

Ch 8. Learning and Memory

Cognitive Neuroscience: The Biology of the Mind, 3rd Ed.,
M. S. Gazzaniga, R. B. Ivry, and G. R. Mangun, Norton, 2008.

Summarized by

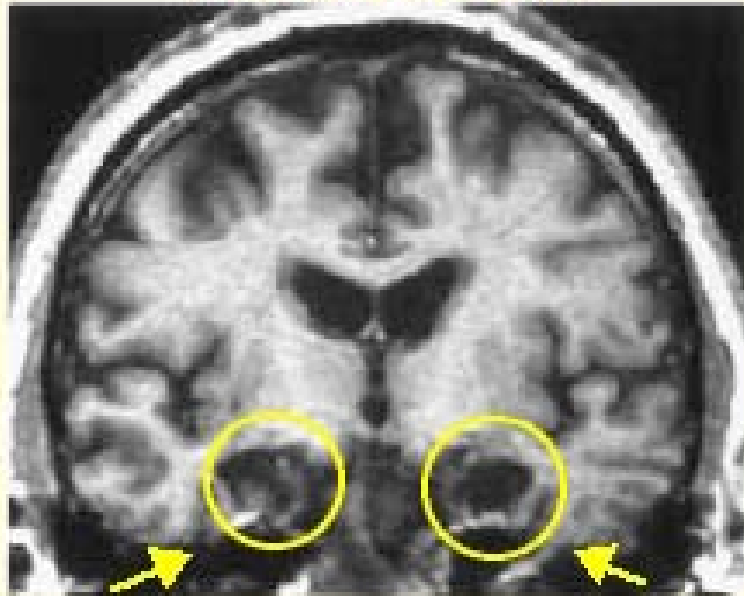
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Introduction – H.M.

MRI scan of "H.M."



NOTE THE RESULTS OF HIS BILATERAL
MEDIAL TEMPORAL LOBE RESECTION AND
THE REMOVAL OF THE HIPPOCAMPUS

- Epileptic patient
- Temporal lobectomy
→ “Amnesia”

Contents

- Theories of Learning and Memory
 - ◆ Sensory, short-term and long-term memory mechanisms
- Memory and brain
- Cellular bases of learning & memory

Theories of Memory

- ◆ Sensory and short-term memory mechanisms
- ◆ Models of short-term memory
- ◆ Models of long-term memory
- ◆ Summary of memory models

Theories of Memory

- **Learning**

- ◆ The process of acquiring new information
- ◆ Learning happens when a memory is created or is strengthened by repetition .

- **Memory**

- ◆ Persistence of learning in a state that can be revealed at a later time

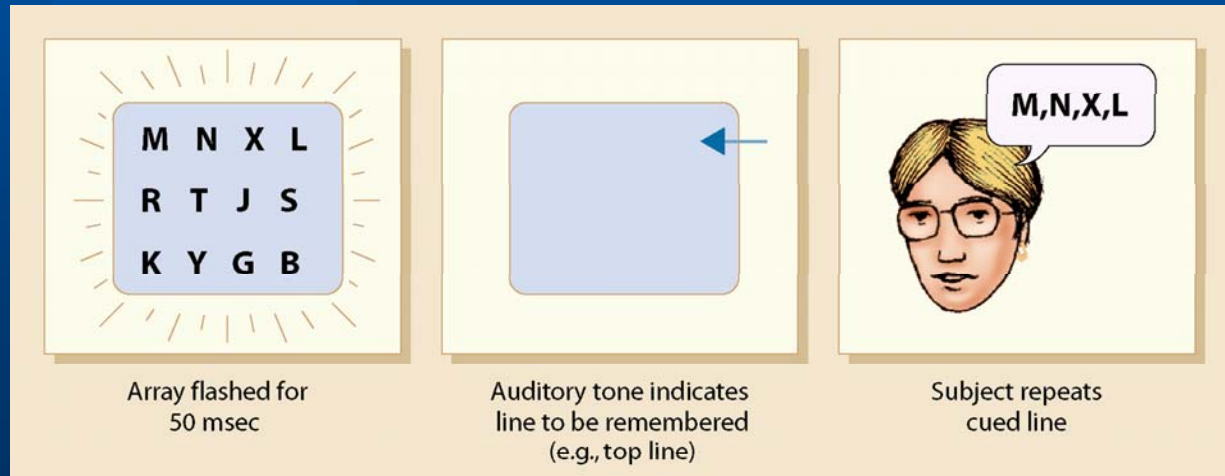
- **Encoding**

- ◆ Processing of incoming information to be stored
- ◆ **Acquisition** registers inputs in sensory buffers and sensory analysis stages.
- ◆ **Consolidation** creates a stronger representation over time.
- ◆ **Storage** creates and maintains a permanent record.
- ◆ **Retrieval** utilizes stored information to create a conscious representation.

Sensory and short-term memory mechanisms

/Sensory memory

- Sensory memory
 - ◆ Decaying relatively swiftly
 - ◆ Partial report
 - ◆ Echoic memory: audition
 - ◆ Iconic memory: vision



Partial report experiment

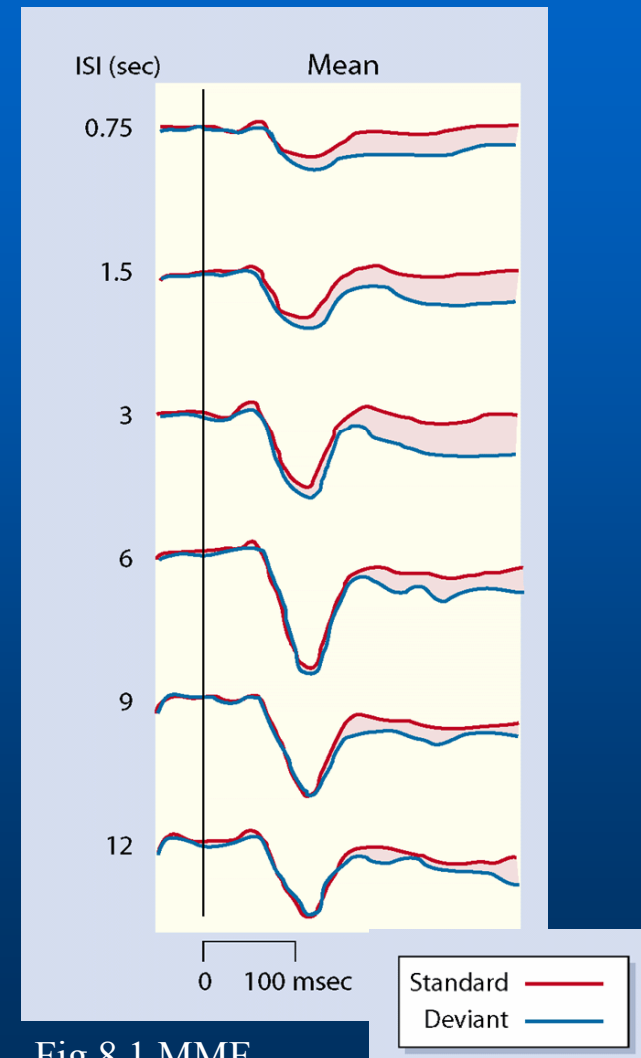
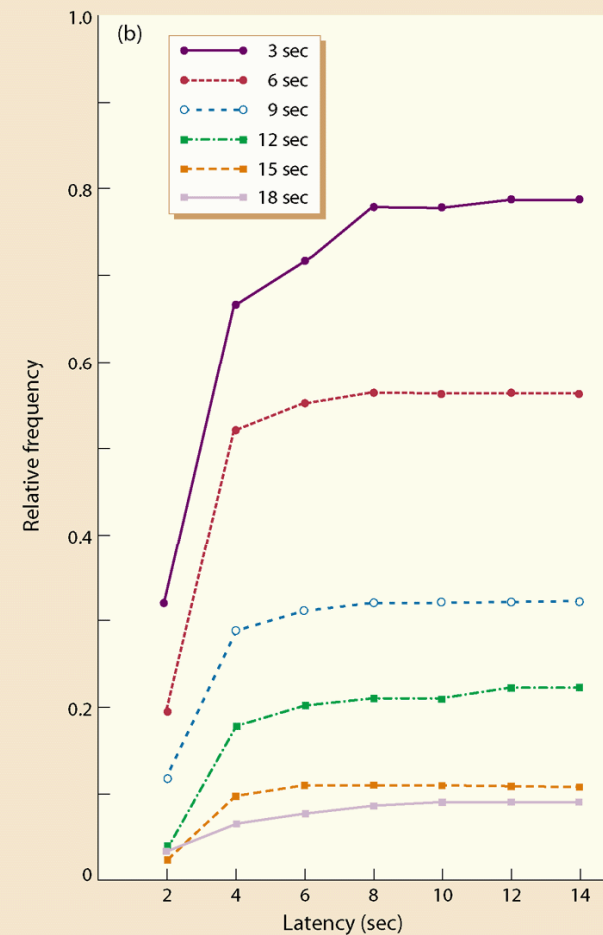


Fig 8.1 MMF

Sensory and short-term memory mechanisms / Short-term memory (1/2)

- Limited capacity
- Seconds ~ minutes



Short-term retention of verbal items

Sensory and short-term memory mechanisms / Short-term memory (2/2)

