

# COSC451: Artificial Intelligence

## Lecture 10: Episodic memory representation of a reach-to-grasp action

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# Recap

In Lectures 2-8, I introduced a model of the SM processes involved in ‘experiencing’ an agent grabbing a cup.

I argued:

- *Perception* of the cup-grabbing event involves a sequence of three sensorimotor operations.
- *Execution* of the cup-grabbing event involves a very similar sequence.

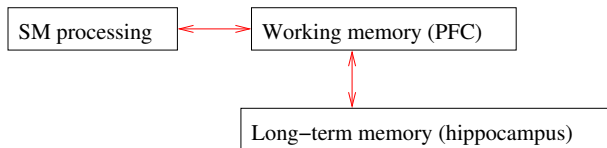
In Lecture 9 I argued that a cup-grabbing event is stored in working memory as a *prepared sequence*, which can be *internally simulated*.

# Today's lecture

In today's lecture, I'll talk about how the cup-grabbing event is stored in long-term (episodic) memory.

The basic idea:

- The event is first buffered in working memory, in **prefrontal cortex**.
- Then it's replayed to the **hippocampus**, which is involved in storing the event in episodic memory.



# Outline of today's lecture

- 1 Working memory and long-term memory: recap
- 2 The role of the hippocampus in episodic memory
- 3 The hippocampus as a memory for sequences
- 4 Encoding and retrieval of episodic memories
- 5 Summary

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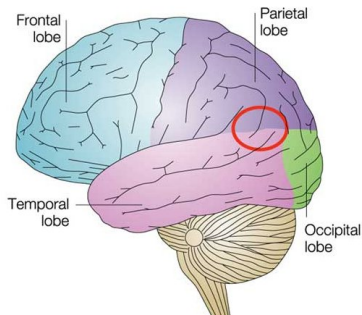
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# Working memory and long-term memory: recap

Recall the distinction between working memory (WM) and long-term memory (LTM).

The basic idea:

- WM involves **frontal cortex** and the temporoparietal junction.

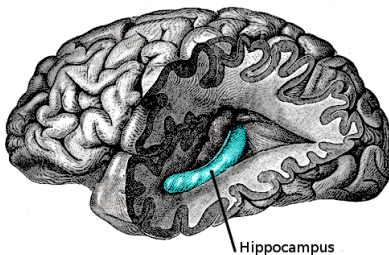


# Working memory and long-term memory: recap

Recall the distinction between working memory (WM) and long-term memory (LTM).

The basic idea:

- WM involves **frontal cortex** and the temporoparietal junction.
- LTM involves the **hippocampus**, and adjacent regions of temporal cortex.



# Working memory and long-term memory

Summary:

	WM	LTM
Duration	seconds/minutes	days/years
Stored in	frontal cortex/TP	hippocampus (→cortex)
Represented as	sounds/meanings	meanings
Implemented as	neural activity	synaptic strengths

# Episodic and semantic LTM

There are actually two forms of LTM.

**Episodic memory:** memory for specific episodes in an agent's life.

- E.g. 'Yesterday, John grabbed this cup here'.

**Semantic memory:** memory for generic facts.

- E.g. 'Cups tend to have handles'.

I'll be focussing on episodic memory.

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# Hippocampal and cortical LTM

The hippocampus is required to form new long-term memories.

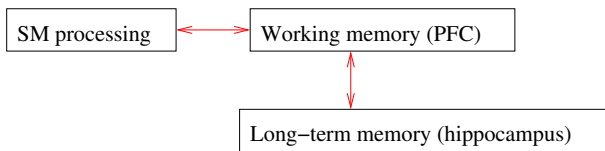
- Patient HM had surgery to remove both hippocampi (and associated cortical areas). He developed a very pure form of **anterograde amnesia**: he couldn't store episodes which happened *after surgery*. (Scoville and Milner, 1957).

Hippocampal damage is also associated with a degree of **retrograde amnesia**.

- E.g. HM couldn't remember episodes that occurred *shortly before* surgery.

