

# CRISP: Challenging the Standard Framework of Hippocampal Memory Function

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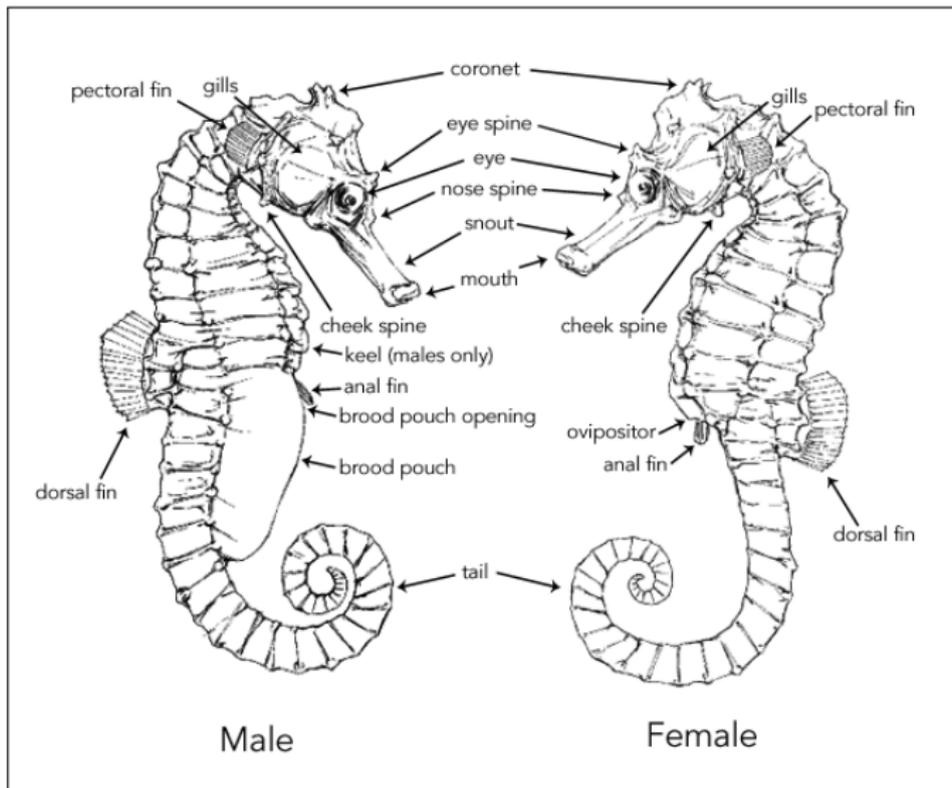
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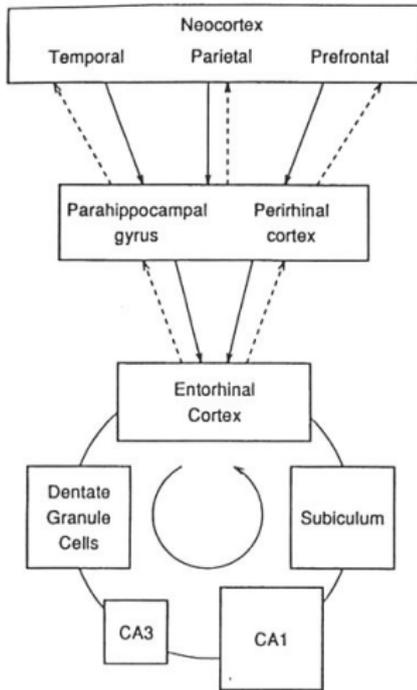
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# Theories of the Hippocampus