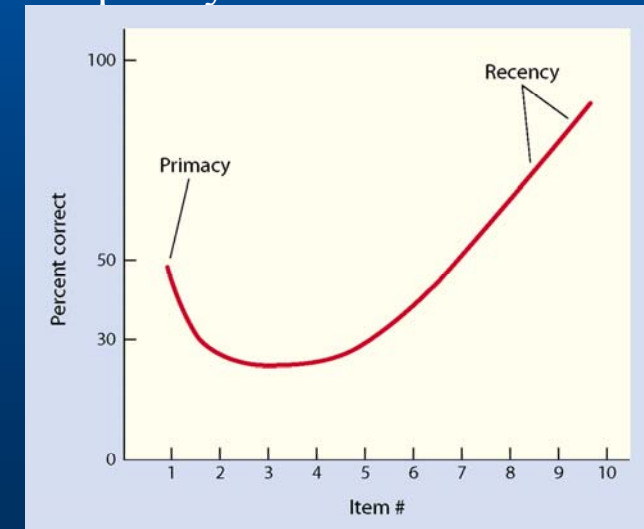
- Serial position effect

- ◆ Primacy effect

- At the beginning of the list
- Enough capacity to transfer from short- to long-term memory
- Unchanged by adding a distracting task at the end of the list
- Eliminated if the list items were presented more quickly

- ◆ Recency effect

- At the end of the list
- Available in short-term memory



Serial position effect

Models of short-term memory

/Modal model

- The Atkinson and Shiffrin modal model of memory. Sensory information enters the information-processing system and is first stored in a sensory register. Items that are selected via attentional processes are then moved into short-term storage. With rehearsal, the item can move from short-term to long-term storage

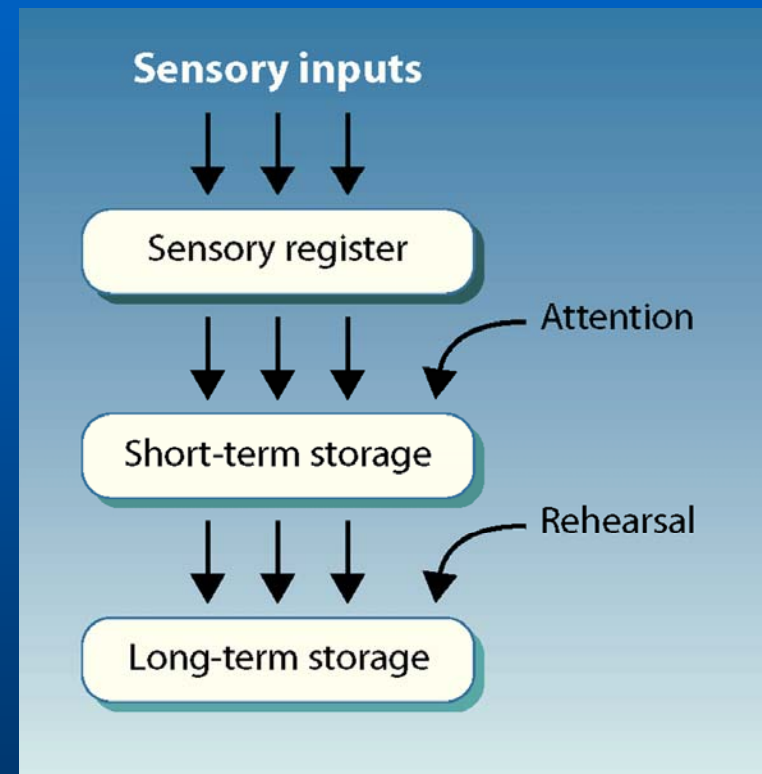


Fig 8.2 Modal model of memory

Models of short-term memory /Levels of processing models

- Levels of processing model
 - ◆ The deeper (more meaningful) an item was processed, the more it was consolidated and stored in long-term memory
 - ◆ Experiments by Fergus Craik and Robert Lockhart (1972)
 - Superficial level: whether the words were composed of uppercase or lowercase letters
 - Intermediate level: whether a word rhymed with another word
 - Deep level: making a judgment about the meaning of the word
 - Subjects showed better subsequent memory for items more deeply processed during learning
 - ◆ Deep or elaborate rehearsal and encoding create meaning-based codes that relate information directly to previously acquired knowledge

Models of short-term memory

/Neuropsychological evidence against the modal model of memory

- Evidences against the modal model
 - ◆ The patient who displayed reduced digit span ability still retained the ability to form new long-term memories
 - ◆ A patient E. E. showed below-normal short-term memory ability but preserved long-term memory
 - ◆ Information from sensory memory registers can be encoded into long-term memory directly

Models of short-term memory

/Working memory models

- A limited-capacity store for retaining information over the short term and for performing mental operations on the contents of this store
- Three-part working memory
 - ◆ The central executive mechanism
 - ◆ The phonological loop
 - ◆ The visuospatial sketchpad

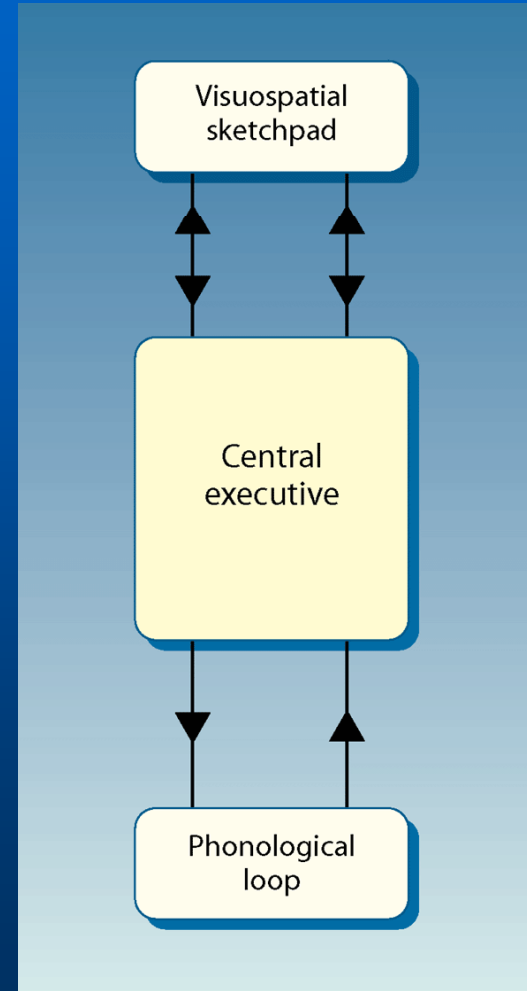


Fig 8.4 Working memory model

Models of long-term memory

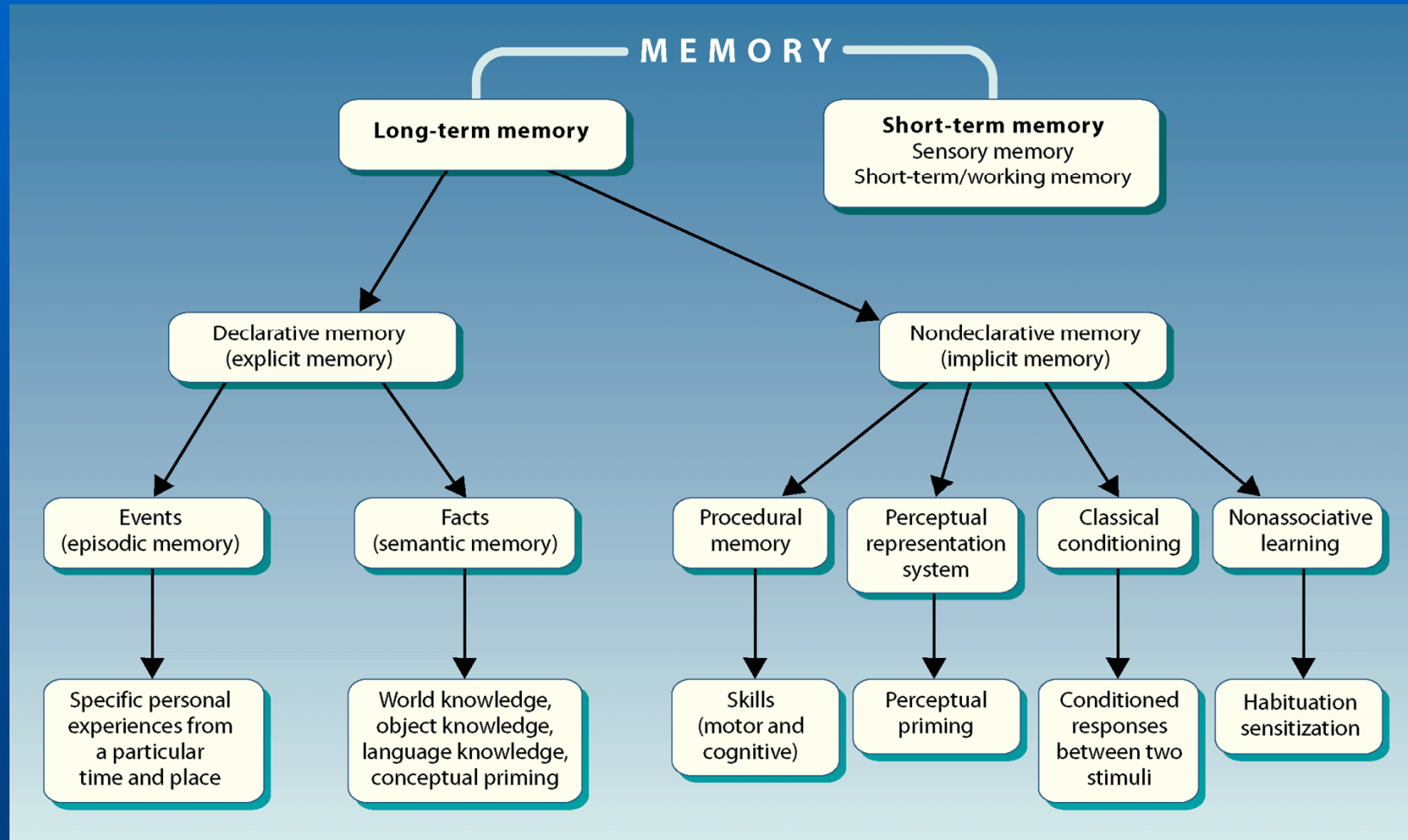


Fig 8.7 The hypothesized structure of human memory

Memory & Brain

- ◆ Human memory, brain damage, and amnesia
- ◆ Animal models of memory and the medial temporal lobe
- ◆ Imaging the human brain and memory

