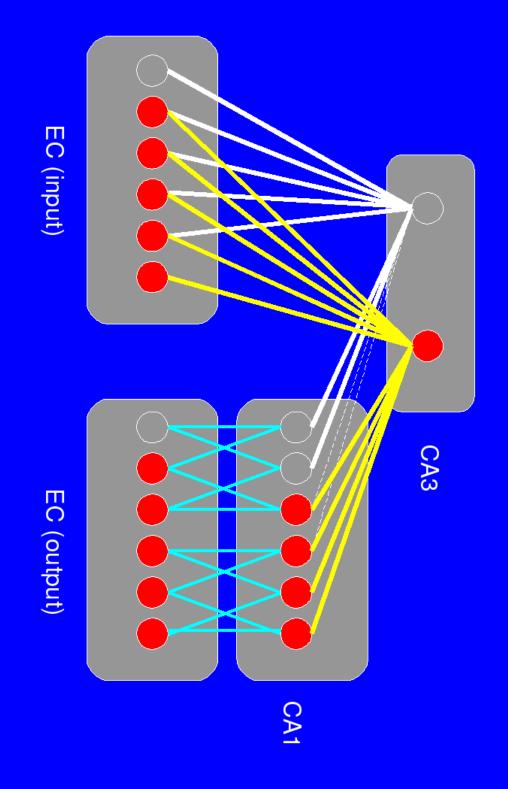


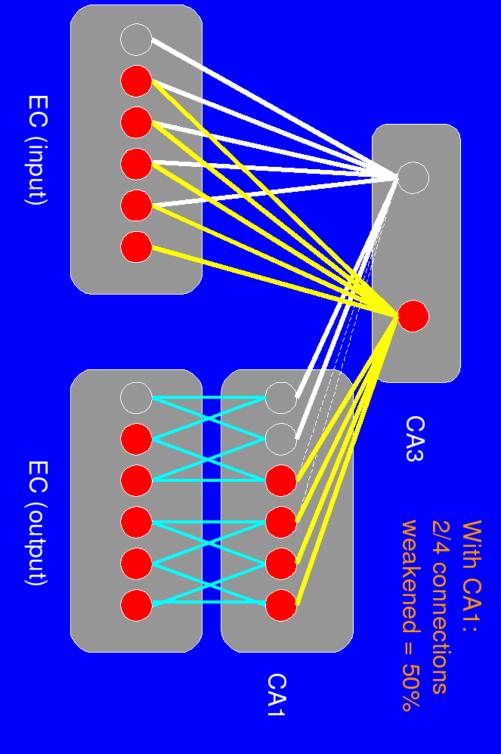


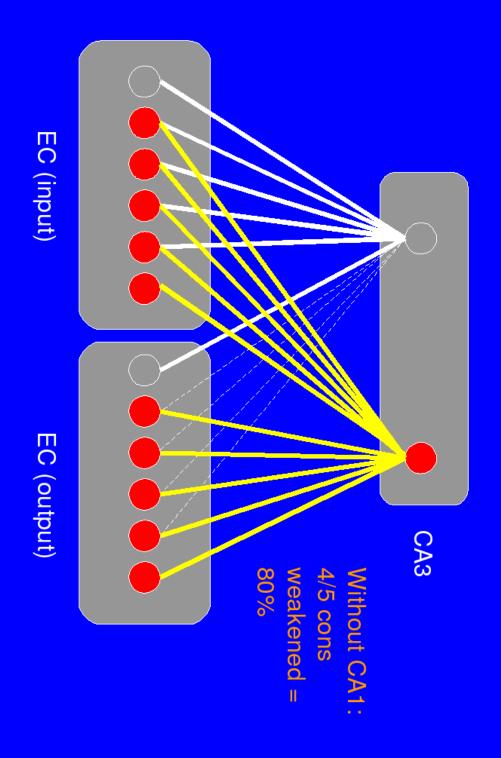












Hippocampus: Summary

- CA3 stores sparse, pattern-separated representations of cortical input patterns
- Recurrent self projections in CA3 facilitate recall (pattern completion)
- Dentate Gyrus (DG) acts as a removable pattern separation turbocharger