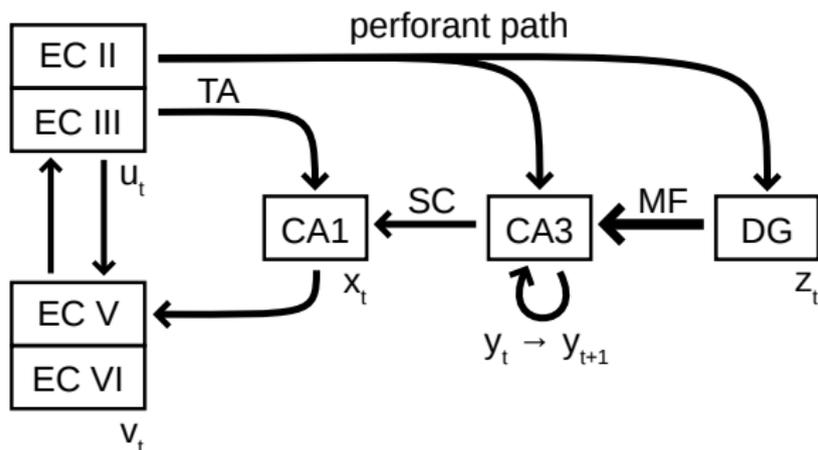
# Standard Framework of the Hippocampus



- ▶ Entorhinal cortex (EC) serves as an interface between association areas of neocortex and the hippocampus.
- ▶ The subareas of the hippocampus are connected in a loop: EC - DG - CA3 - CA1 - subiculum - EC.
- ▶ Because of its recurrent connectivity, CA3 serves as the central autoassociative memory.
- ▶ Dentate gyrus (DG) orthogonalizes similar patterns by sparsification.
- ▶ CA1 helps expanding the highly compressed representation in CA3 on the way back to the association areas.
- ▶ Subiculum has no specific function associated with it.
- ▶ The entorhinal-hippocampal part has been implemented as a connectionist model.

(Treves and Rolls, 1994, *Hippocampus* 4(3):374–391)

# CRISP Theory



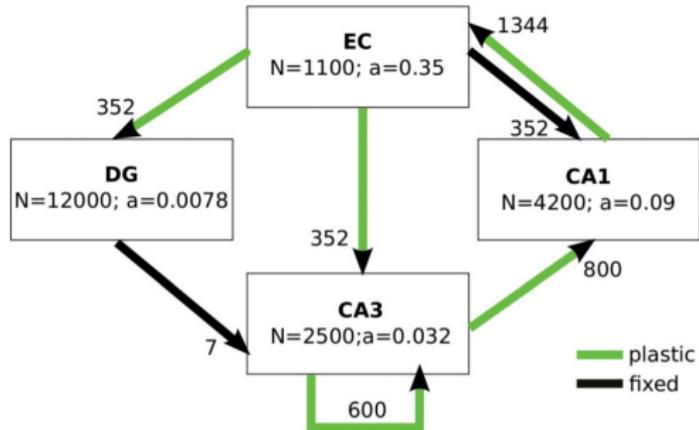
- ▶ **C**ontext **R**eset by dentate gyrus (DG)
  - ▶ Dentate gyrus performs disambiguation of similar patterns.
- ▶ **I**ntrinsic **S**equences in CA3
  - ▶ Patterns are connected by association with pre-existing sequences.
- ▶ **P**attern completion in CA1
  - ▶ Pattern storage and retrieval is done through feedforward hetero-association.
- ▶ This is a conceptual model.

# Memory Fidelity of Single Patterns



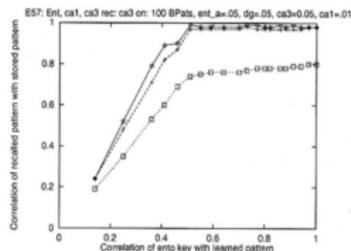
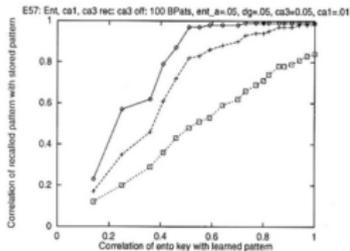
(2018-01-26 <https://pixabay.com/en/loving-memory-memorial-grief-1207568/>)

# Network

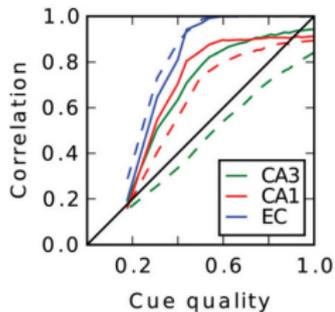


- ▶ Cell numbers, connectivity and sparsity are derived from rat.   
Scaling factor for number of neurons is 100, for connections per neuron is 10.
- ▶ Activation is  $p_i(t+1) = \sum w_{ij} p_j(t)$  with  $k$ -winners-take-all.
- ▶ Autoassociative feedback loop in CA3 is run 15 times per pattern.
- ▶ Learning rules exactly as in (Rolls, 1995).
- ▶ Storage is done via DG, recall via EC→CA3 connections.

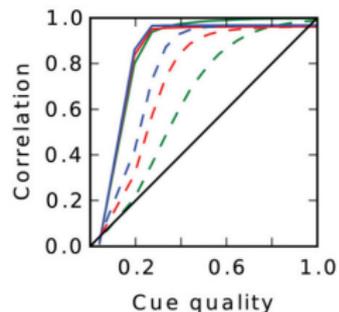
# Following the Rolls (1995) Model



(Rolls, 1995, Intl. J. of Neural Systems 6:51-70)



'Rolls model'

