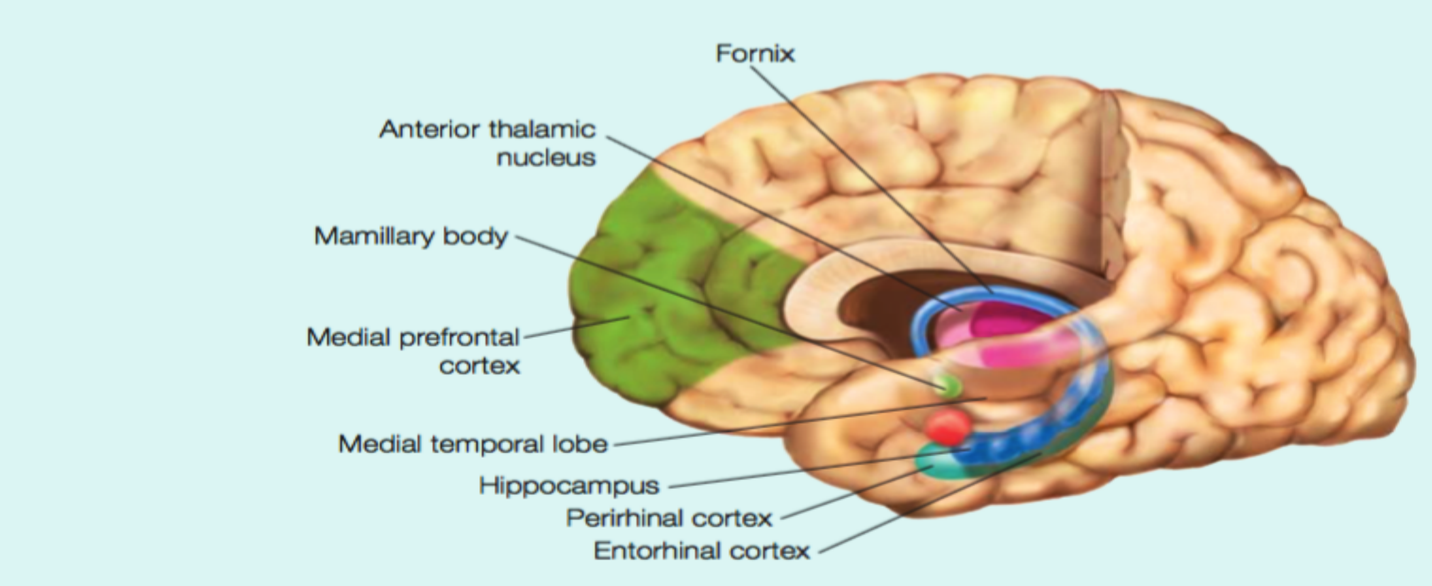
Anatomy of memory

- **Memory** is the outcome of **learning** something through single or repeated exposure. Several types of memory exist, mediated by different neural mechanisms.
- Learning & memory is divided into three major stages
  - **Encoding** = processing of incoming information to create memory traces, consisting of
    - **Acquisition** = certain stimuli are selected from the sensory buffer to enter short-term memory
    - **Consolidation** = brain changes stabilise memory over time (days to months) -> Long-term memory
  - **Storage** = permanent record of information, resulting from acquisition & consolidation
  - **Retrieval** = accessing stored information to act or create conscious representations
- Different forms of memory may retain information in partially or completely different memory systems
  - The **medial temporal lobe memory system** and other, highly interconnected areas, such as amygdala, frontal cortex, basal ganglia, are the neural correlates of memory
    - Bilateral removal -> memory loss as in HM (bad at long-term only), without cognitive deficits
    - Unilateral removal however -> only minor effect



The components of the medial temporal lobe memory system are shown. Other regions of the brain, such as the prefrontal cortex, are involved in storage and retrieval of memories.

Memory Deficits

- **Amnesia** = all memory deficit or loss, affecting all senses, in which each type of functional deficit is associated with a lesion in different brain regions
  - **Anterograde** = loss of memory after lesion -> inability to learn new things
    - **HM** had it & couldn't form new long-term memories, but could learn motor patterns unconsciously -> dissociation between experience of learning & actual process
  - **Retrograde** = loss of memory before lesion -> sometimes scope temporary limited, with loss greatest for most recent events = **temporal gradient/Ribot's law**
    - Patient's score normally on short-term memory tasks

Mechanism of memory

TABLE 9.1 Types of Memory

	Characteristic of Memory			
Type of Memory	**Time Course**	**Capacity**	**Conscious Awareness?**	**Mechanism of Loss**
Sensory	Milliseconds to seconds	High	No	Primarily decay
Short-Term and Working	Seconds to minutes	Limited (7 ± 2 items)	Yes	Primarily decay
Long-Term Nondeclarative	Days to years	High	No	Primarily interference
Long-Term Declarative	Days to years	High	Yes	Primarily interference