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- CA3 stores sparse, pattern-separated representations of cortical input patterns
- Recurrent self projections in CA3 facilitate recall (pattern completion)
- Dentate Gyrus (DG) acts as a removable pattern separation turbocharger
- CA1 helps "translate" sparse, non-overlapping CA3 representations representation back into overlapping EC reps, by providing an intermediately sparse

AB-AC Learning in the Hippo Model

[hip.proj]

AB-AC Learning in the Hippo Model

[hip.proj]

- Unlike cortical model, Hippocampus can rapidly and sequentially interference. learn arbitrary information (AB-AC lists) without huge amounts of
- Cortex still critical for slow learning of overlapping, distributed information, and similarity. representations, supporting generalized knowledge, semantic

AB-AC Learning in the Hippo Model

[hip.proj]

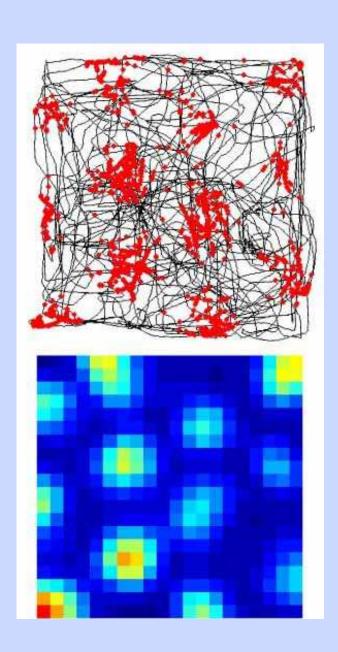
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- waves (Ken Norman) Later: How learning/memory capacity can be enhanced with theta

- 1. Weights (long-lasting, requires re-activation) versus activations (short-term, already active, can influence processing).
- 2. Specialized neural systems: computational tradeoffs. Cortex shows network models? No, hippocampus can learn rapidly without interference using sparse, pattern-separated representations priming, but suffers catastrophic interference. Abandon neural

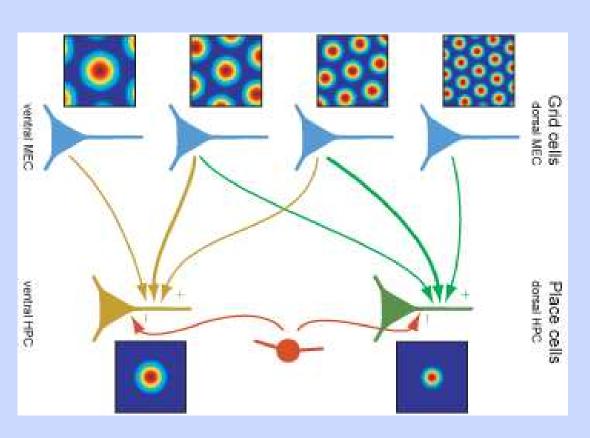
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- 3. Next time: Activation-based memory and activation-weight-based interactions

Hippo and spatial topography: what about "grid cells"?



- Grid cells are in medial entorhinal cortex (Hafting et al, 2005), not hippo proper
- Hippo might integrate location with speed and direction ("head direction cells") to perform path integration
- representations This can be recast as just another example of conjunctive, pattern-separate



Solstad et al, 2006

- 1. Weights (long-lasting, requires re-activation) versus activations (short-term, already active, can influence processing).
- 2. Weight-based: Cortex shows priming, but suffers catastrophic interference. Hippocampus can learn rapidly without interference using sparse, pattern-separated representations.
- 3. Activation-based: Cortex shows priming, but can't do working memory.
- 4. Activation- and weight-based interactions.

Even slow cortical weight changes can yield one-trial learning effects..

