A systems neuroscience approach to memory

- Critical brain structures for declarative memory
- Relational memory vs. item memory
- Recollection vs. familiarity
- Recall vs. recognition
- What about PDs?
- R-K paradigm
- Associative learning
- Why are lesion studies important?
Medial Temporal Lobe Structures

• Hippocampal formation
  – Dentate gyrus
  – Hippocampus
  – Subicular complex
  – Entorhinal cortex

• Perirhinal cortex
  – Receives input from visual association areas and from polymodal and nonvisual unimodal cortices

• Parahippocampal cortex
  – Receives input from visuospatial association areas and from DLPFC and retrosplenial cortex

• Amygdaloid complex
  – Receives a variety of sensory inputs
Does the hippocampus proper support mnemonic functions that are independent of those mediated by adjacent neocortical regions?

- Does recognition memory for individual items depend on the hippocampus?  OR

- Does the hippocampus play a specialized role in the recollection of inter-item associations (relational memory), while memory for individual items (and intra-item features) is mediated by adjacent cortical regions (perirhinal, parahippocampal cortices)
Is there a dissociation of function within the MTL?

- **Logic**: If all MTL structures contribute equally to all forms of declarative learning, then amnesic patients with MTL lesions should show similar magnitudes of impairment across a range of declarative memory tasks.

- **Evidence**: Under certain encoding and retrieval conditions, amnesic patients show surprisingly good recognition memory coupled with poor recall ability.
H.M. showed normal forced-choice recognition up to 1 week after encoding.
Even 6 mo. after learning, H.M. performed within 1 SD of CON Freed, Corkin & Cohen, 1987
6 mo. recognition aided by attention to novelty

Freed, Corkin & Cohen, 1987
In contrast, H.M.’s ability to recall items (or item locations) is at chance
What brain areas support this unexpected learning?
Dual-process Theory

Recognition

Recollection
“I Remember”
- Item-Item
- Item-Context

Item-Context
- perirhinal cortex
- hippocampus

Familiarity
“T Know”
- Item

- parahippocampal cortex
Recall vs. recognition
Direct comparisons between recall and recognition are hard to make

• Why?
  – Because the two memory measures often are not matched in difficulty (recognition is easier than recall)
  – They always differ in their scales of measurement

• How do researchers circumvent these problems?

• Equate amnesic patients and CON on recognition memory performance, and then assess whether, under condition of equated recognition, recall performance is also matched

• The results from several such studies were inconsistent, but Giovanelli & Verfaillie (2001) shed light on at least part of the reason for the inconsistencies
Experiment 1

- Compared recall and recognition performance of AMN and CON
- Matched AMN recognition to CON recognition by giving AMN additional study exposures (6 vs 1)
- Study-test interval 1 min
- Reasoned that recognition and familiarity would contribute to recognition performance of CON, but AMN’s recognition performance would be mediated primarily by familiarity
- Thus, even though the use of multiple learning trials may equate the recognition performance of AMN and CON, it does not equate the processes that mediate such performance.
- The fact that recollection makes a greater contribution to the performance of CON than to the performance of AMN leads to the prediction that despite equated recognition memory, AMN’s recall performance will be worse than that of CON

Giovanello & Verfaellie, 2001
Mean recall and recognition scores of AMN and CON in Experiment 1

- The dissociation between AMN’s recall and recognition performance is inconsistent with the view that AMN have a uniform disruption in all processes that support explicit memory (Squire, 1992)
- Instead, it lends support to the notion that AMN show a relative preservation of familiarity, a process that can support recognition but not recall (Giovanello & Verfaellie, 2001)
Experiment 2

• Compared recall and recognition performance of AMN and CON
• Matched AMN recognition to CON recognition by testing AMN after a 1-min delay and CON after a 24-hr delay
• AMN completed all testing in 1 session
• CON tested on 3 consecutive days
  – Day 1: studied a word list
  – Day 2: performed recall task and studied a different word list
  – Day 3: performed recognition task
• As the study-test delay increases, recollection declines more rapidly than familiarity (Gardiner & Java, 1991)
• Thus, when CON are tested after a delay, their recollection is likely to be impoverished, just as is the case in AMN
• Because the performance of both groups would be mediated primarily by familiarity, Giovanello & Verfaellie (2001) predicted that once recognition was equated, recall performance would be equated as well
Mean recall and recognition scores of AMN and CON in Experiment 2

- Recognition accuracy was successfully matched between the 2 groups.
- AMN recall was not significantly different from CON.
- Testing CON after a delay renders them functionally amnesic.
- Because of the decline in recollection associated with testing after a delay, the performance of CON, like that of AMN, is primarily mediated by familiarity, thus masking the AMN’s deficit in recollection.  