- **Short term forms** of memory
  - **Sensory Memory**: Unconscious **echo** of (large quantity of) sensory information, which is remember for short periods of time, without conscious awareness
    - ERP using mismatch negativity revealed that **echoic memory** (auditory) lasts about 9-10s, while **iconic memory** (visual) lasts about 300-500ms
    - **Example Tasks**: Mismatch component duration of deviant stimulus = duration of sensory memory

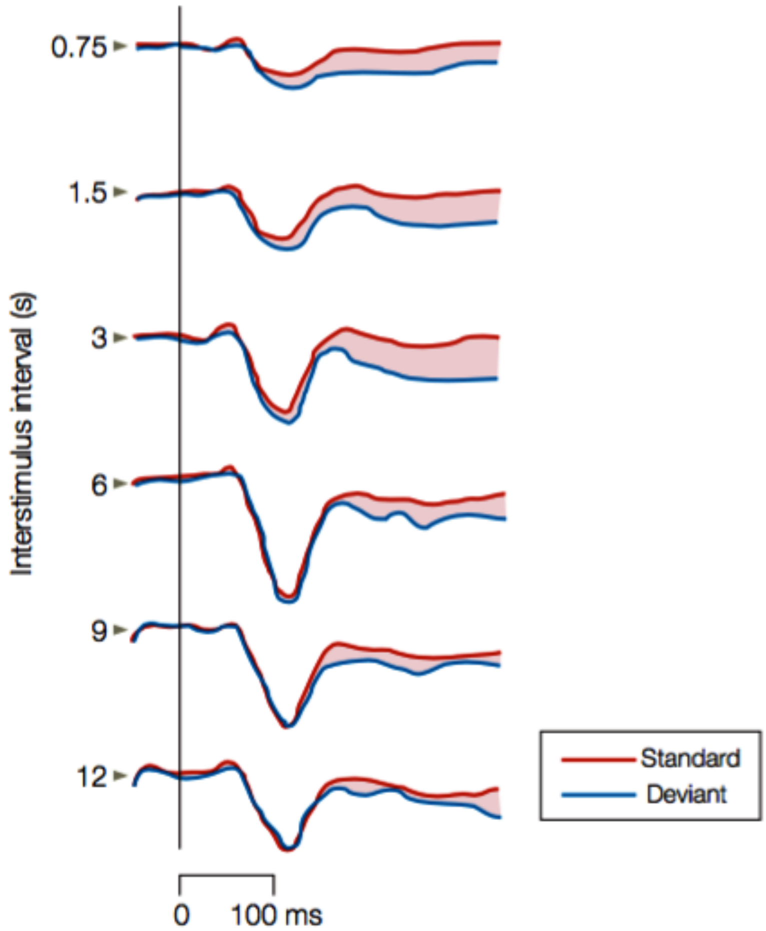


FIGURE 9.4 The mismatch field response.
The magnetic brain response known as the *mismatch field (MMF)* elicited by deviant tones (blue trace) in comparison to the magnetic responses elicited by standard tones (red traces). The amplitude of the MMF (indicated by the shaded difference between the blue and red traces) declines as the time between the preceding standard tone and the deviant tone increases to 12 s. This result can be interpreted as evidence for an automatic process in auditory sensory (echoic) memory that has a time course on the order of approximately 10 s.

  - **Short-term memory**:
    limited capacity (about 7 words of 10 letters each) for seconds to minutes, processed in serial manner (sensory -> selection into short -> long). Information lost through decay or interference.

- **Double dissociation** between short-term & long-term memory (impaired STM, but not LTM or vice-versa)
    - -> short-term memory serial processing might not be necessary before long-term memory is formed -> objection to modal model
- **Example Task**: remembering digits, or locations

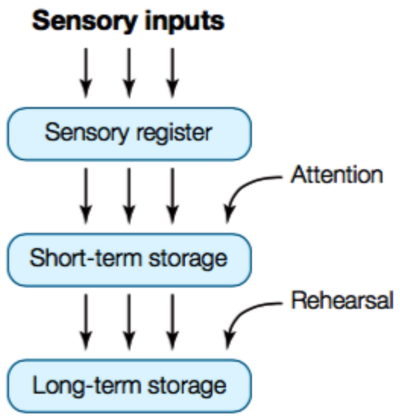


FIGURE 9.5 The Atkinson and Shiffrin modal model of memory. Sensory information enters the information-processing system and is first stored in a sensory register. Items that are selected via attentional processes are then moved into short-term storage. With rehearsal, the item can move from short-term to long-term storage.