W1N____

Even slow cortical weight changes can yield one-trial learning effects..

win____

handle

Even slow cortical weight changes can yield one-trial learning effects..

win____

handle winter

Even slow cortical weight changes can yield one-trial learning effects..

win____

handle winter shower...

Even slow cortical weight changes can yield one-trial learning effects..

win____

handle winter

shower...
win___

Even slow cortical weight changes can yield one-trial learning effects...

win___

handle winter

shower...

win___

Spell $/r\overline{e}d/$.

Even slow cortical weight changes can yield one-trial learning effects..

win____

handle

winter

shower...

win___

Spell $/r\overline{e}d/$.

Name a musical instrument that uses a reed.

Even slow cortical weight changes can yield one-trial learning effects..

win___

handle

winter

shower...

win___

Spell $/r\overline{e}d/$. Name a musical instrument that uses a reed.

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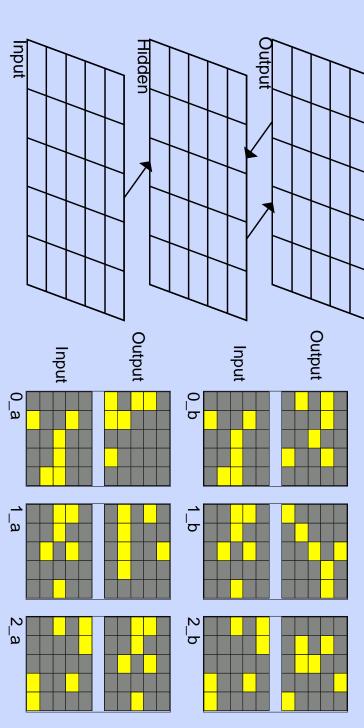
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- Stem-completion & phonetic priming
- Perceptual identification → faster, more accurate detection after recent exposure to words (even hours later)
- Category generation priming: "peach, kiwi"; <many hrs later> → "name some fruits" (in absence of recall)
- Cortex is the key substrate for these priming effects
- Patients with hippocampus damage (sparing cortex) show impaired recall but intact priming
- These priming effects are long-lasting
- This indicates that a weight change is involved (unlikely for activations to persist for long periods)

Simulations of Cortical Priming

- Train a network to learn input-output mappings
- Each input is associated with two valid outputs
- Analogous to:

win___
$$\rightarrow$$
 window
win___ \rightarrow winter
 $/r\overline{e}d/ \rightarrow$ "read"
 $/r\overline{e}d/ \rightarrow$ "reed"

Weight-based Priming Model



Priming Simulations

- After training, the network is equally likely to produce the "a" or "b" output in response to a cue...
- Does not "blend" the two, but instead settles into one of the two valid
- How does one additional study trial with the "a" input affect pertormance?
- Small weight changes (resulting from a single study trial) can "tip the balance" in favor of the recently studied response...

Priming Data

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50
3	2	1	0	12	11	10	9	8	7	9	5	4	3	2	1	0	12	11	10	6	8	7	9	5	4	3	2	1	0
3_b	2_b	1_b	d_0	12_a	11_a			8_a	0	6_a	5_a	4_a	3_a	2_a	1_a	0_a	12_a	11_a	10_a	9_a	8_a		6_a				2_a		0_a
0	0	0	0	0	0	0	0	0	27654	0	0	0	0	0	0	0	0	0	0	0	0	0.605	0	2.2629	0	0	0	.4588	0
3_a	2_a	1_a	0_a	12_b	11_a	10_a	9_a	8_a	7_b	6_a	5_a	4_a	3_a	2_a	1_a	0_a	12_b	11_b	10_a	9_a	8_a	7_b	d_b	5_a	4_b	3_b	2_a	1_b	0_a
1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	0	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Residual activation can also result in priming. (Activation-based priming: later)

Three factors:

- Duration (short-term activations vs long-term weights).
- Content (visual, semantic, etc.)
- Similarity (repetition, semantic relation, etc).

Remember Weight-Based Priming?

Activation-Based Priming

Residual activation can also result in priming: act_priming.proj

No learning (wt changes), to see effects of activation alone.