Human memory, brain damage, and amnesia

/Brain surgery and memory loss (1/3)

- Neurosurgical procedures
 - ◆ Prefrontal lobotomy: removing or disconnecting the prefrontal lobe
 - ◆ Corpus callosotomy: surgically sectioning the corpus callosum
 - ◆ Amygdalotomies: removing the amygdala
 - ◆ Temporal lobe resection: removal of the temporal lobe

Human memory, brain damage, and amnesia

/Brain surgery and memory loss(2/3)

- Patient H.M.
 - ◆ Bilateral medial temporal lobe resection developed dense amnesia
 - ◆ Normal short-term memory, normal digit span abilities
 - ◆ What appeared to be disrupted was the transfer of information from short-term storage to long-term memory

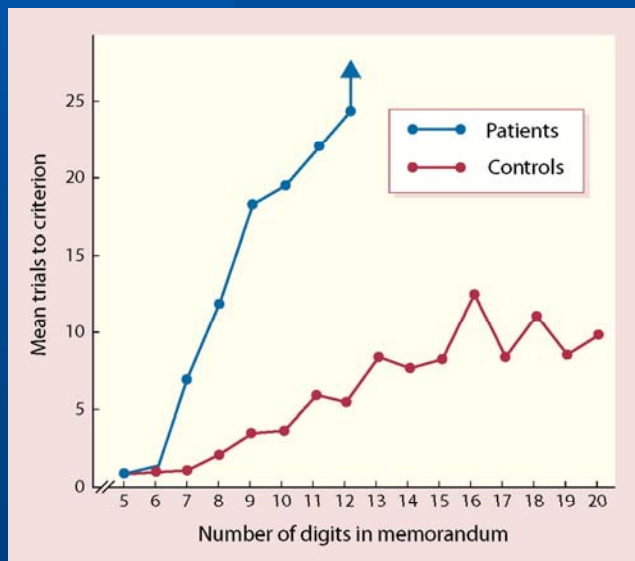


Fig 8.10 Digit span for amnesic patients

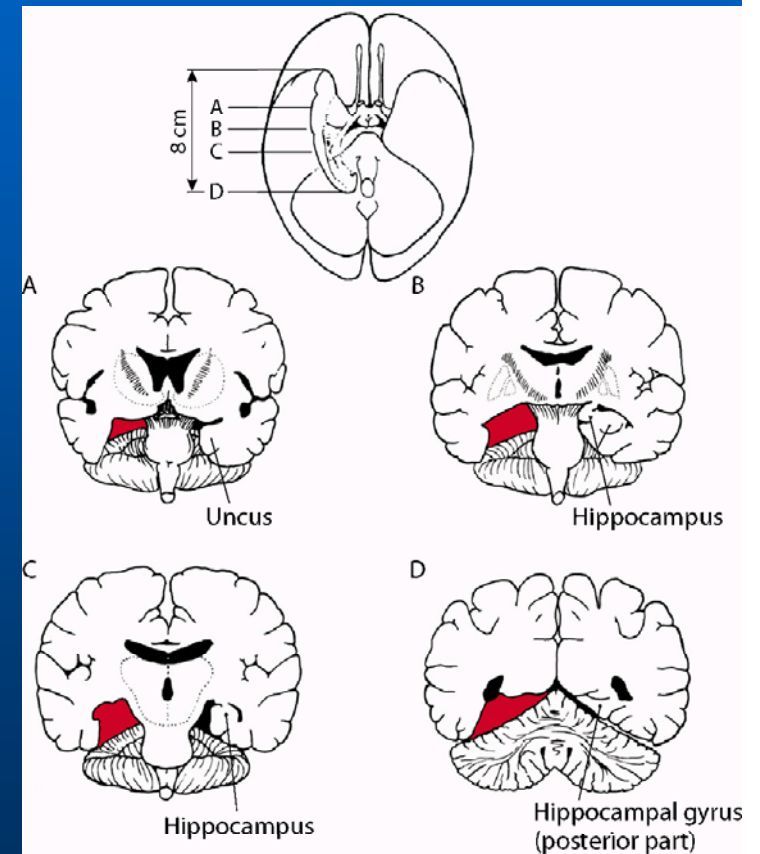


Fig 8.11 The medial temporal lobe & areas believed to have been removed from H.M.

Human memory, brain damage, and amnesia / Brain surgery and memory loss (3/3)

- A patient R.B.
 - ◆ Specific lesion restricted to CA1
 - ◆ Hippocampus is crucial in forming new long-term memories.

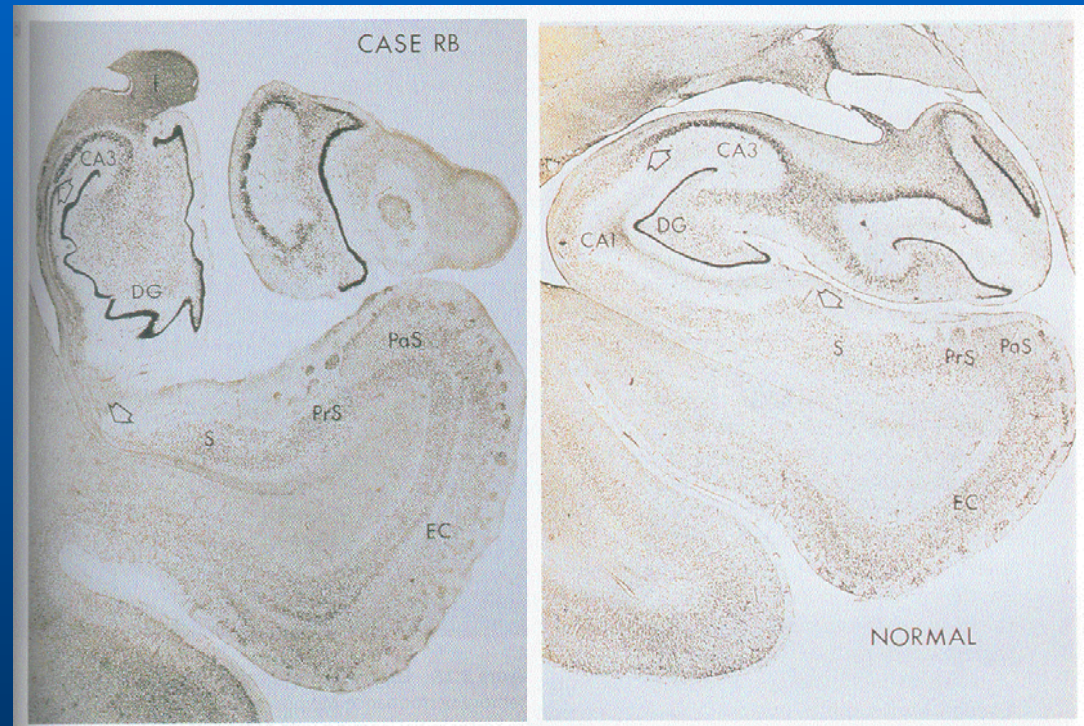


Fig 8.14 Section of brain from R.B. & normal

Human memory, brain damage, and amnesia

/Memory consolidation and the hippocampus

- Memory consolidation
 - ◆ memories are solidified in long-term stores over long-term period
- The hippocampal region is critical for the consolidation of information in long-term memory
 - ◆ Evidence: amnesics have retrograde amnesia for memories from one to a few years prior to the damage to the medial temporal lobe or diencephalon, a pattern that does not support a storage role but rather a role in consolidation
 - ◆ Consolidation strengthens the associations between multiple stimulus inputs and activations of previously stored information
 - ◆ Once consolidation is complete, the hippocampus is no longer required for storage or retrieval

Human memory, brain damage, and amnesia

/Anterior and lateral temporal lobes and memory

- Lesions that damage the lateral cortex of the anterior temporal lobe lead to a dense amnesia that includes severe retrograde amnesia
- The lateral and anterior regions of the temporal lobe: the sites of storage of long-term declarative memories or regions for retrieval of information from long-term stores

Human memory, brain damage, and amnesia

/Amnesics can learn new information (1/2)

- Medial temporal lobe damage generally is associated with the inability to learn new information
- Is it true that damage to the medial temporal lobe memory systems affects both episodic and semantic memory?
- Amnesic's learning of new information includes semantic knowledge

Human memory, brain damage, and amnesia

/Amnesics can learn new information (2/2)

- Patient K. C.
 - ◆ His retrograde amnesia involved episodic information from his entire life
 - ◆ Intact semantic memory for general world knowledge
 - ◆ K. C. demonstrated perceptual priming effects & procedural learning.