- **Working memory**: limited capacity store for retaining information, retrieved from LTS or sensory memory, over short periods (**maintenance**) + performing mental operations on the content of this store (**manipulation**).
    - Coordination through **central executive** integrating information from
        - **Phonological loop**: hypothetical mechanisms for acoustically coding information -> modal-specific working memory, relying on acoustic not semantic processing
            - Close to Broca's & Wernicke's

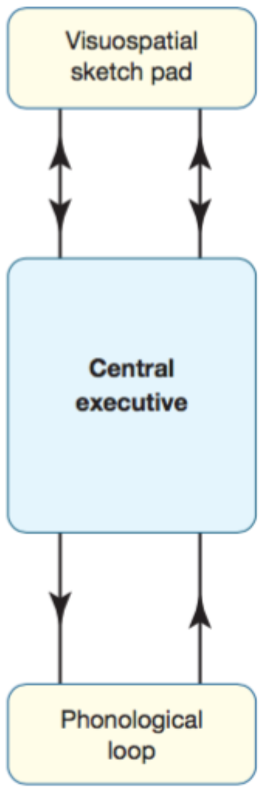


FIGURE 9.7 Simplified representation of the working memory model proposed by Baddeley and Hitch. This three-part working memory system has a *central executive* that controls two subordinate systems: the *phonological loop*, which encodes information phonologically (acoustically) in working memory; and the *visuospatial sketch pad*, which encodes information visually in working memory.

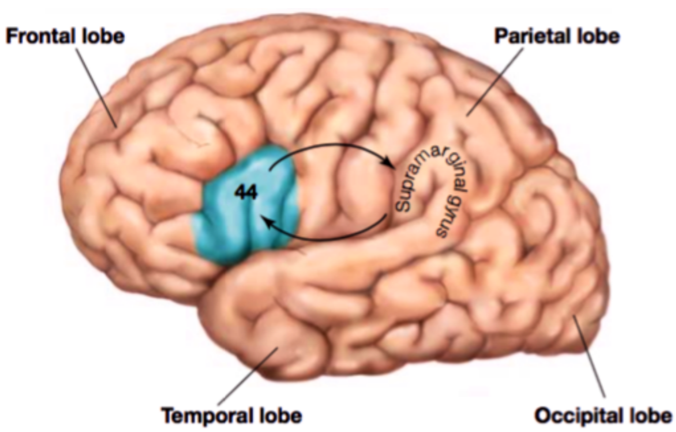


FIGURE 9.8 Lateral view of the left hemisphere, indicating that there is an information loop involved in phonological working memory flowing between BA44 and the supramarginal gyrus (BA40).

- **Visuospatial sketch pad**: equal to phonological loop, but for purely visual/visuospatial information
- -> Parietal cortex

- ○ **Long-term forms** of memory -> hippocampus + rhinal
    - **Declarative memory**: memory for events & facts, which we have conscious access to.
        - **Episodic memory**: of personal experiences = autobiographical memory remembered vividly in first person perspective & context of event
        - **Semantic memory**: objective knowledge/factual knowledge without much context
        - **Example task**: remembering long digits numbers