Activation-based Priming: Residual Activation

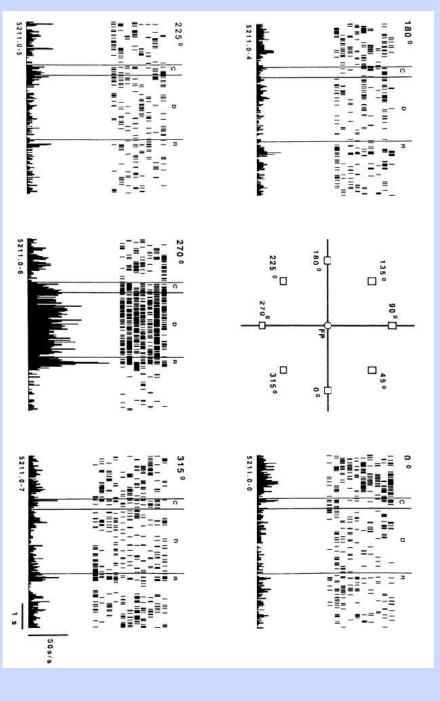
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0.33391	0	1.40431	0	0.337607	0	1.64196	0	0.444151	0	0	0	2.00435	0	2.36882	0	0.663053	0	1.05335	0	0.467382	0	2.06997	0	1.7529	0	d s
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0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	o err

Activation-based Priming: Residual Activation

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5.32969	0	6.4702	0	5.20613	0	7.888	0	9.4205	0	8.85609	0	5.74102	0	4.02698	0	6.26163	0	1.05335	0	5.43822	0	2.18947	0	1.7529	0	s se
0.33391	0	1.40431	0	0.337607	0	1.64196	0	0.444151	0	0	0	2.00435	0	2.36882	0	0.663053	0	1.05335	0	0.467382	0	2.06997	0	1.7529	0	ds
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memory)?? But what about when need to maintain over longer delays (working

Prefrontal Cortex: Delay-related activity



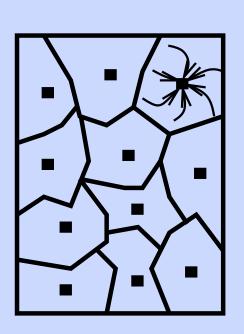
Spatial delayed-response task; Funahashi et al, 1989

Active Maintenance

Maintaining information in active form over longer time periods.

Can be used for working memory (e.g., in mental arithmetic).

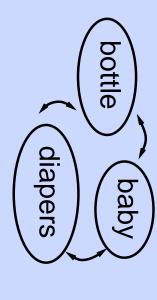
Attractor = stable activation state:



(don't want activity to spread)

Prefrontal vs. Posterior Cortex

Posterior cortex: interactive reps w/spreading activation



Advantages
Semantic associations
Inference (diapers → baby)
Schema (parenting)