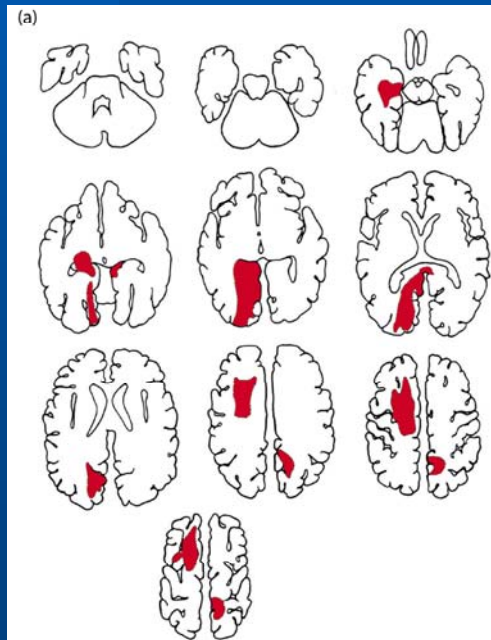


Fig 8.19 K.C.'s major lesions

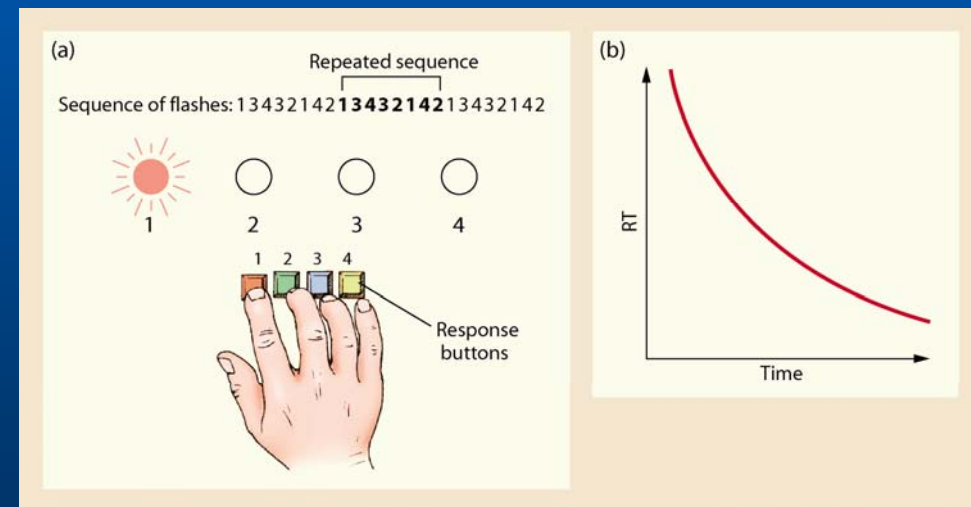


Fig 8.21 procedural learning of sequences

Human memory, brain damage, and amnesia

/Deficits in forming new nondeclarative memories

- The dissociations in what amnestics can learn indicate that distinct neural systems mediate different forms of memory
 - ◆ One alternative interpretation: the differential demands that different types of knowledge place on a single cognitive-neural memory system
 - Declarative memory is more cognitively demanding and thus is first affected by partial damage to a hypothesized unitary memory system
 - ◆ Double associations are the strongest evidence for two separate systems

Human memory, brain damage, and amnesia

/The perceptual representation system (PRS) (1/3)

- Subjects are shown lists of words and then wait varying amounts of time to perform a fragment completion task. Tulving and Schacter (1990) showed that subjects are better at completing fragments of words that were previously shown to them.

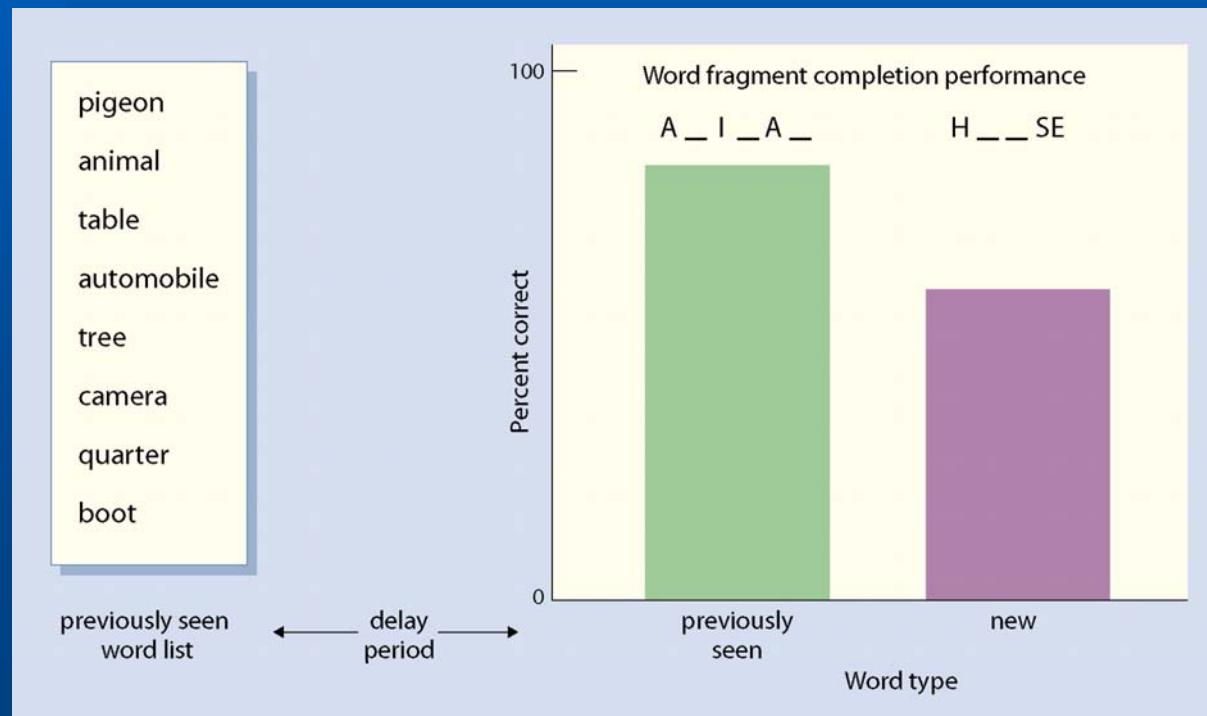


Fig 8.22 A typical word-priming study

Human memory, brain damage, and amnesia

/The perceptual representation system (PRS) (2/3)

- Information is remembered better on recall or recognition tests if it is processed more deeply during encoding
 - ◆ Subjects complete fragments of words and perform better with words previously viewed even without explicitly recognizing them
 - ◆ When the initial words are presented auditorily, and then perform the implicit tests visually, priming from auditory to visual is reduced for the implicit tests
 - ◆ Implicit memory in priming reflects a PRS that subserves structural, visual, and auditory word form representations

Human memory, brain damage, and amnesia

/The perceptual representation system (PRS) (3/3)

- Possible and impossible objects
 - ◆ Subjects were better at deciding on objects previously viewed
 - This occurred only for possible objects, and only when subjects were instructed to pay attention to the global form of the stimulus at the time of encoding
- The PRS apparently mediates word and nonword forms of priming, and so implicit memory of this type is not based on conceptual systems but rather is perceptual in nature
- Patient M. S.
 - ◆ Removing most of areas 18 and 19 of his right occipital lobe<그림 8.23>
 - ◆ Explicit tests of memory (recognition and cued recall) and implicit memory (perceptual priming)
 - ◆ The test materials were words presented briefly and then read aloud
 - ◆ The amnesic patients displayed the expected impairment of explicit word recognition, but they did not show impairment in the implicit perceptual priming
 - ◆ M. S. had the novel pattern of normal performance on explicit recognition but impairment in the implicit perceptual priming test

Animal models of memory

- What structures of the medial temporal lobe systems are involved in episodic memory?

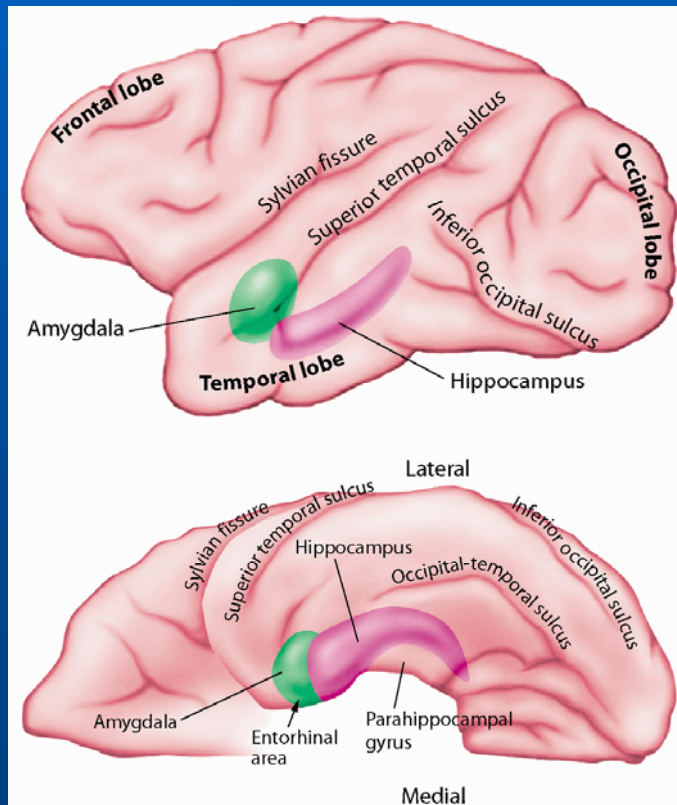


Fig 8.25 Gross anatomy of the medial temporal lobe

- Delayed non-matching to sample task

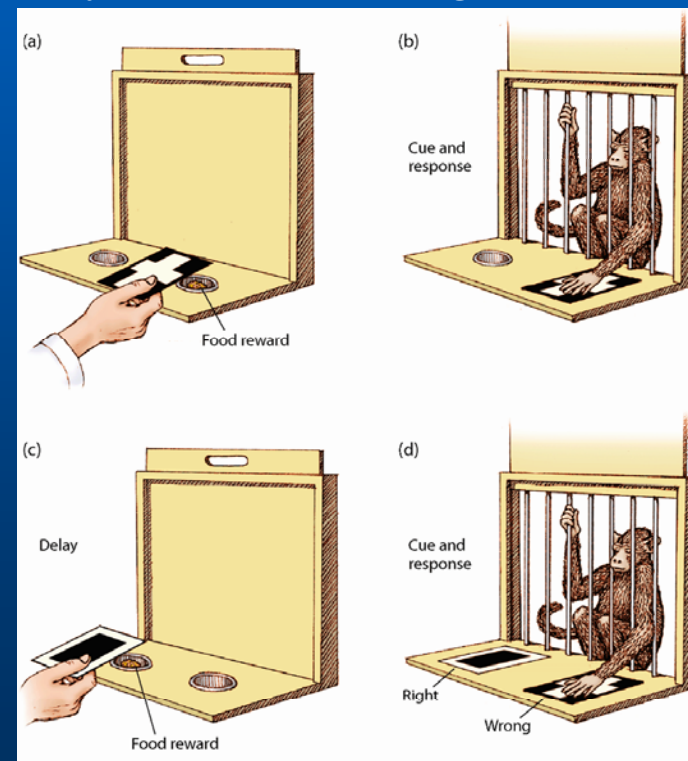


Fig 8.24 Delayed nonmatch-to sample task

Animal models of memory

- Delayed nonmatching to sample task
 - ◆ Memory was impaired only if the lesion included the hippocampus and amygdala
 - ◆ The presence or absence of the amygdala lesion did not affect the monkey's memory → the amygdala could not be part of the system that supports the acquisition of long-term memory