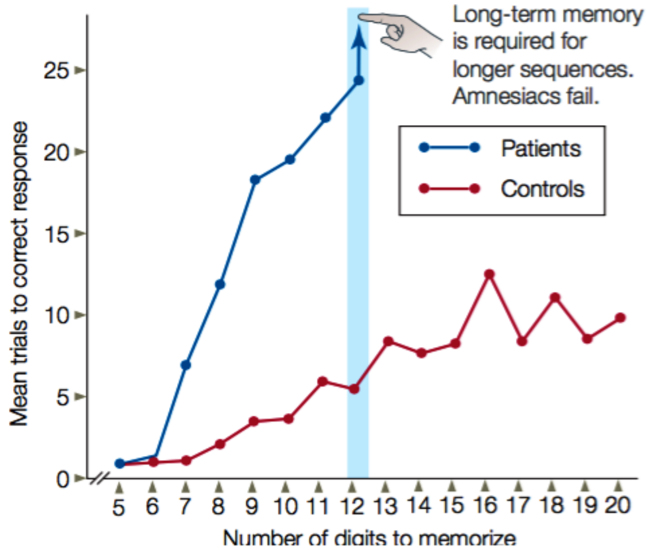
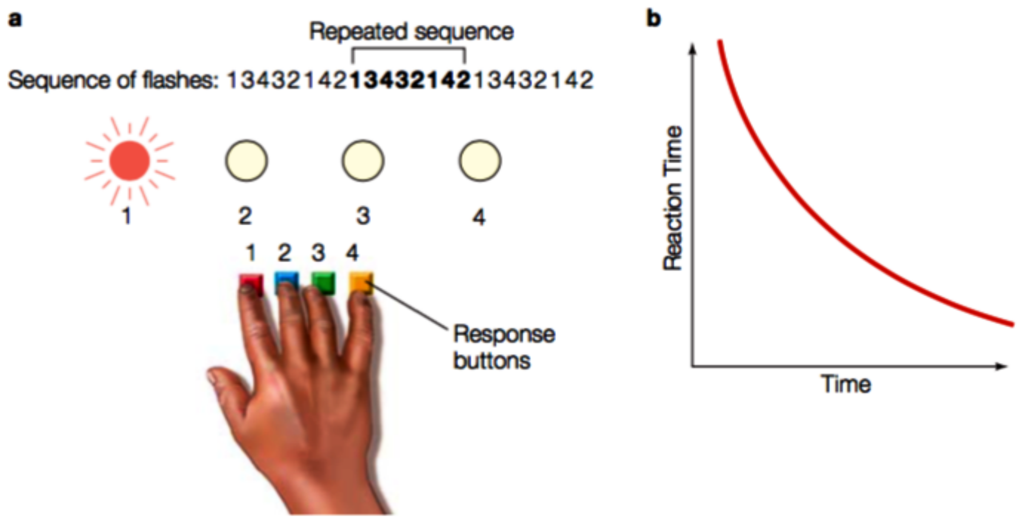


FIGURE 9.3 Digit span for amnesic patients and control participants.
A sequence of five digits was read to the participants, who were then asked to repeat the digits to the experimenter. If the digits were repeated correctly, one more digit was added to the next sequence presented. If the digits in a sequence were reported incorrectly, that sequence was repeated until the participant reported it correctly.

    - **Non-declarative memory**: knowledge that cannot be verbally reported, because implicit, resulting form priming, conditioning, habituation, etc.
        - **Procedural memory**: depends on extensive, repeated experience, like motor skills
            - Often tested through serial reaction time -> HM improved too at this task -> he had declarative memory impairment & episodic memory is different from procedural

FIGURE 9.11 Procedural learning of sequences in the serial reaction-time task.
(a) Using their fingers, participants are asked to push buttons corresponding to flashes of lights in a complex sequence that is repeated but not obvious. (b) Over time, participants reaction time to the repeating sequence becomes faster as compared to a sequence that is totally random, although they apparently do not know that any pattern exists.



        - **Priming**: change in response to stimulus (like faster processing/recognition) following prior exposure to that stimulus, which can be conceptual, perceptual, or semantic
            - Perceptual priming acts with **perceptual representation system PRS**, in which structure & form of objects is primed
            - Priming also occurs for conceptual & semantic features, but lasts much shorter (seconds)
        - **Classical conditioning & non associative learning** = stimulus pairing & habituation