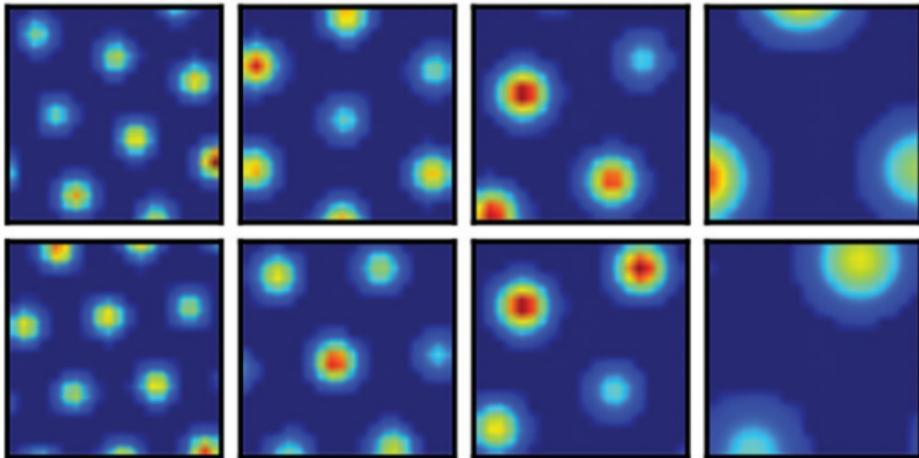


'modified Rolls model'

Solid/dashed lines: with/without recurrent dynamics in CA3.

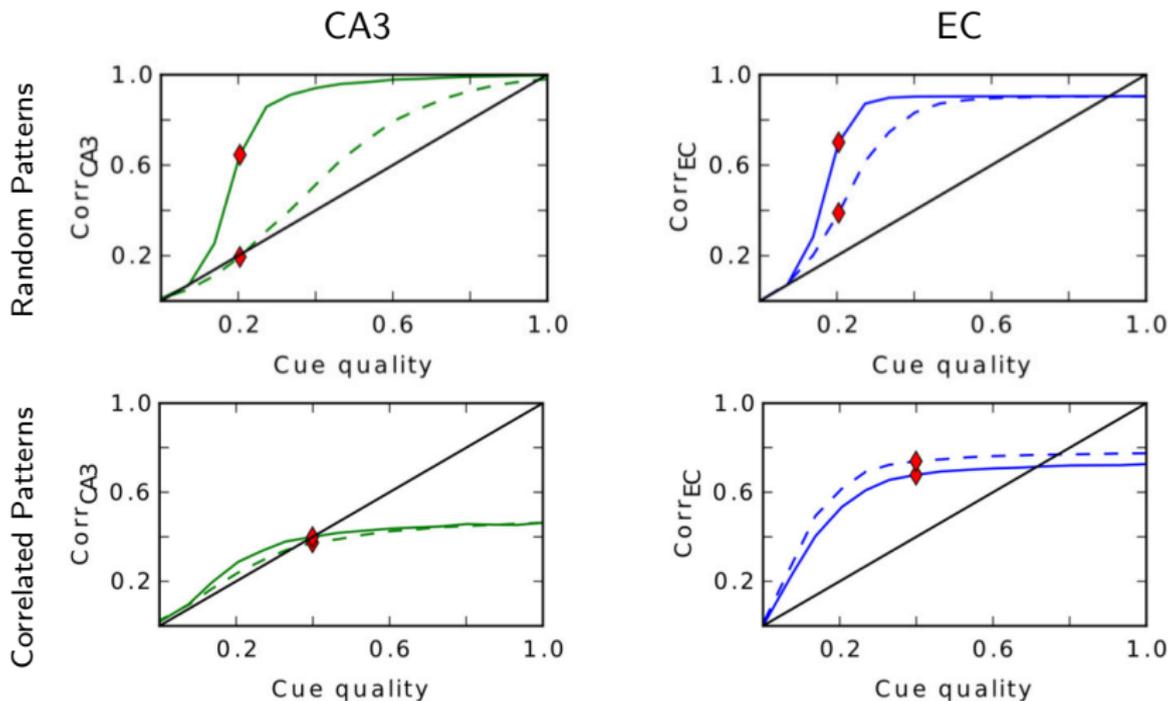
The Rolls model (top and lower left) used 1% activity in CA1 for 100 patterns and full connectivity from CA1 to EC. We changed that to 10% and sparse connectivity from CA1 to EC, and during storage CA1 was activated by EC→CA1.

## Correlated Input



- ▶ Four modules of grid cells as mEC input.
- ▶ Population activity at random locations serves as input.