Disadvantages
Memory confusion

Prefrontal: isolated reps, maintenance w/out activation spread

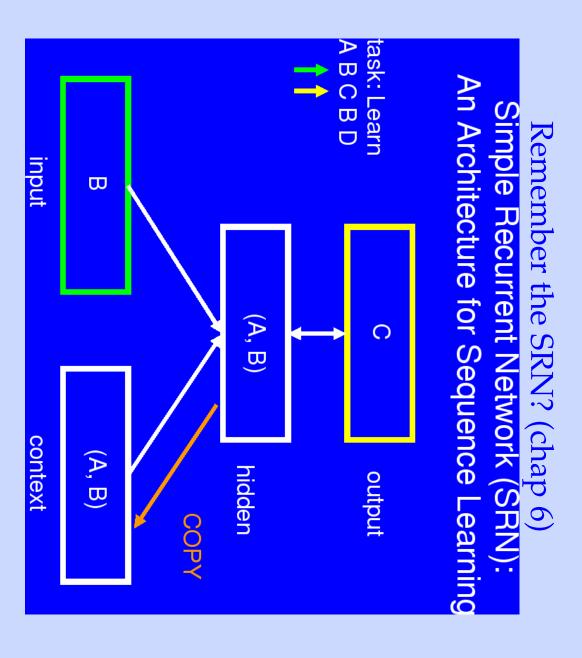
Attractors: Summary

- To get robustness from noise, you need isolated representations with strong recurrent connections
- This prevents activity from spreading
- Tradeoff #1: Preventing spreading activation (active maintenance) vs. allowing spreading activation (inference)
- Solution: Posterior cortex uses interconnected representations → spreading activation; prefrontal cortex (PFC) uses isolated reps \rightarrow prevents spreading activation
- Evidence for isolated stripes in PFC (Levitt et al, 93; Pucak et al, 96)

Attractors: Summary

- Tradeoff #2: Within PFC, need for robust maintenance vs. need to update PFC activation when appropriate
- Strong recurrents (weak inputs) = robust maintenance
- Weak recurrents (strong inputs) = rapid updating
- We need a mechanism for switching PFC between the two modes
- Also, how to *learn* when to update?

ABCBD task: Learn An Architecture for Sequence Learning Simple Recurrent Network (SRN): Remember the SRN? (chap 6) input W (A, B) C context (A, B) output hidden COPY

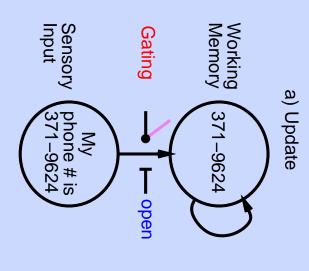


this is a gating network: context only updated at discrete timepoints

Simple SRN story is not flawless

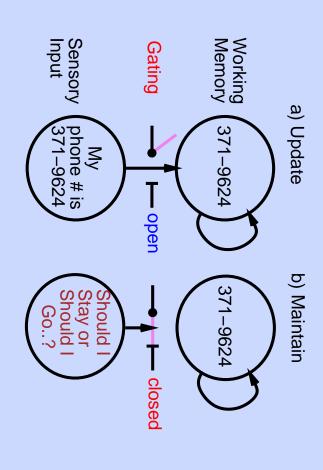
- How is hidden→ "copy" function implemented biologically?
- During settling, context must be actively maintained (ongoing hidden activity has no effect on context).
- Assumes all context is relevant: What if distracting information context. presented in middle of sequence? Want to only hold on to relevant
- What if want to hold on to more than one piece of information in WM to robustly maintain others? at a time?? Or to selectively update one part of WM while continuing
- And what if the decision of whether or not to update information depends on currently internal WM state?

Working Memory Demands: Updating & Maintenance



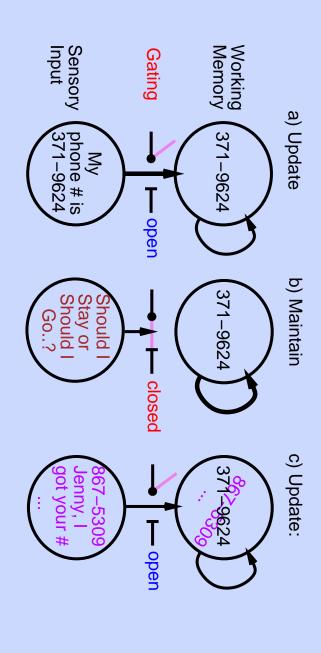
- Working memory: robust maintenance of information, but must also have ability to be rapidly updated — requires gating.
- You've got to know when to hold 'em, know when to fold 'em.