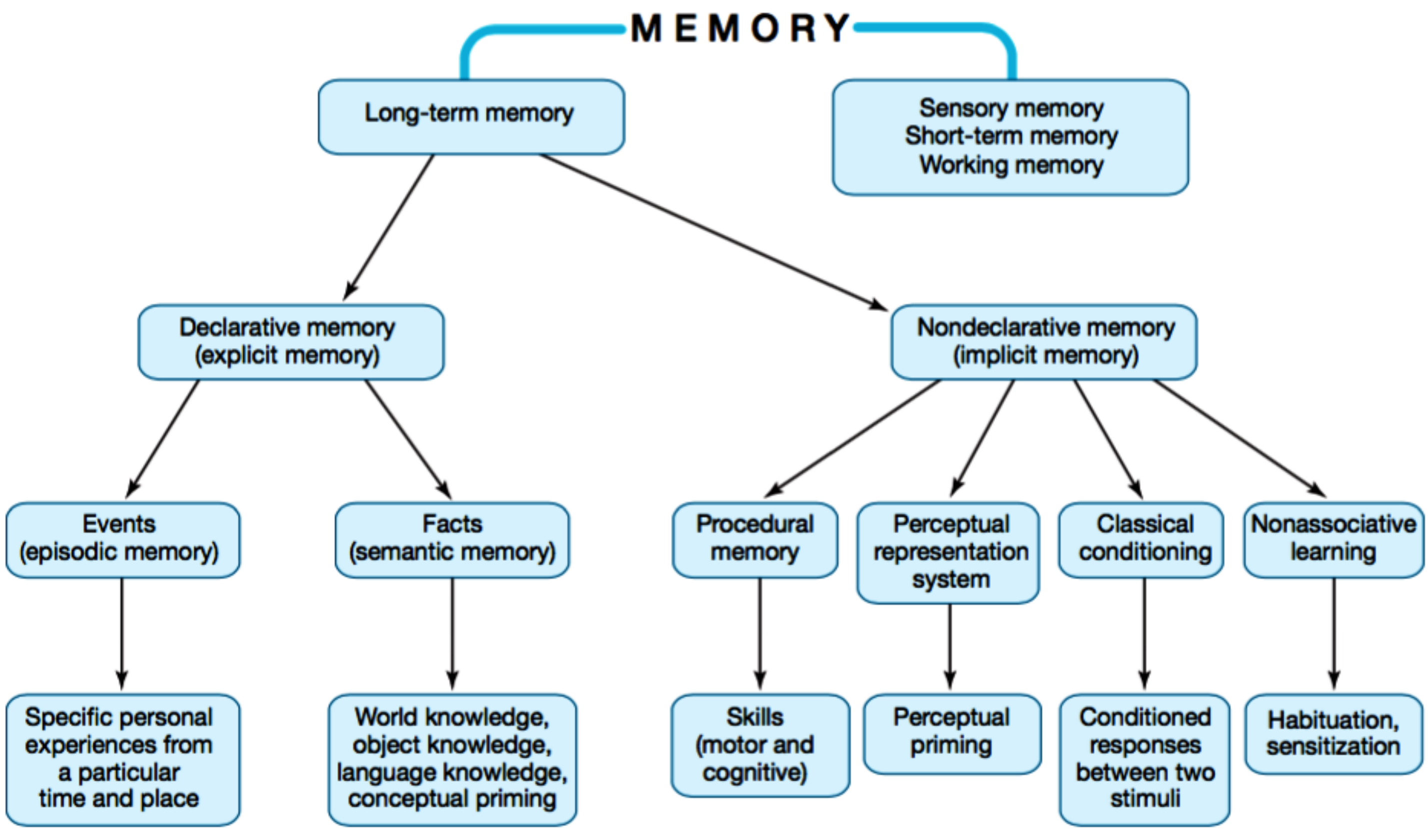
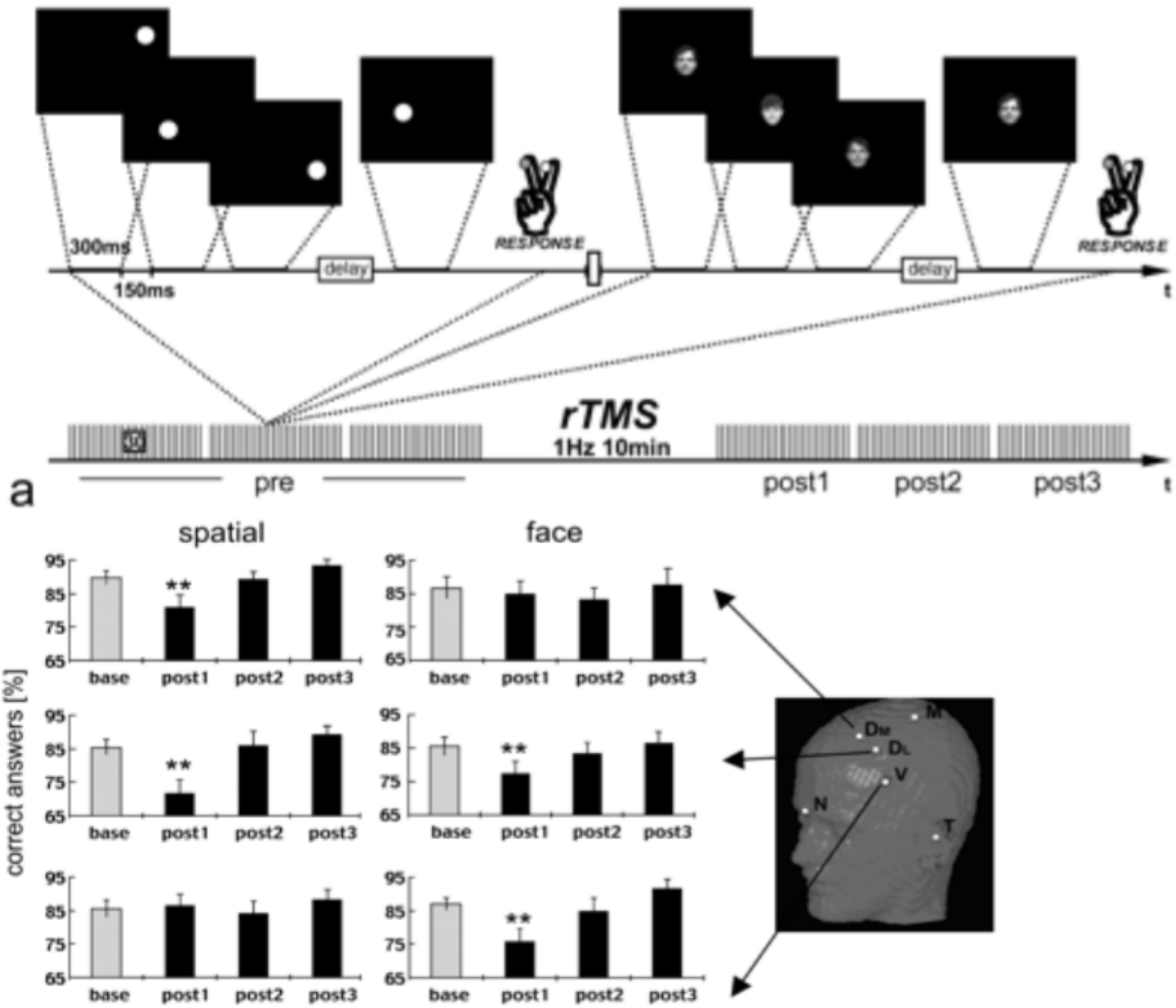