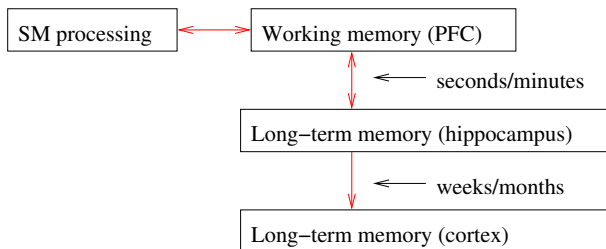
## Consolidation of hippocampal memories in cortex

An influential idea: the hippocampus creates new memories, which are progressively **consolidated** into more permanent storage in cortex (Marr, 1971; McClelland *et al.*, 1995).



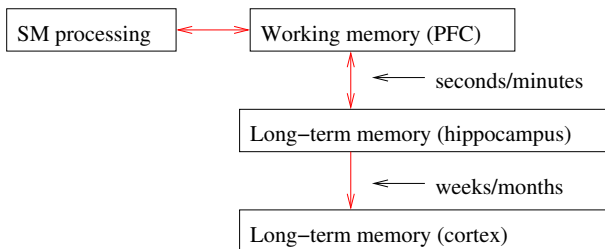
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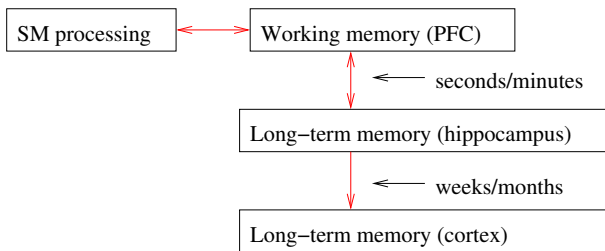
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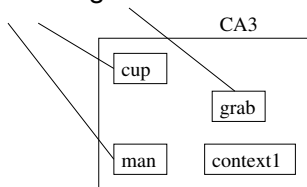


Anthony Robins has an account of how consolidation solves the **catastrophic forgetting problem**.

I'll focus on hippocampal (rather than cortical) LTM.

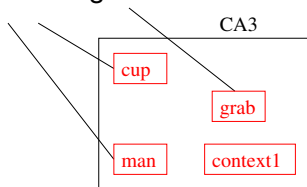
# The hippocampus as an autoassociative network

In Rolls and colleagues' model of the hippocampus, memories are stored in associations between representations originating from different SM modalities in a region called **CA3**.



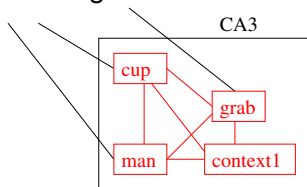
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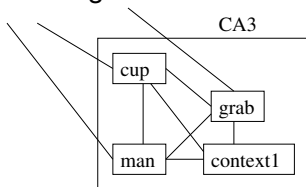
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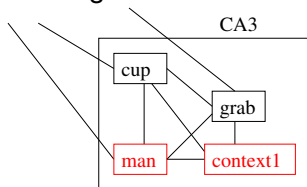
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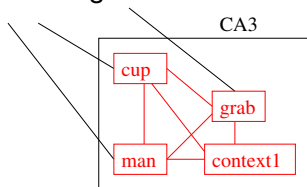
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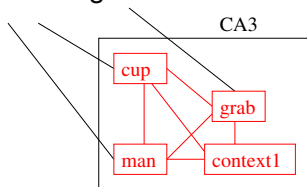
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Note:

- The hippocampus doesn't store object and event representations.
- It stores *associations* between representations held elsewhere in cortex.

# Representing contexts in the hippocampus

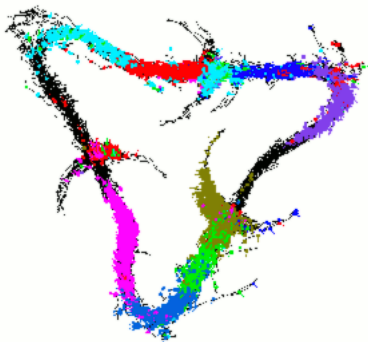
Episodic memories must be tied to specific spatiotemporal **contexts**.