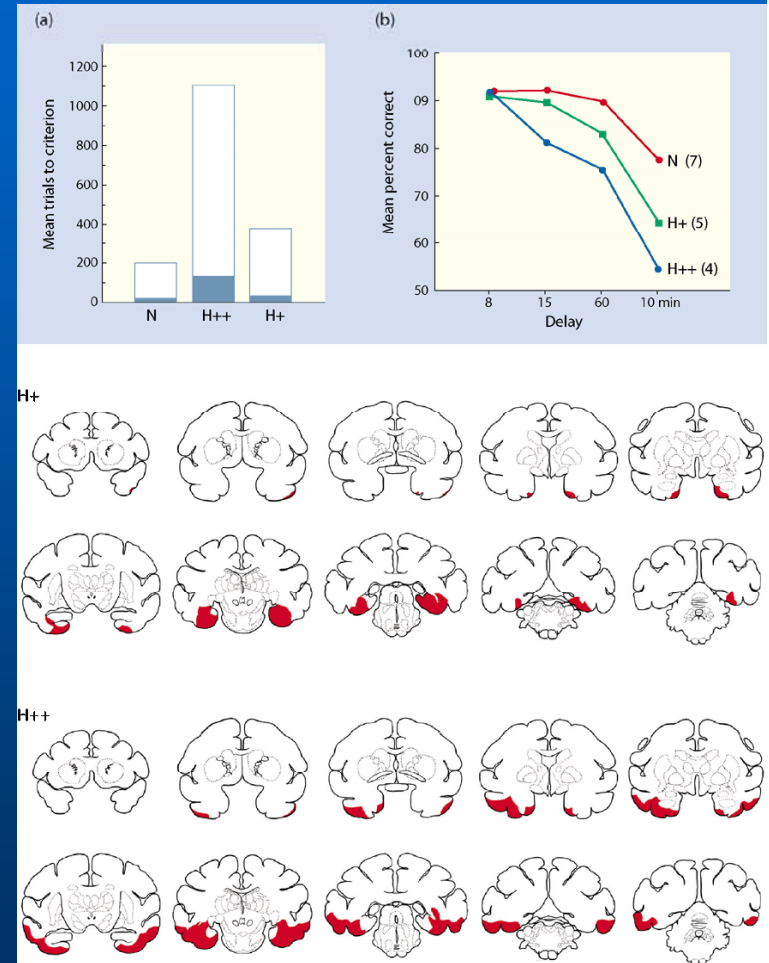


Fig 8.27 The delayed nonmatching for normal monkey vs. monkeys with lesions

Animal models of memory

- The hippocampus cannot function properly if the parahippocampal and perihinal regions are damaged
- These regions are involved in much processing themselves
- Lesions restricted to the hippocampus do not produce as severe a form of amnesia as do lesions that include surrounding cortex

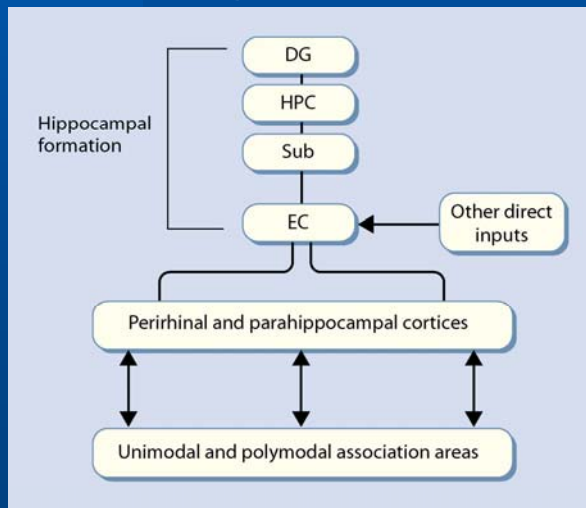


Fig 8.26 Flow of information between the neocortex and the hippocampus system

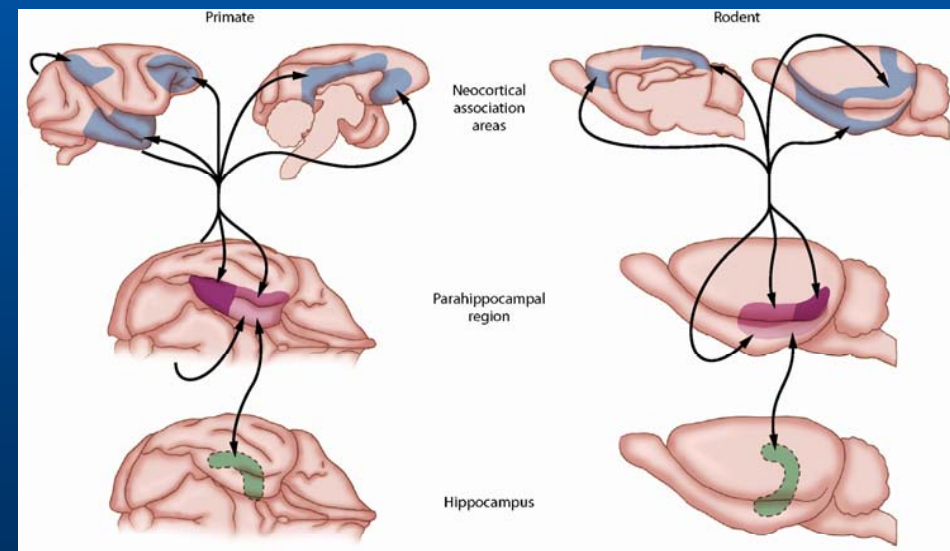


Fig 8.28 Anatomy of the hippocampal memory system in monkeys and rats

Imaging the human brain and memory

/Episodic encoding and retrieval (1/3)

- Whether the hippocampus becomes active when encoding new information
 - ◆ The right hippocampal region was activated during encoding of the face but not during recognition, where retrieval processes should have been engaged
 - ◆ Encoding also activated the left prefrontal cortex, whereas recognition activated the right prefrontal cortex
 - ◆ When subjects were asked to perform a retrieval task for episodic memories, the right, not the left, hemisphere was activated
- The left prefrontal region and hippocampal region were active during the intentional encoding of information, whereas the right prefrontal region was activated during episodic retrieval

Imaging the human brain and memory /Episodic encoding and retrieval (2/3)

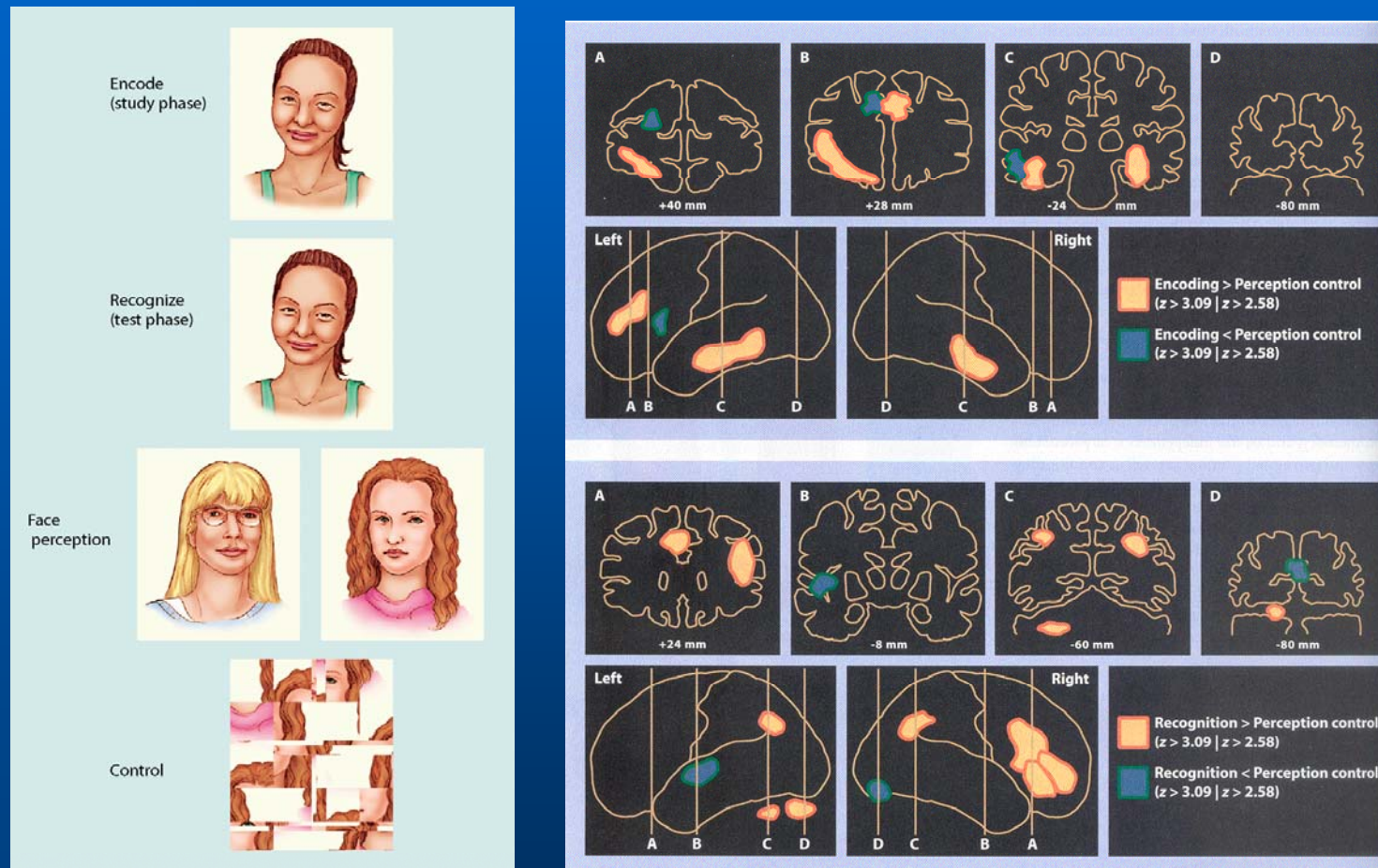


Fig 8.30-31 A PET study of encoding and retrieval of face information

Imaging the human brain and memory /Episodic encoding and retrieval (3/3)