FIGURE 9.2 The hypothesized structure of human memory, diagramming the relationships among different forms of memory.

Mottaghey - Segregation of areas related to visual working memory in prefrontal cortex, reveals by rTMS

- Role of prefrontal cortex in higher cognitive functions = different kinds of memory, is uncertain. Information processing segregation could depend on nature of cognitive task or nature of stimulus -> Two executive processing systems proposes
    - Ventral frontal system: serving as interaction between STM & LTM & executive processing - would be activated by face stimuli ("what" visual system)
    - Dorsal frontal system: serving as interaction between memory & working memory, only recruited when active manipulation & monitoring of information required, which would be activated by spatial stimuli ("where" visual system)
- **RQ**: Can segregation of areas within prefrontal cortex involved in WM tasks for faces or spatial locations, be demonstrated using rTMS
- **Method**
    - Subjects: 8 right-handed males
    - Task: delayed WM paradigm -> 30 blocks = 15A + 15B of random presentation of
        - A: spatial locations = white dots on black screen at different locations with respect to fixation cross
        - B: unfamiliar faces = black/white images
        - -> rTMS to dorsal or ventral frontal cortex -> comparison versus baseline
- **Results**
    - TMS to left or right dorsal -> much poorer spatial task performance & no effect on facial/nonspatial task performance

- TMS to ventral -> much poorer facial/nonspatial task performance & no effect spatial task performance
- **Conclusion**
  - -> Human working memory follows dorsal = spatial & ventral = object axis as shown through segregation of effects on task performance following inhibition of ventral or dorsal prefrontal cortex
- **Problems**
  - Poor spatial resolution of rTMS & possible dynamic compensation = interaction between "distinct" modalities



<u>Owen - Functional organization of spatial/non-spatial working memory</u>

- FMRI to reveal that performance of visual-spatial & non-spatial prefrontal cortex is not mediated by dorsal/ ventral system respectively, but that specific regions of frontal cortex make equal contribution to spatial / non-spatial working memory.
    - Hypothesis: segregation idea resulted from flawed design, as type of executive processing underlying monitoring & manipulation account for differences between those two regions-> if controlled for executive processing through keeping task the same, there will be no difference+
- **RQ**: are the same of different areas of the lateral prefrontal cortex involved in spatial/nonspatial working memory when executive processing is the same?
- **Method**
    - FMRI scans, blocked design, n-Back task
    - Tasks: 2 different experimental tasks, with same executive requirements: monitoring & manipulating ongoing series of visual stimuli within working memory, but different type of visual stimuli = locations versus abstract patterns
        - Spatial versus control should yield greater dorsal & non spatial versus control greater ventral activation if stimulus type is critical variable. If type of executive processing critical variable -> dorsal activation should appear in both tasks
- **Results**
    - Increase in dorsal in spatial versus control
    - No increase in dorsal in non spatial versus control
        - But peaks in temporal cortex
    - TMS to ventral -> much poorer facial/nonspatial task performance & no effect spatial task performance
- **Conclusion**
    - -> Spatial & non-spatial working memory tasks activate similar regions in prefrontal cortex, regardless of nature of stimulus -> no distinction between dorsal/ventral regarding functional processing of different types of stimuli, but type of executive processing is important