It's known that one of the key functions of the hippocampus is in representing space.

- In most?/all? mammals, the hippocampus is used to represent the spatial structure of the local environment.
- The environment representation is stable over movements of the animal.
- Hippocampal **place cells** fire when the animal is in a particular place in the environment.

## Hippocampal place cells

Here's a diagram showing the activity of 7 different place cells in a rat running a triangular route. (Skaggs *et al.*, 1996)



The place cell circuit converts 'egocentric' sensory information into *environment-centred coordinates*.

# Spatiotemporal contexts

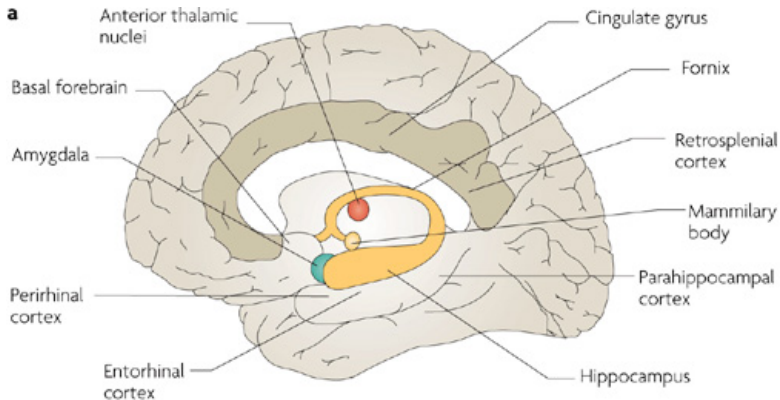
Animals store knowledge of the different spatial environments they encounter in the hippocampal region.

- Different environments are stored as different **spatial contexts**.
- Spatial contexts are probably stored in the **parahippocampal cortex** (see e.g. Eichenbaum *et al*, 2007).
- The activity of place cells depends partly on perception and partly on the active spatial context. (Evidence from the *remapping* of place cells when an animal moves to a new environment.)

Episodic memories involve associations between objects, actions and spatial contexts. (Probably temporal contexts too.)

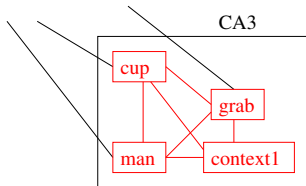
# Parahippocampal cortex

Parahippocampal cortex is part of the medial temporal cortex, adjacent to the hippocampus.



# Representing episodes in the hippocampus

There's a problem: how do we represent the *structure* of an episode?



- Who's the agent?
- Who's the patient?

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# Hippocampal memory traces as sequences

Suggestion: if the experience of an action is associated with a characteristic *sequence* of SM states, then perhaps the action can be encoded in episodic memory using this sequence.

- The first SM item is the 'agent'...
- The second SM item is the 'patient'...
- The third SM item is the 'action category'...

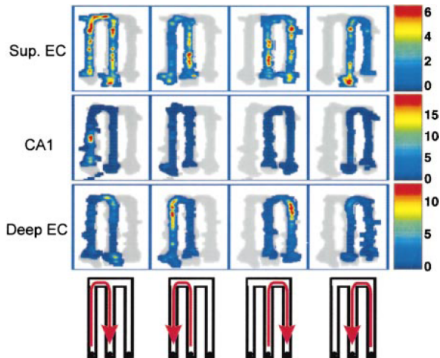
The idea that episodic memory is sequential is not new:

- Tulving (1983): episodes are *organised into sequences*.
- I'm proposing an additional level of granularity, where individual episodes are *also* organised as sequences.

# Evidence that the hippocampus stores sequences

## Evidence in rats:

- Frank *et al.* (2000): some hippocampal place cells encode 'trajectories', rather than single locations.



# Evidence that the hippocampus stores sequences

## Evidence in rats:

- Nàdasdy *et al.* (1999): sequences of hippocampal place cell activity which occur during waking experience tend to be **replayed** during sleep (at a much faster speed).
- Sequences of nonspatial stimuli are also stored in hippocampus (Fortin *et al.*, 2002; Kesner *et al.*, 2002).