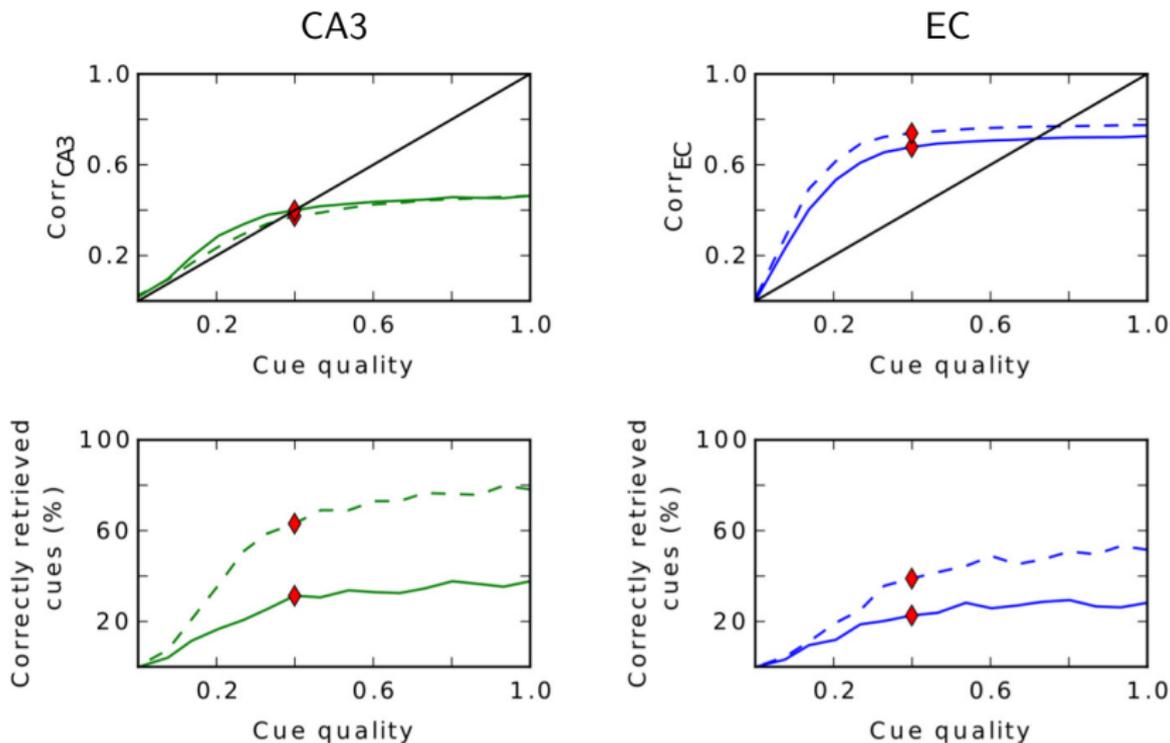
# Performance on 252 Random and Correlated Patterns



Solid/dashed lines: with/without recurrent dynamics in CA3.

Learning in DG is disabled, because it drops performance. 252 patterns were used.

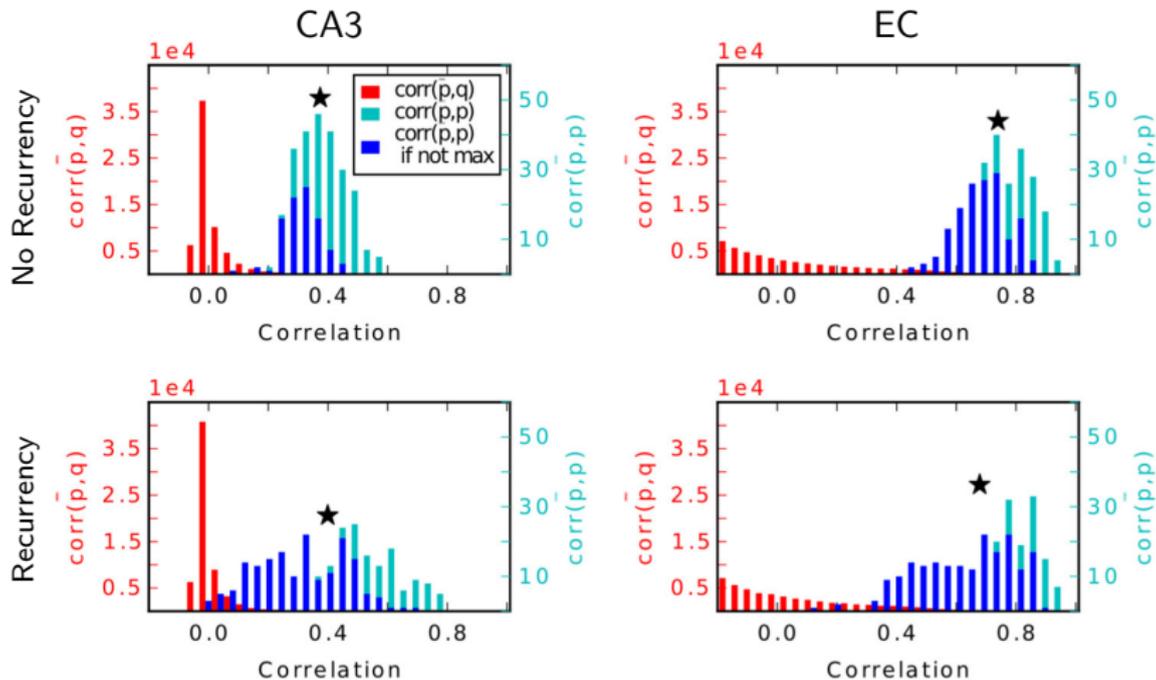
# Performance on 252 Correlated Patterns



Solid/dashed lines: with/without recurrent dynamics in CA3.