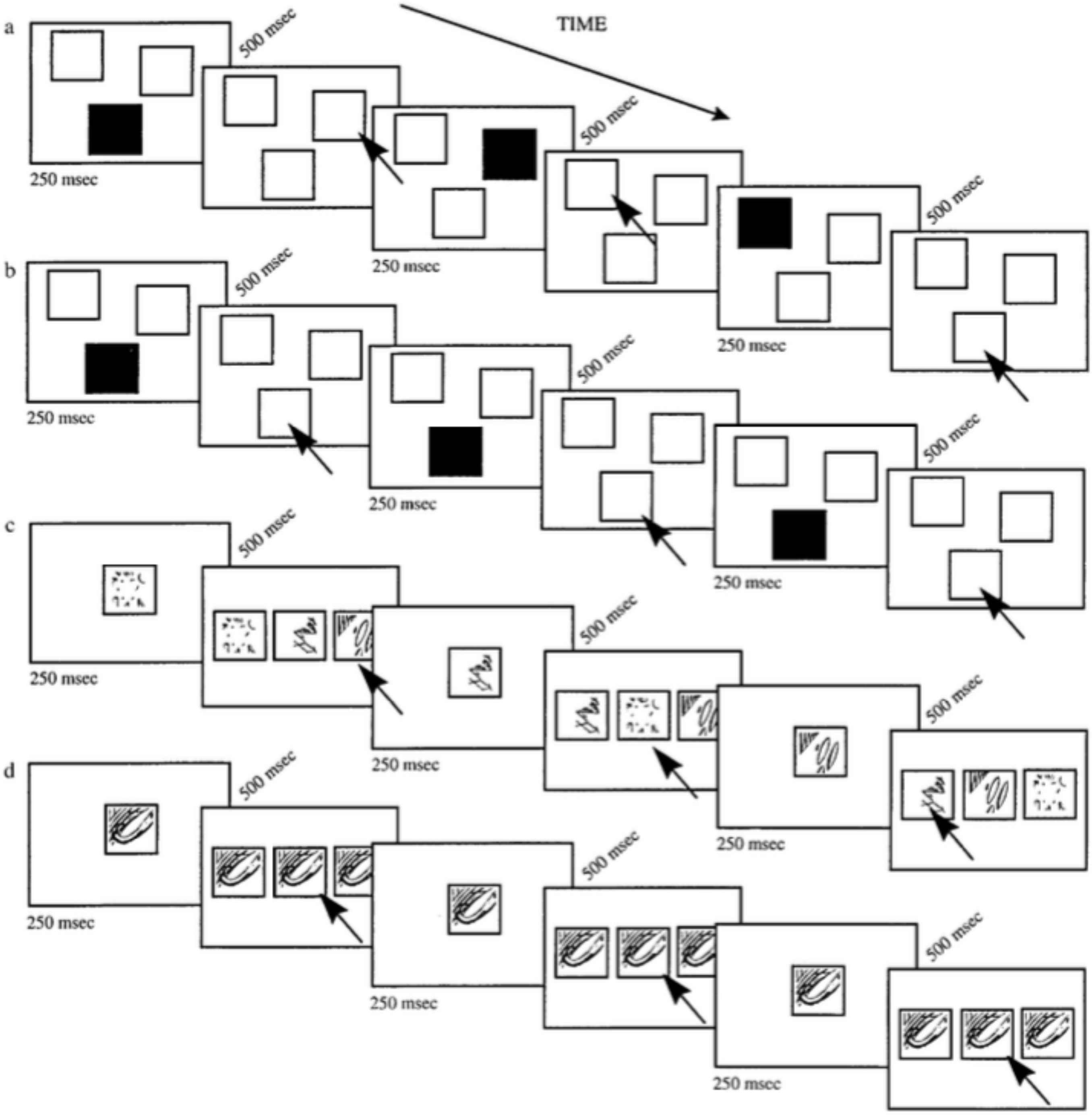


FIG. 1. Illustrated are: (*a*) the spatial working memory task, (*b*) the spatial control task, (*c*) the nonspatial working memory task, and (*d*) the nonspatial control task. A number of trials are shown in each case. Trials were presented sequentially with a constant 500-ms interval in between. Black arrows, subjects' responses.

After the surgery, H.M. knew the autobiographical details of his life and all the other things he had learned in his life up to the 2 years immediately before his surgery. For those 2 years before surgery, however, he could not remember anything. He also showed selective memory loss for *events* as far back as a decade before the surgery. H.M. had normal short-term memory (sensory registers and working memory) and procedural memory (like riding a bicycle). Like many other amnesics (Figure 9.3), H.M. had normal *digit span* abilities (how many numbers a person can hold in memory over a short period of time) and did well at holding strings of digits in working memory. Unlike normal participants, however, he did poorly on digit span tests that required the acquisition of new long-term memories. It appeared that the transfer of information from short-term storage to long-term memory was disrupted. H.M. had anterograde amnesia, and could form no new long-term memories. Interestingly, even though he could not consciously remember new experiences, his behavior would be affected by them. The researchers were surprised when they discovered that H.M. could learn some things: tasks that involved motor skills, perceptual skills, or procedures became easier over time, though he could not remember practicing the new skill or being asked to learn it. There was a dissociation between remembering the experience of learning and the actual learned information.

