Why do we have a hippocampus? Short-term memory and consolidation
So far we have talked about the hippocampus and:

- coding of spatial locations in rats
- declarative (explicit) memory
- experimental evidence for LTP
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**TODAY:**
- role of the hippocampus in short term storage and memory consolidation
Remember patient H.M.

since bilateral surgical removal of the hippocampus and surrounding areas, H.M. cannot form new declarative memories but can acquire new skills.

experiments in non-human primates have attempted to reproduce these observations
Concurrent object discrimination in monkeys

100 pairs of easily discriminable objects

animals learn that pointing to one, or touching one is rewarded, but not the other

\begin{tabular}{ll}
\textit{rewarded} & \textit{non-rewarded} \\
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<table>
<thead>
<tr>
<th>rewarded</th>
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<tbody>
<tr>
<td><img src="smiley.png" alt="Smiley Face" /></td>
<td><img src="cube.png" alt="Cube" /></td>
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<tr>
<td><img src="triangle.png" alt="Triangle" /></td>
<td><img src="moon.png" alt="Moon" /></td>
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<tr>
<td><img src="sun.png" alt="Sun" /></td>
<td><img src="cross.png" alt="Cross" /></td>
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animals are trained on this task every day

pairs of objects are presented over and over in randomized order
Once animals have learned this task, they remember the pairs of objects over several weeks.

Several weeks later, they can be tested on the task by presenting each pair once and scoring the number of correct choices and animal makes.
In experiments testing the role of the hippocampus in memory consolidation, hippocampal lesions were performed in animals at various time points AFTER they has learned the task.
Timeline for these experiments

5 groups of 20 pairs of items are used
Results for control monkeys (sham surgery, no damage to hippocampus)

Control animals have good memory for recently learned pairs; memory declines as time between training and testing decreases.
Lesioned monkeys are severely impaired on object pairs learned shortly before the surgery but perform normally on those learned long before the surgery.
Learn 20 pairs of objects

Delay
2, 4, 8, 12, 16 weeks

Surgery
Delay
2 weeks

Testing

Unrewarded

Rewarded

28 42 70 98 126

Controls exhibit normal forgetting

Hippocampal lesions impair memory formation only when they occur < 30 days after learning occurred
These results show that the hippocampal formation is required for memory storage for only a limited period of time after learning. As time passes, its role in memory diminishes, and a more permanent memory gradually develops independently of the hippocampal formation, probably in neocortex.

The following model, by the same group, suggests a temporal role for the hippocampal formation in memory consolidation.
These observations led to a theory for the role of hippocampus in memory consolidation. This theory, proposed by Alvarez and Squire (among others) is based on the following ideas:
(1) several areas of neocortex and the medial temporal lobe (MTL) structures participate in the formation, maintenance and recall of long-term declarative memory events;
(2) the neocortex communicates with the MTL via reciprocal connections;
(3) within the neocortex, memory consolidation consists of gradually binding together the elements that form a given memory;
(4) the MTL learns quickly, but has a reduced storage capacity and
(5) the neocortex learns more slowly but has a large capacity.
The model

Short term storage

MTL

Long term storage

NC

Auto-associative memory
The model

MTL: Medial temporal lobe
1. Neurons are organized in groups of 4

2. In each group, only one neuron can be active (“winner-take-all”)

3. Synapses between MTL and cortex are very plastic (higher learning rate, fast changing).

4. Synapses between cortical areas are less plastic (lower learning rate, slow changing)
Exercise: Write down the equation that describes a continuous output leaky integrator. 

**Winner-take-all:** Remember, this refers to a network in which only the most strongly activated unit in each layer stays active and all others are silent. Cortex 1 and cortex 2 consist of two layers, MTL of a single layer.

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Exercise: Draw a winner-take-all network and describe a neural mechanism that can implement this idea. Write down all equations necessary.
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Leaky continuous firing rate neurons:
\[ a_i = v a_i + \sum w_{ij} a_j + \text{noise} + \text{external input (cortical neurons only)} \]
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Learning rule with build in LTD:

\[ \Delta w_{ij} = \lambda a_i (a_j - \text{average}) \]

-- if presynaptic neuron less active than average, weight decreases, if more active than average, weight increases
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Slow forgetting (very slow):
\[ \Delta w_{ij} = -\rho \cdot \Delta w_{ij} \]
Goal: To reconstruct a "stored" or "learned" pattern of input from an incomplete version of that input. Each pattern consisted of two units activated in cortex 1 and two units activated in cortex 2.

Exercise: What type of network we talked about in class can do this? What are the equations involved?
How it works

1. Events to be memorized activate cortical neurons. *only one in each group of 4 is activated by external input.*

2. Initially weak synaptic weights with randomized values activate MTL neurons to various degrees.
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4. The Hebbian learning rule increases the weights between simultaneously active neurons in the two cortical areas and the MTL (in addition, very small weight increases between active neurons in the two cortical layers.)
5. If only part of the cortical activation pattern is activated by external inputs, the network can restore the originally learned pattern VIA the MTL.
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6. In this scenario, if the MTL is lesioned shortly after the learning process, the pattern cannot be recalled.
7. To simulate consolidation, no activity is imposed on the cortical neurons; MTL neurons are randomly activated.

8. When neurons with strong connections to the cortical areas are activated in the MTL, they reactivate previously stored combinations of cortical neurons. If this reactivation happens often enough (over weeks), the slow changing connections between cortical neurons are increased and the pattern association is stored.
9. After this consolidation process, patterns can be recalled even in the absence of the hippocampus due to the connections between cortical areas.
Discussion points: What are the assumptions in this model? How do they correspond to known data? Which choices of parameters are necessary to make this model work? Which are not?
Random activation during consolidation:

Some researchers believe that neurons in the hippocampus “replay” events that have been lived during the day during REM sleep. Some evidence for this idea exists.
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2) During the experiment, rats were first moved onto a circular platform on which movement was restricted (PRE). They then ran on a linear track (RUN) and were returned to the platform immediately after (POST)
A: Firing raster of cells during running on linear track
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B: Place fields of recorded cells on linear track
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C: Cells recorded during sleep firing in the same sequence than on the linear track
Results show a high correlation between the sequences of cell firing during POST sleep and RUN, but no correlation between the sequences of cell firing during PRE sleep and RUN.
Tricks:

1. Winner take all scheme
2. Numbers of neurons in each group have to be the same
3. Synaptic distribution weird
4. LTP/LTD between MTL and cortical areas not shown
5. Only non-overlapping patterns used
6. Number of neurons in MTL exactly same as number of patterns