Learning in DG is disabled, because it drops performance. 252 patterns were used.

# Performance on Correlated Patterns

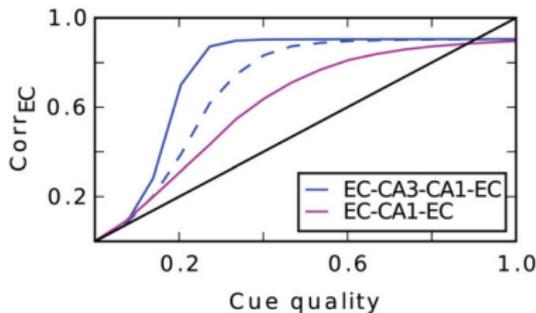


Top/bottom: without/with recurrent dynamics in CA3. Red: correlations with wrong patterns. Blue/cyan: correlations with correct pattern. Blue: cases where the recalled pattern is closer to a wrong than to a correct pattern. Black star: average correlation with correct pattern. Histograms taken at cue quality levels marked by red diamonds in previous graphs.

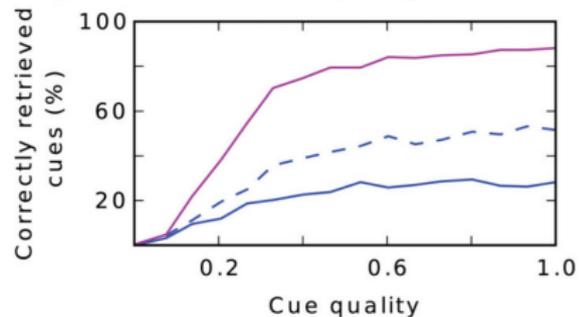
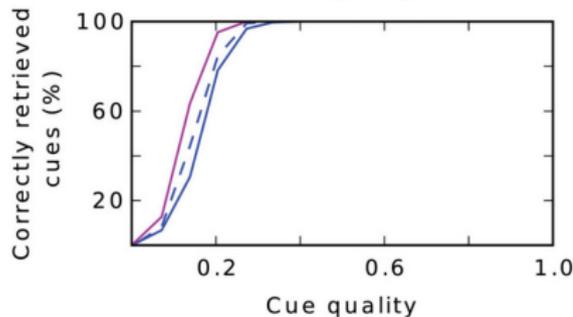
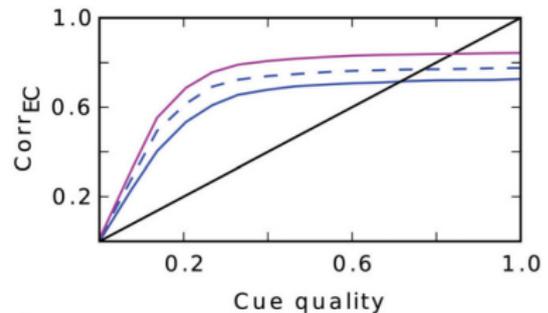
# Performance with EC→CA1→EC Network

- ▶ Storage: Activity in CA1 triggered by EC→CA3→CA1, without plasticity. Connections EC→CA1→EC are plastic.
- ▶ Retrieval: EC→CA1→EC only is effective.