Giovanello & Verfaellie, 2001
Conclusions

• The relation between AMN’s recall and recognition performance depends on the method by which AMN’s recognition is matched to CON’s recognition
• This finding does not imply that one method of equating is better than another
• Which method is selected depends on the goals of a particular study
• The contribution of familiarity and recollection differed across experiments
  – In Exp 1, recollection made a larger contribution to the performance of CON than to that of AMN; recall in the CON exceeded that in the AMN group
  – In Exp 2, the performance of both groups was supported largely by familiarity; recall performance was equivalent across both groups

Giovanello & Verfaellie, 2001
What about PDs?

• If PDs are impaired on familiarity but not recollection, then the following predictions should be upheld:

• Procedure 1: study-test interval 1 min
  – Recall (recollection): PD=CON
  – Recognition (recollection makes a larger contribution than familiarity): PD=CON

• Procedure 2: study-test interval 24 hr
  – Recall (recollection): PD=CON
  – Recognition (supported largely by familiarity): PD<CON
Remember-know paradigm
Gardiner & Java, 1991
Response probability as a function of retention interval

Response Probability as a Function of Retention Interval in Experiment-1

<table>
<thead>
<tr>
<th>Retention Interval</th>
<th>Target Words</th>
<th>Lures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&quot;Remember&quot;</td>
<td>&quot;Know&quot;</td>
</tr>
<tr>
<td>10 min</td>
<td>.49</td>
<td>.26</td>
</tr>
<tr>
<td>1 hr</td>
<td>.42</td>
<td>.24</td>
</tr>
<tr>
<td>1 day</td>
<td>.27</td>
<td>.27</td>
</tr>
<tr>
<td>1 week</td>
<td>.25</td>
<td>.23</td>
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</tbody>
</table>

Over retention interval, the mean proportion of correct “remember” responses declined sharply, but the mean proportion of correct “know” responses showed little change “Know” responses to lures exceeded “remember” responses to lures (FA) Recognition w/out recollective experience persists for at least 1 week, but recognition w/out recollective experience declines sharply.

Response Probability as a Function of Retention Interval in Experiment-2

<table>
<thead>
<tr>
<th>Retention Interval</th>
<th>Target Words</th>
<th>Lures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&quot;Remember&quot;</td>
<td>&quot;Know&quot;</td>
</tr>
<tr>
<td>1 week</td>
<td>.24</td>
<td>.25</td>
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<tr>
<td>4 weeks</td>
<td>.19</td>
<td>.21</td>
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<tr>
<td>6 months</td>
<td>.15</td>
<td>.17</td>
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</tbody>
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Broadly similar pattern for “remember” and “know” responses (unlike Exp 1) Although performance was low at 6 months, “remember” and “know” responses to target words exceeded those to lures No tendency for FA rates to increase systematically Recognition w/ recollective experience and recognition w/out recollective experience persist for at least 6 months.

Figure by MIT OCW.
Response probability as a function of log hours

**Left side:** classic forgetting functions

**Right side:** recognition memory w/ recollective experience and recognition memory w/out recollective experience have different forgetting rates up to 24 hr

*Gardiner & Java, 1991*
Evidence using the R-K paradigm suggests that the familiarity-based contribution to recognition memory performance is preserved in AMN, whereas the recollective-based component is drastically impaired (e.g., Aggleton et al., 2005)
What’s wrong with the remember-know procedure?

• Recollection is categorical, but familiarity is continuous
• The method relies on participants’ subjective reports
• How do we know that YA and OA interpret “remember” and “know” responses the same way? Or OAs and PDs?
• Is the sense of remembering qualitatively similar for the two groups being compared?
• When a participant endorses an item as “remembered,” it is not clear what types of info the participant has retrieved
• A “remember” response can signify retrieval of info ranging from a variety of contextual elements (e.g., remembering a feeling elicited by the stimulus, or remembering the item that preceded the stimulus) to memory for the exact features of the stimulus (e.g., remembering the font in which the word was written)
• It is likely that memory for these different types of information is supported by different processes
To circumvent these issues, researchers have adopted paradigms that require recognition confidence judgments (e.g., Ranganath et al.) and paradigms that more directly compare memory for associations or relations with memory for isolated items (e.g., Hockley & Consoli; Giovanello, Verfaellie & Keane; and Davachi & Wagner).
Lesion studies

- Neuroimaging studies cannot speak to the necessity of particular brain regions for specific memory functions.
- To fill this void, several studies have investigated the degree to which lesion locus or extent affects the likelihood that AMNs are impaired specifically on the recollective or associative components of a memory task.
- If the hippocampal formation is disproportionately engaged during recollective or associative processing, compared to familiarity-based processing, then AMN patients with damage limited to the hippocampus should show a relative sparing of item recognition relative to associative recognition (e.g., Vargha-Khadem et al., 1997; Mayes et al., 2004).