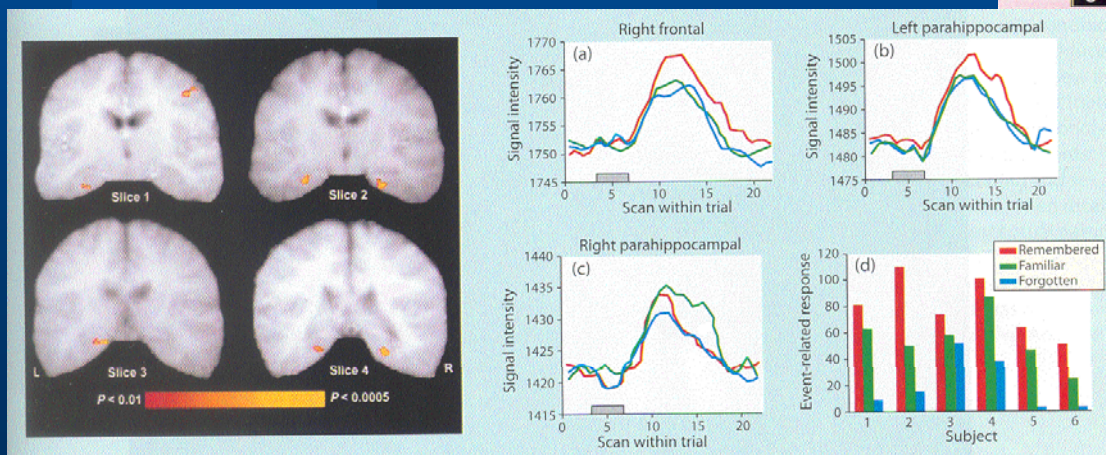
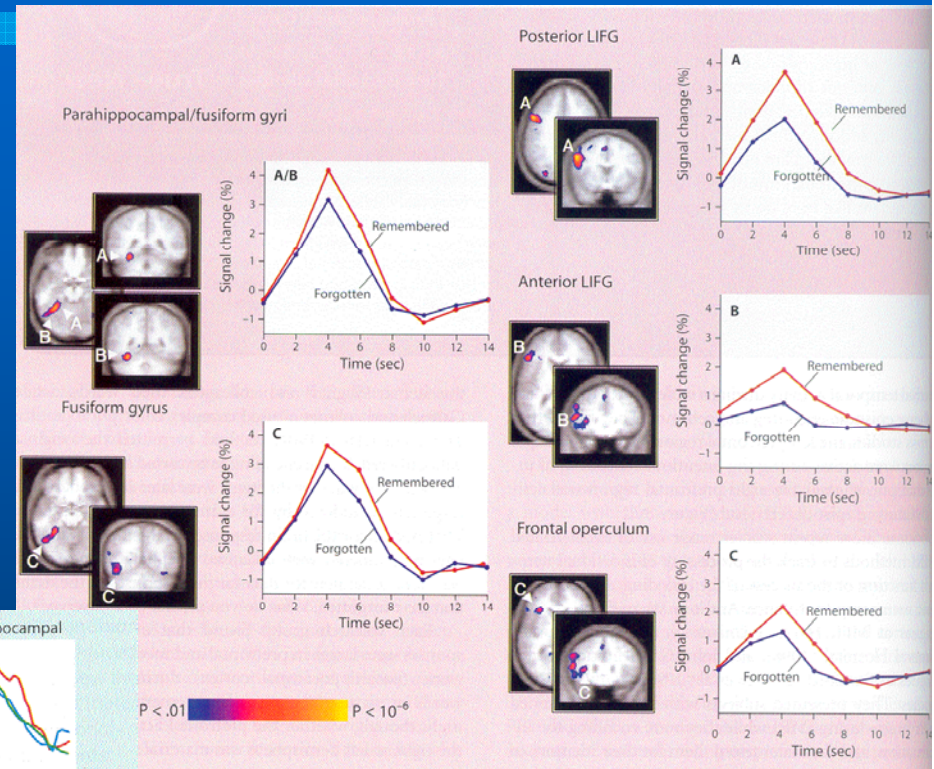
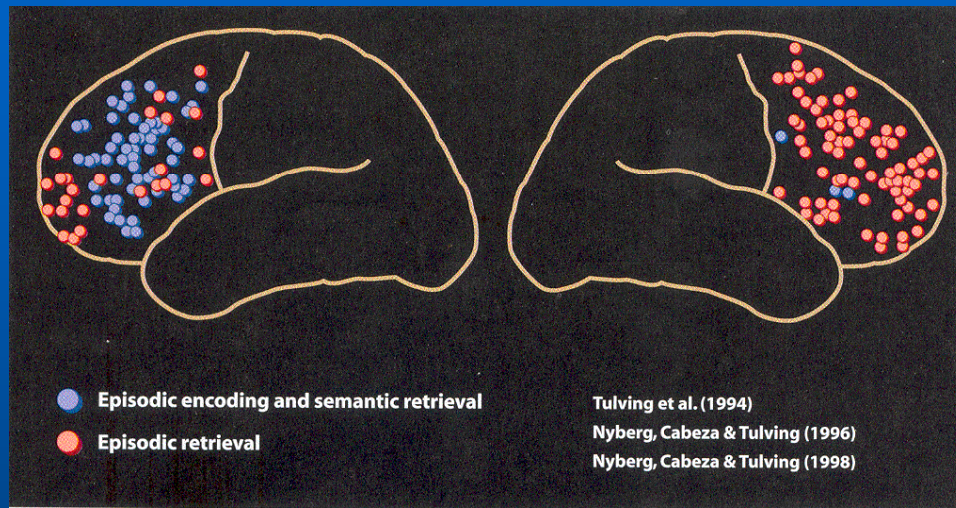


Fig 8.36 and extra
Brain imaging :
Brain activation
by episodic encoding & retrieval

Imaging the human brain and memory

/Procedural memory encoding and retrieval

● Experiment

- ◆ The subjects responded to stimulus sequences by pushing a button with their right hand while monitoring a sequence of tones and counting those of lower frequency
- ◆ Activated region: the motor cortex, the supplementary motor area of the left hemisphere, the putamen in the basal ganglia bilaterally, the rostral prefrontal cortex, and parietal cortex
- ◆ When the auditory task was removed: the right dorsolateral prefrontal cortex, right premotor cortex, right putamen, and parieto-occipital cortex

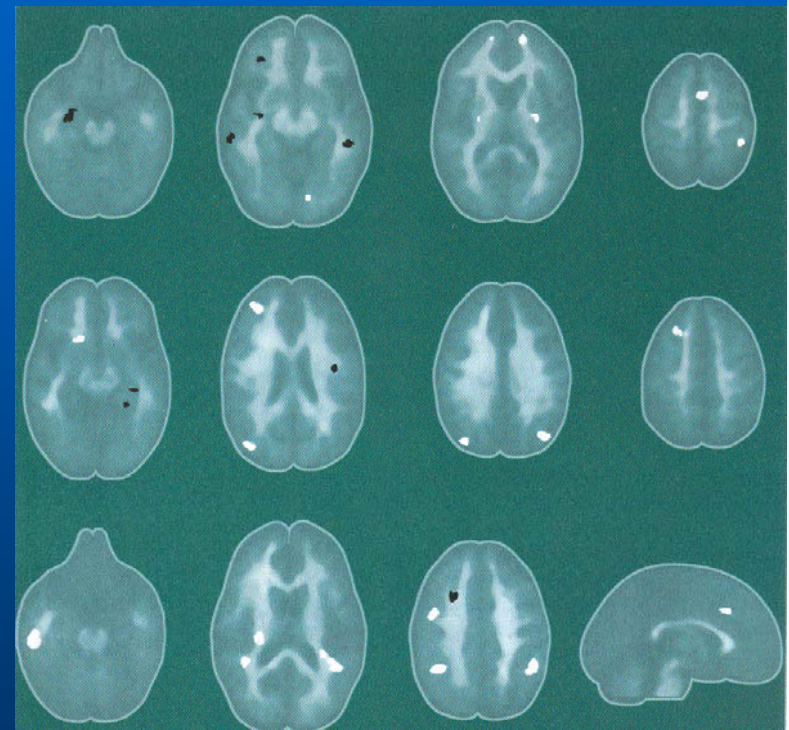


Fig 8.38 Activations corresponding to implicit learning of motor sequences in normal subjects