Working Memory Demands: Updating & Maintenance

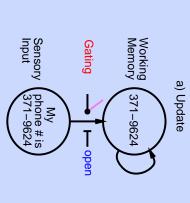


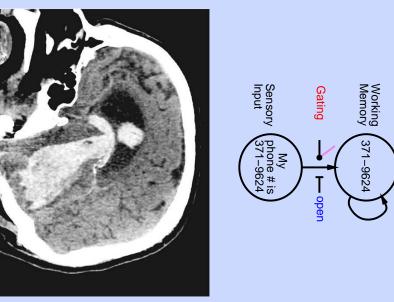
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Working Memory Demands: Updating & Maintenance



- Working memory: robust maintenance of information, but must also have ability to be rapidly updated — requires *gating*.
- You've got to know when to hold 'em, know when to fold 'em.







Dopamine provides dynamic gating mechanism: [First pass story (Braver & Cohen, '00 and text):]

- Positive TD δ (reward) = DA burst = update PFC.
- No TD δ = constant DA = maintain PFC.
- Negative TD δ (error) = DA dip = clear PFC.

The same DA signal that learns to predict reward can be used to drive updating of PFC states!

DA solves part of the problem

- Learning signal for gating.
- But DA is very global signal projecting to all of PFC sufficent for updating and maintaining one item at a time
- How to selectively update some aspects of WM but not others?
- Also prev DA-PFC model had awkward catch-22 problem: the stimulus is only predictive of reward if it is maintained (ie in PFC). But then stim needs to be gated into PFC in the first place to generate DA!

DA solves part of the problem

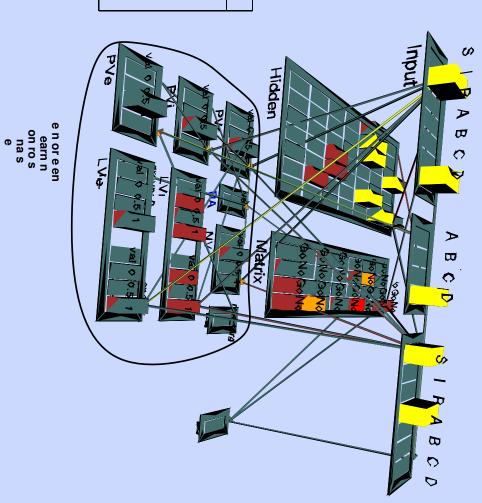
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- Also prev DA-PFC model had awkward catch-22 problem: the then stim needs to be gated into PFC in the first place to generate DA! stimulus is only predictive of reward if it is maintained (ie in PFC). But
- Solution: separate learning from gating... and link to now well established role of basal ganglia-thalamus in gating.

Dynamic Gating: Current Story

- DA signals are important for learning/knowing when to gate
- But actual gating signals are implemented via more complex circuit interactions with the Basal Ganglia Go/NoGo system
- DA used to train Go/NoGo system exactly like in the motor and simple decision making domains...
- BG-gating solves multiple computational and biological plausibility issues that are problematic with pure-DA based gating
- Goto BG_PFC_WM1.pdf slides for more info and evidence

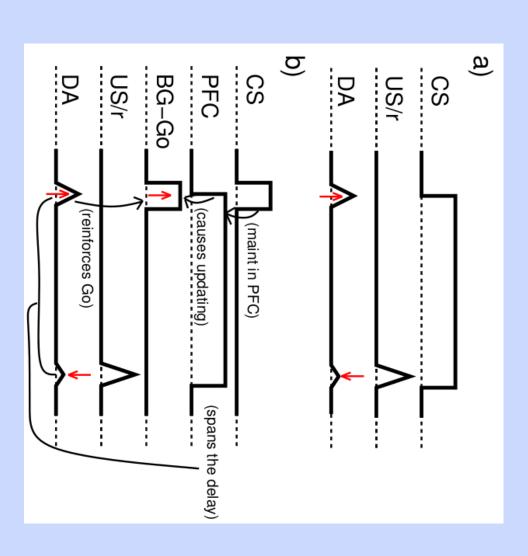
A Simple WM Task

3 12	4 ω 4
IGNORE-B IGNORE-C	IGNORE-B IGNORE-C IGNORE-D
\triangleright	\triangleright