Random Input



Correlated Input

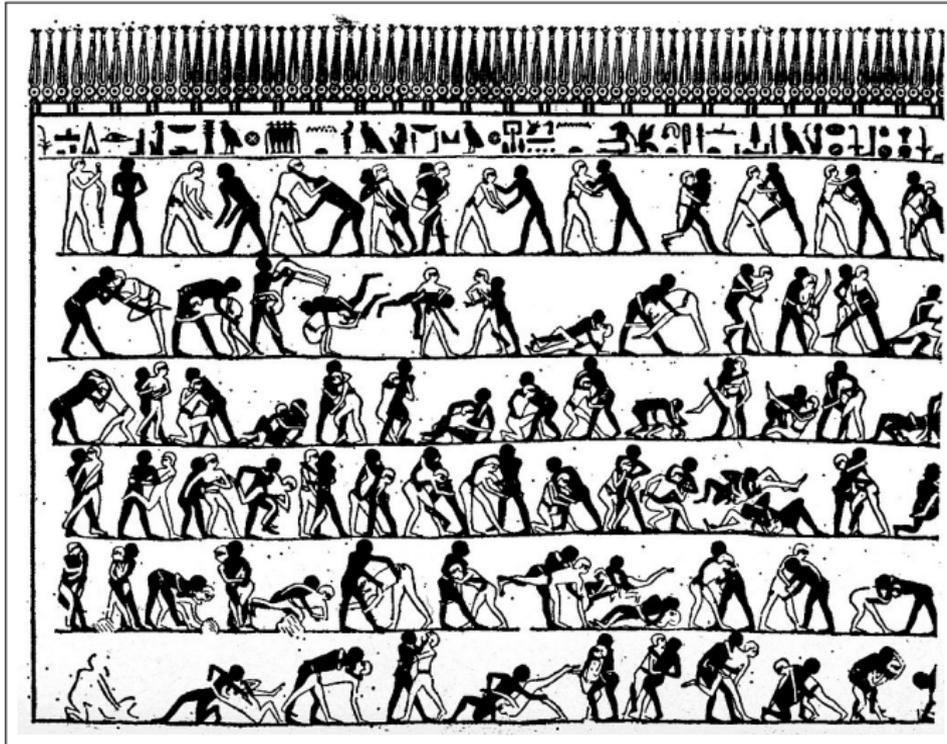


Solid/dashed lines: with/without recurrent dynamics in CA3.

# Summary

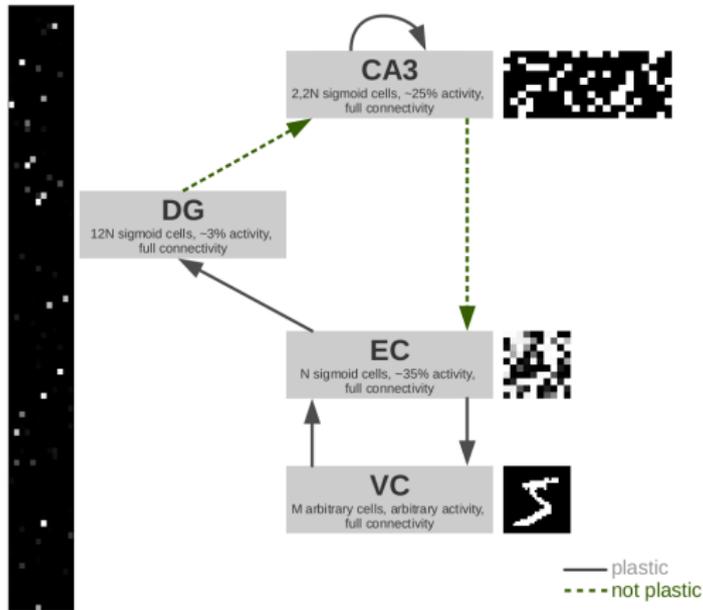
- ▶ Qualitative behavior of a network can be very different for random and for more natural input patterns.
- ▶ Correlation between stored and retrieved patterns is only one measure of performance. Confusion rate might be more important.
- ▶ We found feed-forward hetero-association to be more powerful than recurrent auto-association.
- ▶ Recurrent dynamics in CA3 was even harmful.
- ▶ A simple  $EC \rightarrow CA1 \rightarrow EC$  performed best on correlated input.

# Instantaneous Sequential Storage and Retrieval of Pattern Sequences



(2018-02-07 <https://commons.wikimedia.org/wiki/File:Egyptmotionseries.jpg>)

# Network



- ▶  $N = 200$ .
- ▶ Fixed connections were pre-trained with gradient descent, plastic connections were trained with Hebbian learning plus weight decay.

## Raw Input Patterns



- ▶ A random sequence of 200 handwritten digits of size  $28 \times 28 = 784$  from the MNIST database serves as raw input, shown here by rows from top left to bottom right.

## Reconstructed Input Patterns



- ▶ Raw images are compressed with an auto-encoder network down to 220 dimensions to yield the EC representation.
- ▶ This image shows the reconstructed images from the auto-encoder.

## Full Recall from Cue 10 Without Noise



- ▶ Cue image is shown negative. Retrieved sequence is rotated for easier comparison.
- ▶ The recently stored patterns (lower right) are clearer than the earlier stored patterns (upper left). The quality loss is roughly linear.
- ▶ In this run 196/200 of the retrieved sequences are correct.

## Full Recall from Cue 10 With 20% Input Noise



- ▶ Same as before but with 20% input pixel noise.