Imaging the human brain and memory

/Procedural memory encoding and retrieval

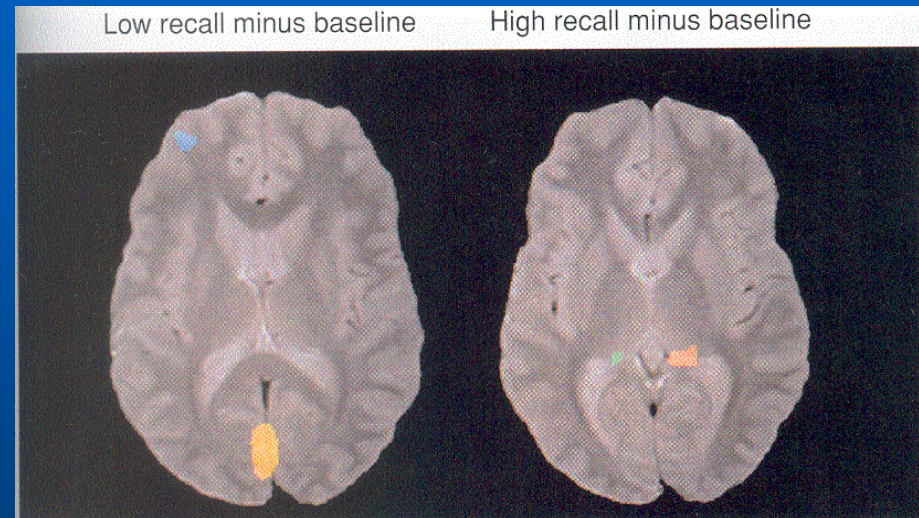
- Motor cortex is critical for implicit procedural learning of movement patterns
- The supplementary motor cortex may be part of the cortical-subcortical motor loop, which regulates voluntary movements
- Explicit learning and awareness of the sequences required increased activity in the right premotor cortex, the dorsolateral prefrontal cortex associated with working memory, the anterior cingulate, areas in the parietal cortex concerned with voluntary attention, and the lateral temporal cortical areas that store explicit memories

Imaging the human brain and memory

/Perceptual priming and implicit and explicit memory (1/2)

● Experiment

- ◆ Schacter et al. showed the subjects the words but required them to process the words only for surface perceptual features
- ◆ Subjects were assigned an implicit stem-completion task in which some experimental blocks had stems from previously presented words and other blocks had stems of new words
- ◆ Result
 - Subjects manifested implicit priming behaviorally
 - No activations or deactivations were noted in the hippocampus, but blood flow in the bilateral occipital cortex (area 19) decreased
 - The hippocampus was not activated, even though implicit perceptual priming was obtained



PET scans during recall of words

Imaging the human brain and memory

/Perceptual priming and implicit and explicit memory (2/2)

- Implicit and explicit retrieval of information is subserved by separate brain systems
- The hippocampus is activated most when explicit retrieval includes significant experience with the material, not merely an attempt to retrieve information
- The hippocampus encodes new information but also retrieves recent information when explicit recollection is involved
- Deactivation of the visual cortex for previously seen words is a correlate of perceptual priming

Cellular Bases of Learning & Memory

- ◆ Long-term potentiation and the hippocampus

Long-term potentiation and the hippocampus (1/4)

- Three major excitatory neural components of the hippocampus
 - ◆ *Perforant pathway*
 - forms excitatory connections between the parahippocampal cortex and the granule cells of the dentate gyrus
 - ◆ *Mossy fibers*
 - connect the granule cells of the dentate gyrus to the CA3 pyramidal cells
 - ◆ *Schaffer collaterals*
 - connect the CA3 pyramidal cells to the CA1 pyramidal cells

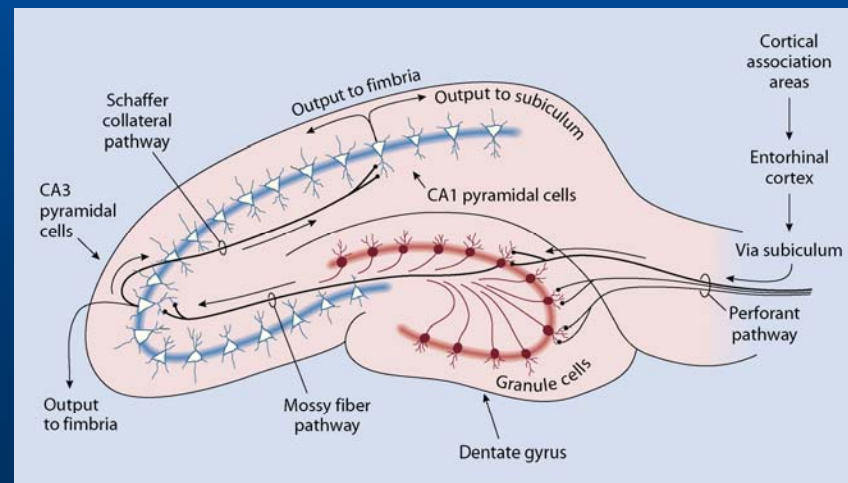


Fig 8.40 Synaptic organization of the rat hippocampus

Long-term potentiation and the hippocampus (2/4)

- LTP (long-term potentiation)
 - ◆ Stimulation of axons of the perforant pathway leads to greater synaptic strength in the perforant pathway such that later simulation created larger postsynaptic responses in the granule cells of the dentate gyrus
- LTD (long-term depression)

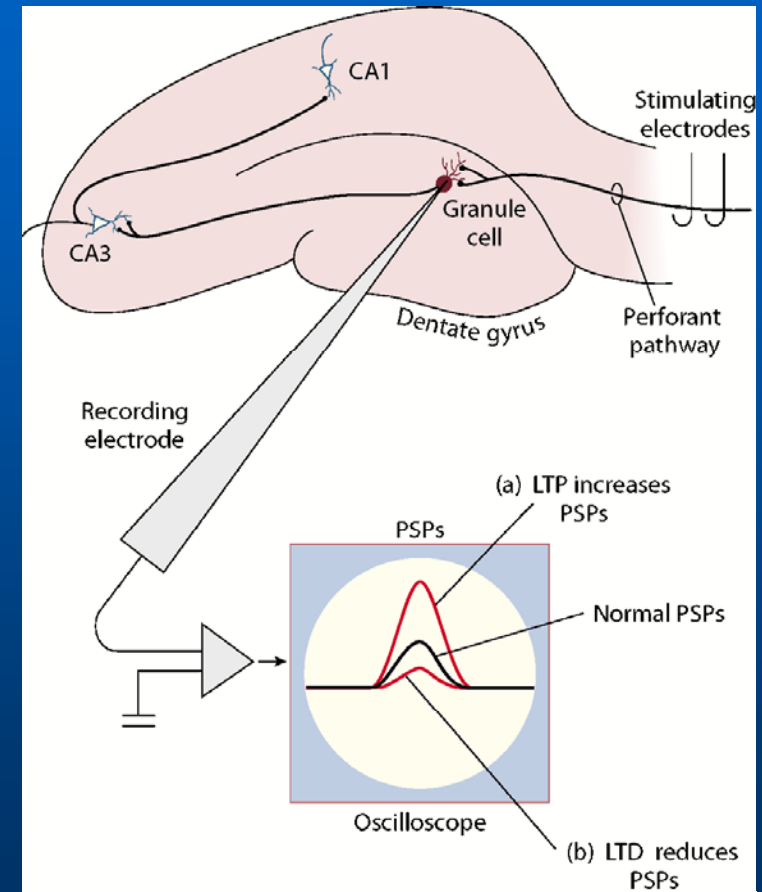


Fig 8.41 Stimulus and recording setup for the study of LTP in perforant pathways

Long-term potentiation and the hippocampus (3/4)

- Hebbian learning
 - ◆ If a synapse is active when a postsynaptic neuron is active, the synapse will be strengthened
- Associative LTP
 - ◆ If a weak and a strong input act on a cell at the same time, the weak synapse becomes stronger
 - ◆ When two weak inputs (W1 and W2) and one strong input (S1) are given to the same cell, and when W1 and S1 are active together, W1 is strengthened whereas W2 is not. Subsequently, if W2 and S1 are active together, W1 is not affected by the LTP induced from W2 and S1

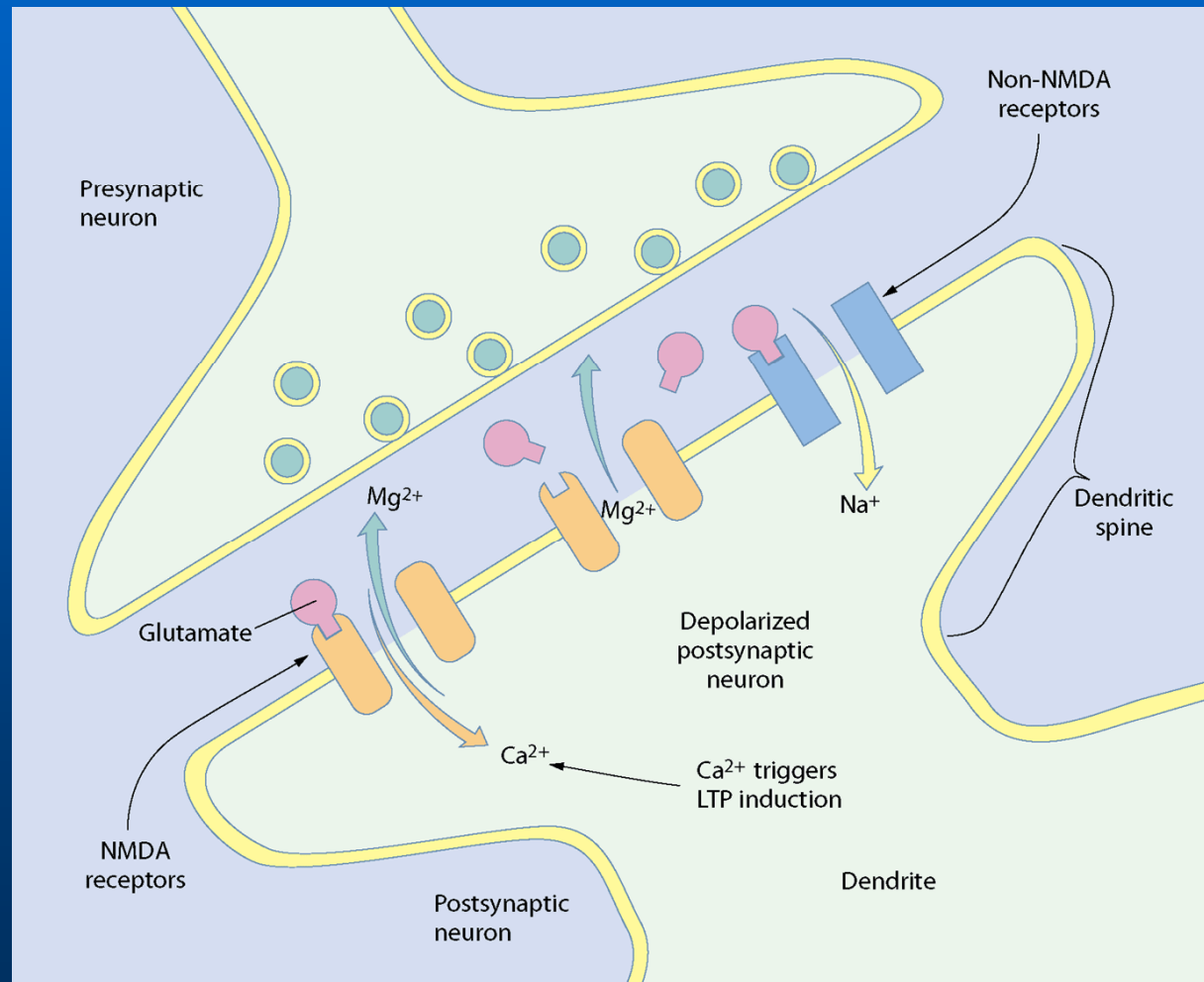
Long-term potentiation and the hippocampus (4/4)