## Evidence in humans:

- Hippocampal patients have impaired memory for sequences of words (Shimamura *et al.*, 1990) and faces (Holdstock *et al.*, 2005).
- Kumaran and Maguire (2006) fMRI study: hippocampal activity during sequence encoding correlates with later retrieval success.

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# Encoding and recall of episodic memories

What are the processes by which episodic memories are encoded and recalled?

- These processes are mainly cortical.
- PFC / working memory is heavily involved.

# Encoding of episodic memories

There is evidence that PFC is involved in the process of encoding episodic memories.

- Stimuli which are processed semantically are subsequently better recalled ( Craik and Lockhart, 1972). Semantic processing correlates with left PFC activity (Kapur *et al.*, 1994).
- PFC activity during encoding correlates with retrieval success (ERP data in Rugg, 1995; fMRI data in Rotte *et al.*, 2000).

# Encoding of episodic memories

One interesting model (Jensen and Lisman, 1996; Baddeley, 2000): episodic memories are first **buffered in working memory** before being replayed to hippocampus.

- Synapses in hippocampus are strengthened by **LTP**.
- LTP only occurs between cells active within 100ms of one another.
- 'Episodes' often take tens of seconds to be experienced. So there must be a buffering mechanism.

# Encoding of episodic memories

Interesting evidence from the **Hebb repetition effect (HRE)**.

Hebb (1961): gave subjects a series of digit sequences in an immediate serial recall task.

- There was a repeated sequence: e.g. XXXX, **4967**, XXXX, **4967**.
- ISR *gradually improved* for the repeated sequence.

Milner (1971): hippocampal patients don't show the HRE, suggesting that WM representations are gradually consolidated in hippocampus.

Burgess and Hitch (2005): HRE is unaffected by phon. similarity and articulatory suppression. (So the WM buffer interfacing with hippocampus probably isn't the phon. loop.) But it *is* affected by variations in chunking. So maybe the WM buffer is the 'episodic buffer'.

# Encoding of episodic memories

My suggestion: the episodic buffer in PFC holds a *planned SM sequence*, which can be *replayed* (fast) to the hippocampus.

Note: the PFC doesn't actually 'send information' to the hippocampus.

- Parahippocampal cortex evokes a context representation  $C1$ .
- PFC evokes a sequence of representations in sensory/motor cortex. E.g. *man, cup, grab*.
- The hippocampus learns the sequence:

*$C1, man, cup grab$* .

# LTM representations of objects

We also need to maintain representations of *objects* in LTM.

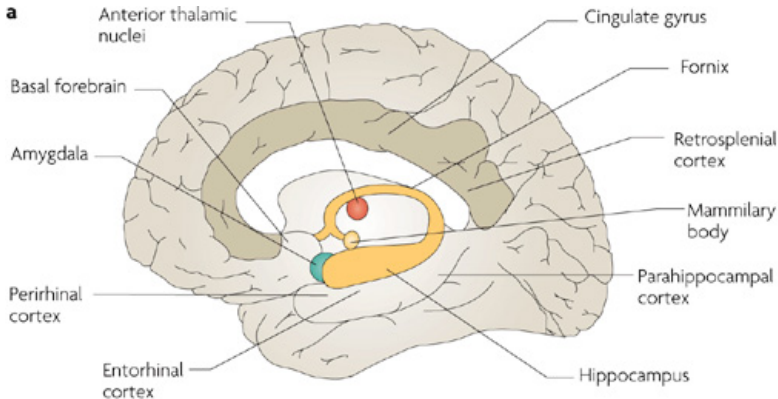
- We have memories of many *individuals*: e.g. people, pets, cars etc.
- There's an important difference between *categorising* an individual ('it's a dog!') and *recognising* it ('it's my dog Fido!').

There's evidence that individuals are stored in LTM in the **perirhinal cortex** (see e.g. Diana *et al.*, 2007).

- Perirhinal cortex is particularly involved in the encoding and identification of *familiar objects*.

# Perirhinal cortex

Perirhinal cortex is part of the medial temporal cortex, anterior to parahippocampal cortex.