Studies of H.M. changed how people thought about the brain's memory processes. Previously, it was thought that memory could not be separated from perceptual and intellectual functions. These latter functions, however, remained intact in H.M., implying that memory was to some degree distinct from these processes. From H.M., researchers also learned that the medial temporal lobes are necessary for forming long-term memory and for transferring information about events and facts from short-term memory into long-term memory. Studies of H.M. also suggest that the medial temporal lobes are not necessary for the formation and retrieval of short-term memories or for learning new long-term memory that involves learning procedures or motor skills. Thus, the medial temporal lobe memory system is involved in certain memory functions, but not others, and is not critical for general intelligence, cognitive control, language, perception, or motor functions.

Studies in H.M. and other patients with amnesia have also shown that they can learn some forms of new information in addition to procedures, motor skills, and perceptual skills. They can also learn new concepts and world knowledge (semantic memory). But the amnesic patients, nonetheless, do not remember the *episodes* during which they learned or observed the information previously. The growing evidence from cases of amnesia suggests that long-term memories for events, facts, and procedures can be partially dissociated from one another, as expressed in their differential sensitivity to brain damage. Throughout this chapter, we explore additional studies that used patients with amnesia as participants.

tures, shapes, and faces. In summary, the PRS mediates word and non-word forms of priming. Moreover, it is not based on conceptual systems, but rather is perceptual in nature. Interestingly, this type of priming is also found in amnesia patients like H.M. H.M. would show evidence of priming even when he could not remember ever having seen the word list or ever having done a fragment-complete task before. This behavior tells us that the PRS system does not rely on the medial temporal lobe, because both of H.M.'s were removed surgically. But this is merely a single dissociation. Is there any evidence that brain lesions can affect the PRS system while leaving long-term memory intact?

continue to evolve, and different models emphasize different factors in the organization of learning and memory. Many different memory models have been proposed, including, for example, those based on how long memories persist, the type of information that is retained, whether memories are conscious or unconscious, and the time it takes to acquire them (see Figure 9.2 for a summary of the essential relations among different forms of long-term and short-term memory). In the next few sections, we discuss different forms of memory, and describe some of the evidence supporting theoretical distinctions among them.

Studies of patients with brain damage permit a test of the hierarchically structured modal model of memory. In 1969, neuropsychologists Tim Shallice and Elizabeth Warrington at University College London reported that a patient (K.F.) with damage to the left perisylvian cortex (the region around the Sylvian fissure) displayed reduced digit span ability (about 2 items, as opposed to 5 to 9 items for healthy persons). The test involves first reading lists of digits for the participants to remember and then, after a delay of only a few seconds, having participants repeat those digits. The lists can be from two to five or more digits long, and the maximum number that a person can recall and report is known as his digit span ability (see Figure 9.3).

Remarkably, however, in a long-term memory test of associate learning that pairs words, K.F. retained the ability to form certain types of new long-term memories that could last much longer than a few seconds. Therefore, it seemed that the patient displayed an interesting dissociation between short-term and long-term memory. If this interpretation of the finding is true, it has important implications for models of memory: Short-term memory might not be required in order to form long-term memory. This conclusion is in contrast to how the information flows in the modal model (Figure 9.5), which requires serial processing. One issue with this view is that the two tests presented to K.F. were different (digit span and word association), and it's hard to pinpoint whether the dissociation is one of memory processes or actually due to the different tasks.

A more recent example of a similar patient comes from the work of Hans Markowitsch and colleagues (1999) at Bielefeld University in Germany. Their patient, E.E., had a tumor centered in the left angular gyrus. The tumor affected the inferior parietal cortex and posterior superior temporal cortex (Figure 9.6), regions similar to but slightly different from those affected in patient K.F. After undergoing surgery to remove the tumor, E.E. showed below-normal short-term memory ability but preserved long-term memory—a pattern similar to K.F.'s. E.E. showed normal speech production and comprehension, and normal reading comprehension. He had poor short-term memory for abstract verbal material, however, as well as deficits in transposing numbers from numerical to verbal, and vice versa, even though he could calculate normally. Interestingly, on tests of his visuospatial short-term memory and both verbal and nonverbal long-term memory, E.E. performed normally.