- Three rules for associative LTP
 - ◆ Cooperativity: more than one input must be active at the same time
 - ◆ Associativity: weak inputs are potentiated when co-occurring with stronger inputs
 - ◆ Specificity: only the stimulated synapse shows potentiation
- LTP production
 - ◆ For LTP to be produced, the postsynaptic cells must be depolarized in addition to receiving excitatory inputs
 - ◆ If an input that is normally not strong enough to induce LTP is paired with a depolarizing current to the post-synaptic cell, LTP can be induced
- LTP prevention
 - ◆ LTP is reduced by inhibitory inputs to postsynaptic cells
 - ◆ When postsynaptic cells are hyperpolarized, LTP is prevented

Long-term potentiation and the hippocampus

/The NMDA receptor (1/3)

Fig 8.43 The role of Mg^{2+} and Ca^{2+} in the functioning of the NMDA receptor



Long-term potentiation and the hippocampus

/The NMDA receptor (2/3)

- NMDA receptors are central to producing LTP but not maintaining it
 - ◆ When AP5 is introduced to CA1 neurons, NMDA receptors are chemically blocked and LTP induction is prevented. But the AP5 treatment does not produce any effect on previously established LTP in these cells
 - ◆ NMDA receptors are normally blocked by Mg^{2+}
 - ◆ The Mg^{2+} ions can be ejected from the NMDA receptors only when the neurotransmitter glutamate binds to the receptors and when the membrane is depolarized → Mg^{2+} is ejected and Ca^{2+} can enter the cell
 - ◆ Ca^{2+} acts as an intracellular messenger conveying the signal which changes enzyme activities that influence synaptic strength

Long-term potentiation and the hippocampus

/The NMDA receptor (3/3)

- LTP induction likely include presynaptic and postsynaptic mechanisms
 - ◆ Hypothesis 1
 - LTP raises the sensitivity of postsynaptic non-NMDA glutamate receptors and prompts more glutamate to be released presynaptically
 - ◆ Hypothesis 2
 - Changes in the physical characteristics of the dendritic spines transmit EPSPs more effectively to the dendrites
 - Via a postsynaptic to presynaptic cell message, the efficiency of presynaptic neurotransmitter release is increased

Long-term potentiation and the hippocampus

/Long-term potentiation and memory performance

- LTP and spatial learning
 - ◆ Chemically blocking LTP in the hippocampus of normal mice impairs their ability to demonstrate normal place learning
 - ◆ Genetic manipulations that block the cascade of molecular triggers for LTP also impair spatial learning
- Conclusions
 - ◆ NMDA receptors may be needed to learn a spatial strategy but not to encode a new map
 - ◆ The pretraining merely allowed the motor-related side effects of NMDA receptor blockage to be avoided
- LTP does exist at the cellular level and that NMDA receptors play a crucial role in LTP induction in many pathways of the brain

Summary

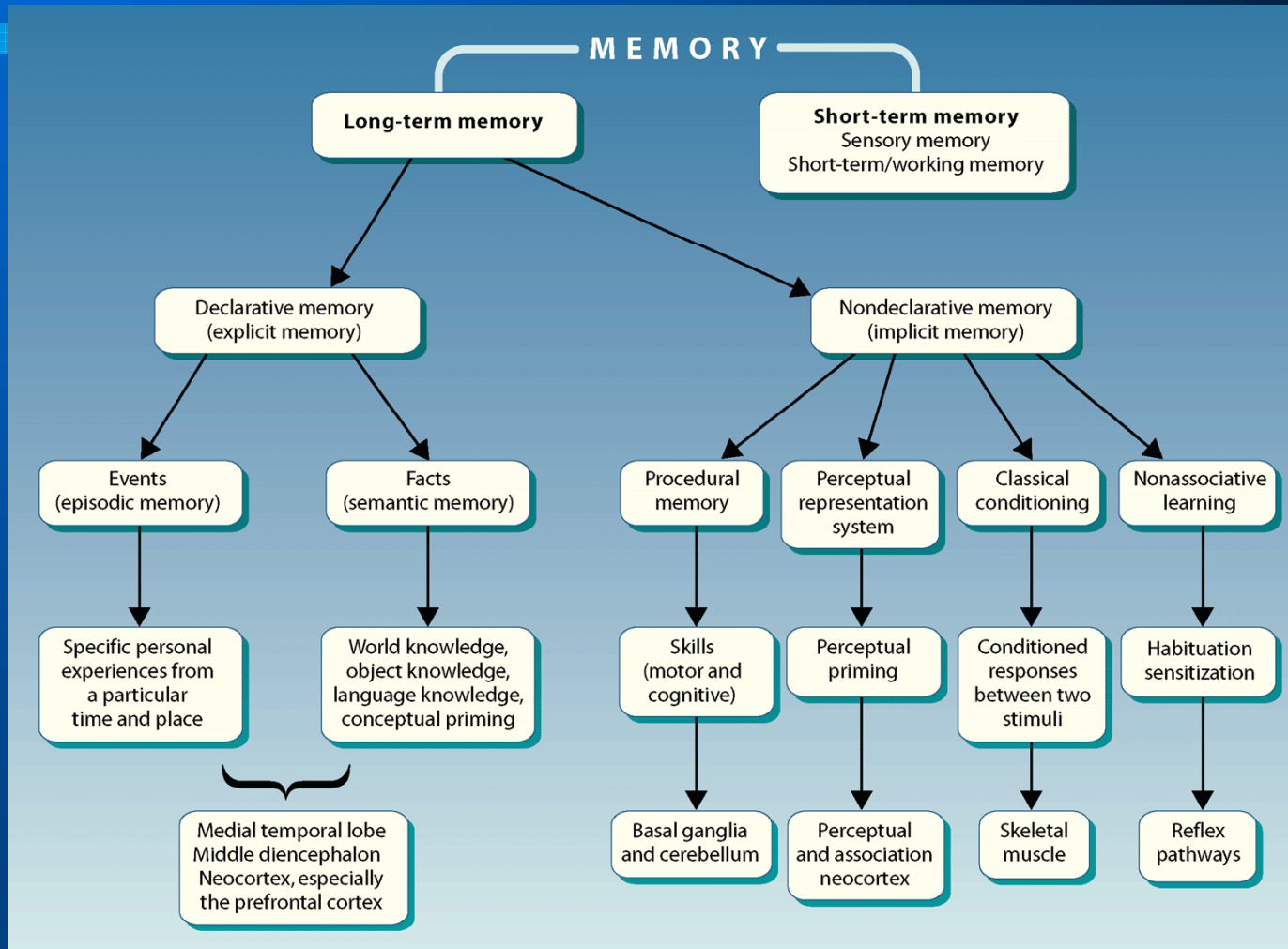


Fig 8.44 Generalized diagram of the relationships of long-term memory systems to the underlying brain systems.

Key Terms

acquisition

anterograde amnesia

declarative memory

encoding

hebbian learning

long-term memory

nondeclarative memory

procedural memory

retrograde amnesia

short-term memory

working memory

amnesia

consolidation

distributed representation

familiarity

learning

memory

perceptual representation system (PRS)

retrieval

sensory memory

storage

Thought Questions (1/3)

- Compare and contrast the different forms of memory on the basis of their time course. Does the fact that some memories last seconds while some last a lifetime necessarily imply that different neural systems mediate the two forms of memory?
- Patient H.M. and others with damage to the medial temporal lobe develop amnesia. What form of amnesia do they develop? For example, is it like the amnesia most often shown in Hollywood movies? What information can such amnesia patients retain, what can they learn, and what does this tell us about how memories are encoded in the brain?

Thought Questions (2/3)

- Can you ride a bike? Do you remember learning to ride a two-wheeler? Can you describe to others the principles of riding a bike? Do you think that, if you gave a detailed set of instructions to another person who had never ridden a bike, he or she could carefully study your instructions and then hop on a bike and ride happily off into sunset? If not, why not?
- Describe the subdivisions of the medial temporal lobe and how they contribute to long-term memory. Consider both encoding and retrieval.

Thought Questions (3/3)

- Relate models of long-term potentiation (LTP) to changing weights in connectionist networks. What constraints do cognitive neuroscience findings place on connectionist models of memory?