# LTM object representations in episodic memory

An important thing about LTM individuals:

- They persist over time.
- A single individual can participate in many episodes.

Episodes stored in the hippocampus must refer to individuals, not just to types.

- The WM sequence which represents an episode activates WM representations of individuals.
- These **WM individuals** must activate **LTM individuals**, so that the hippocampus can store a sequence involving LTM individuals.

*LTM\_man1, LTM\_cup1, grab*

# Recall of episodic memories

Recall has three phases:

- **Cue creation**: creation of a memory cue
- **Retrieval**: presentation of the cue to the hippocampus
- **Post-retrieval**: monitoring of the hippocampus' response.

# Cue creation

PFC seems to be involved in the creation of memory cues.

- Gershberg and Shimamura (1995): frontal patients are generally worse at **recall** tasks than **recognition** tasks.
- Buckner *et al.* (1998): activity in PFC during recall correlates with retrieval *effort* rather than retrieval success.

Proposal:

- Memory cues are originally created in PFC-based WM, and then communicated to hippocampus.

Note: this echoes the story about the role of WM in episodic memory creation.

# A model of retrieval as rehearsal

A common suggestion: retrieving a memory involves 'reliving it' (see e.g. Tulving 1983; 2002).

Some evidence that the hippocampus reactivates SM representations:

- Hippocampus projects to a wide range of SM areas.  
Damasio & Damasio (1994): hippocampus is a **convergence zone**
- Burgess *et al.* (2000) fMRI study on humans: recall activates parietal cortex (holding allocentric SM representations)
- Ji and Wilson (2007) study on rats: fast replay of hippocampal place cell sequences during sleep coincided with replay of sequences of cells in *visual cortex*

# The retrieval phase

The retrieval operation is mainly a *control operation*, which activates certain interfaces and deactivates others.

- It must open a connection from PFC to hippocampus, to communicate the cue to the hippocampus.
- If retrieval is rehearsal, the retrieval operation must also establish a special **retrieval mode**, in which sensory cortices receive input from hippocampus rather than from the world.

Neural correlates of the retrieval operation?

- Several ERP studies find a short burst of activity in left parietal cortex occurring early in recall tasks (Allan *et al.*, 1998; Johansson & Mecklinger, 2003).

## The post-retrieval phase

During the post-retrieval phase, there are several types of activity:

- Hippocampal activity
- Re-evoked activity in sensory areas (see above)
- A late, sustained right frontal ERP signal, signalling PFC processing of the recalled material (Allan *et al.*; Johansson & Mecklinger)

What processing is PFC doing in the post-retrieval phase?

- If material recalled from hippocampus is mainly sensorimotor, maybe PFC needs to recompute an intentional representation.
- Suggestion: **PFC recreates a representation in the episodic buffer, similar to that created when an event is first experienced.**

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# Summary

- An event is *experienced* as a *SM sequence*.
- It is stored in *working memory* (in PFC) as a *planned SM sequence*.
- To store the event in *episodic memory*, the planned sequence is *replayed* to the hippocampus.
- The hippocampus also stores the event as a sequence.
- When the event is retrieved, the sequence is replayed from hippocampus, and a sequence plan is recreated in PFC, similar to the plan created when the event was experienced.

The process of *replaying a planned sequence to episodic memory* is the key process in the linguistic model I'll propose.

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# Replaying a planned sequence: timecourse of signals

Sustained PFC signal	Transient signals		
	Context signals	Action signals	Reafferent signals
$plan_{attend\_agent/attend\_cup/grasp}$ ↓ ↓	$C_1$	$attend\_agent$	$attending\_to\_agent$
$plan_{attend\_agent/attend\_cup/grasp}$ ↓ ↓	$C_2$	$attend\_cup$	$attending\_to\_cup$
$plan_{attend\_agent/attend\_cup/grasp}$ ↓ ↓	$C_3$	$grasp$	$attending\_to\_agent$
$plan_{attend\_agent/attend\_cup/grasp}$ ↓ ↓	$C_4$		$attending\_to\_cup$