PFC/BG Model: sir.proj

PFC maintenance enables RL to train BG



Reinforcement learning and WM gating

- Network learns to associate stimuli with rewards via PVLV / DA system (like TD)
- PVLV gets information not only from outside world, but also PFC state
- Desired outcome: Network learns that having the STORE pattern in PFC leads to rewards, but having the IGNORE pattern does not

Reinforcement learning and WM gating

- Bursts and dips of DA train the basal ganglia Go/NoGo gating system
- If BG system gates an input into PFC and that PFC pattern had been PFC pattern as rewarding) associated with reward → DA burst (DA system recognizes this new
- This DA burst reinforces Go activity in the BG units that caused the drive updating itself, but is a learning signal) gate this pattern into PFC on future trials. (phasic DA does not directly gating in the first place, making it even more likely that the BG will
- Desired outcome: Networks learns "Go" to gate STORE into PFC, but learns "NoGo" to IGNORE

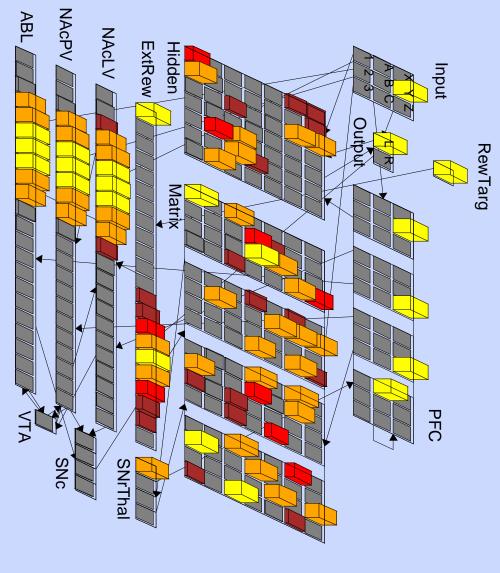
Sketch of how the network learns

- Begins with trial-and-error learning (both at response output and in BG gating system)
- Explore different gating "policies" and reinforce ones that work. (some amount noise helpful!)
- If correct response happens to occur when STORE is active in PFC (initially due to guessing) \Rightarrow Reward
- Resulting DA burst trains PVLV (or TD) system to learn that having "STORE" in PFC is a good thing

Sketch of how the network learns

- Next time STORE is represented in PFC, PVLV system triggers a DA external reward) burst, based on its learned PFC-reward association (without needing
- This DA burst drives BG Go learning so that good stimuli are more likely to be gated
- In turn, stored information is more likely to be present in PFC during RECALL trial.
- At this point, Hidden layer simply has to learn to map PFC representation of stored stimulus to the Output response
- This leads to increased rewards, further training gating system, and leading to stable state.

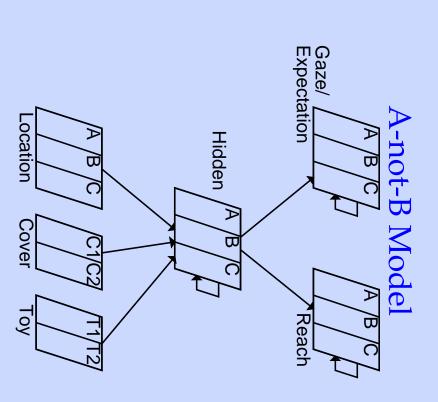
Four "Stripe" PFC/BG Model, Learns with DA (O'Reilly & Frank, 2006) RewTarg



Weight- and Activation-Based Memory Interactions

A-not-B task

- Perseverative searching at A also seen in patients with PFC damage
- Better peformance in gaze/expectation
- Inhibition problem?
- Model demonstrates maintenance problem.
- Same model accounts for various effects in different versions of 1998). A-not-B task not explained by any other unified theory (Munakata,



Knowledge-action dissociations in card-sort task

- Kids can tell you where trucks go in the shape game, even after sorting according to color!
- But if you ask "where do red trucks go in the shape game" they still fail! (Morton & Munakata, 2002)
- Explained by different levels of conflict experienced when faced with multiple stimuli-response associations..