## Full Recall from Cue 10 Without Noise

5	0	4	7	9	2	1	3	1	4	3	5	3	2	1	7	2	8	6	9
4	0	9	1	1	2	9	3	2	2	2	8	6	9	0	5	6	0	7	6
1	8	1	9	3	2	8	5	9	3	5	0	7	4	9	9	0	9	4	1
4	4	6	0	4	5	6	1	0	0	2	7	1	6	3	0	2	1	1	7
9	0	2	6	7	8	3	9	0	4	6	7	4	4	8	0	7	8	3	1
5	7	1	7	1	1	6	3	0	2	9	3	1	1	0	4	9	2	0	0
2	0	2	7	1	8	6	4	1	6	3	4	5	9	1	3	3	8	5	4
7	7	4	2	8	5	8	6	7	3	4	6	1	9	9	6	0	3	7	2
8	2	9	4	4	6	4	9	7	0	9	2	9	5	1	5	9	1	0	3
2	3	5	9	1	7	6	2	8	2	2	5	0	7	4	9	7	8	3	2

## Full Recall from Cue 10 With 20% EC Noise

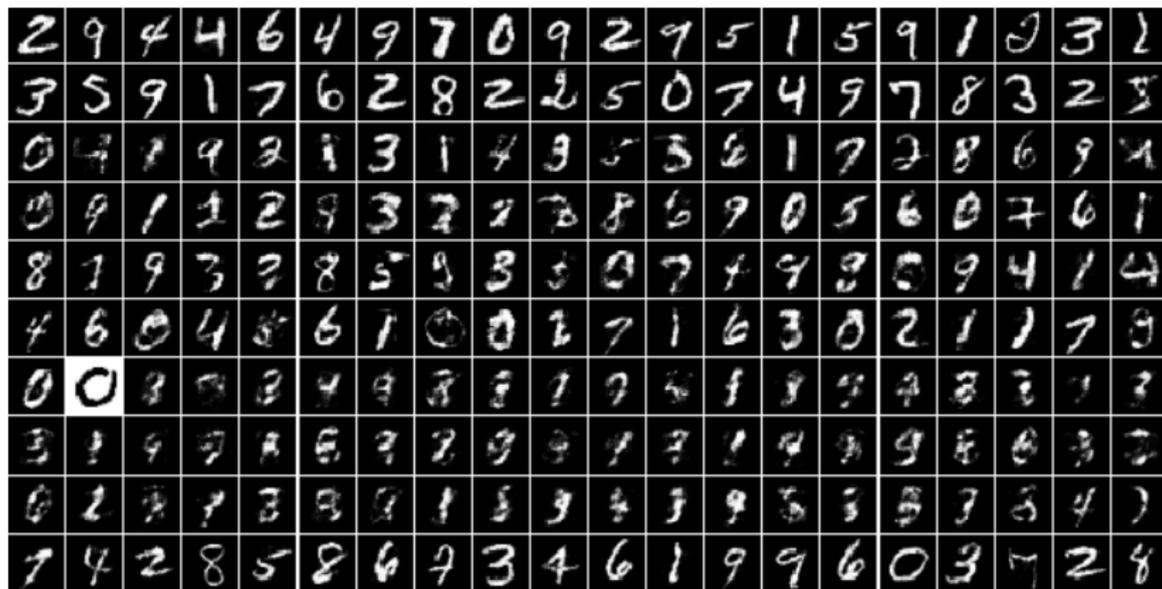
5	0	4	7	9	2	1	3	1	4	3	5	5	2	1	7	2	8	6	9
4	0	9	1	1	2	9	3	2	2	2	8	6	9	0	5	6	0	7	6
1	8	1	9	3	2	8	5	9	3	5	0	7	4	9	9	0	9	4	1
4	4	6	0	4	5	6	1	0	0	2	7	1	6	3	0	2	1	1	7
9	0	2	6	7	8	3	9	0	4	6	7	4	4	8	0	7	8	3	1
5	7	1	7	1	1	6	3	0	2	9	3	1	1	0	4	9	2	0	0
2	0	2	7	1	8	6	4	1	6	3	4	5	9	1	3	3	8	5	4
7	7	4	2	8	5	8	6	7	3	4	6	1	9	9	6	0	3	7	2
8	2	9	4	4	6	4	9	7	0	9	2	9	5	1	5	9	1	0	3
2	3	5	9	1	7	6	2	8	2	2	5	0	7	4	9	7	8	3	2

- ▶ Same as before but with 20% noise in EC.

## Reconstructed Input Patterns

5	0	4	1	9	2	1	3	1	4	3	5	3	6	1	7	2	8	6	9
4	0	9	1	1	2	4	3	2	7	3	8	6	9	0	5	6	0	7	6
1	8	7	9	3	9	8	5	9	3	3	0	7	4	9	8	0	9	4	1
4	4	6	0	4	5	6	7	0	0	2	7	1	6	3	0	2	1	1	7
8	0	2	6	7	8	3	9	0	4	6	7	4	6	8	0	7	8	3	1
5	7	1	7	1	1	6	3	0	2	9	3	1	1	0	4	9	2	0	0
2	0	2	7	1	8	6	4	1	6	3	4	5	9	1	3	3	8	5	4
7	7	4	2	8	5	8	6	7	3	4	6	1	9	9	6	0	3	7	2
8	2	9	4	4	6	4	9	7	0	9	2	9	5	1	5	9	1	0	3
2	3	5	9	1	7	6	2	8	2	2	5	0	7	4	9	7	8	3	2

## Full Recall from Cue 121 Without Noise



- ▶ Cue 121 does not trigger the correct sequence.

## Full Recall from Cue 121 Without Noise Shifted by 39

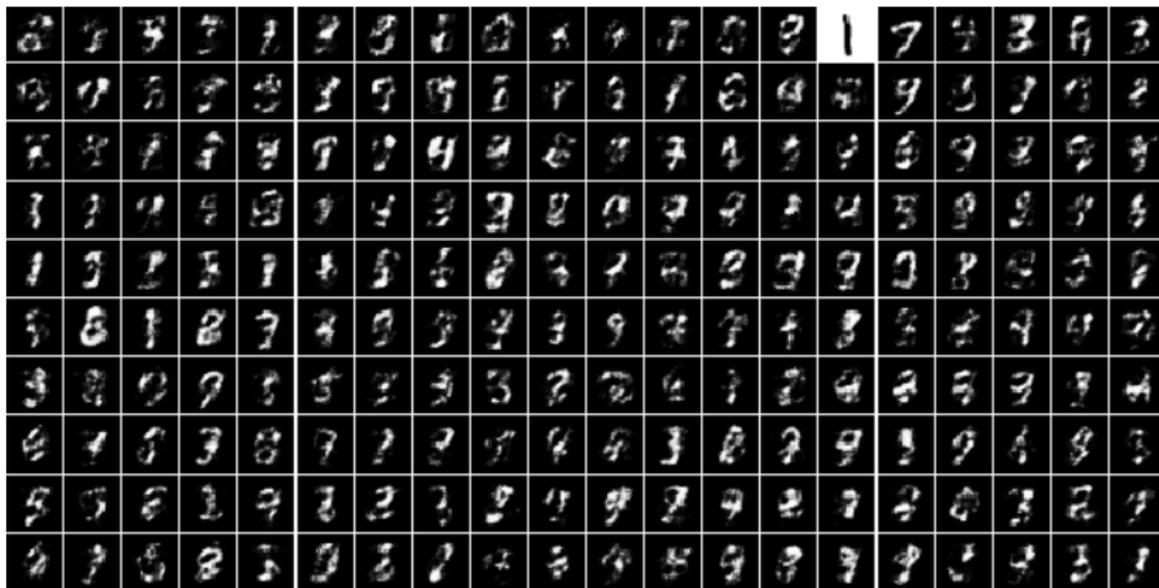


- ▶ But after about 60 time steps CA3 converges to the correct sequence shifted by 39.

## Reconstructed Input Patterns

5	0	4	1	9	2	1	3	1	4	3	5	3	6	1	7	2	8	6	9
4	0	9	1	1	2	4	3	2	7	3	8	6	9	0	5	6	0	7	6
1	8	7	9	3	9	8	5	9	3	3	0	7	4	9	8	0	9	4	1
4	4	6	0	4	5	6	7	0	0	2	7	1	6	3	0	2	1	1	7
8	0	2	6	7	8	3	9	0	4	6	7	4	6	8	0	7	8	3	1
5	7	1	7	1	1	6	3	0	2	9	3	1	1	0	4	9	2	0	0
2	0	2	7	1	8	6	4	1	6	3	4	5	9	1	3	3	8	5	4
7	7	4	2	8	5	8	6	7	3	4	6	1	9	9	6	0	3	7	2
8	2	9	4	4	6	4	9	7	0	9	2	9	5	1	5	9	1	0	3
2	3	5	9	1	7	6	2	8	2	2	5	0	7	4	9	7	8	3	2

## Full Recall from Cue 14 Without Noise



- ▶ Cue 14 does not trigger the correct sequence and CA3 does not recover into the correct sequence at all.
- ▶ CA3 fluctuates around a spurious attractor state.

# Summary

- ▶ It is possible to store a sequence of up to  $1.5N$  random patterns in a recurrent CA3 network of  $N$  units with gradient descent.
- ▶ It is possible to do instantaneous sequential hetero-association of a sequence of correlated patterns to the intrinsic sequence of patterns in a CA3 with some preprocessing (auto-encoder + DG).
- ▶ The system has no catastrophic interference/forgetting, quality of retrieved patterns degrades linearly.
- ▶ Sequential order is preserved reliably even for similar stimuli and overlapping sequences.

Thank you!