The last 20 years have seen a bedrock change in how psychologists think about memory, largely due to findings from neuropsychology. Until the early 1970s, psychologists viewed the memory system of the human brain as unitary. Today, human memory is more often viewed as a confederation of systems, each serving a different function, each subserved by different neural structures, and each capable of operating independently (see Schacter and Tulving, 1994, for a number of perspectives). What used to be called simply "memory" is today often referred to as explicit (or declarative) memory: memory that is associated with awareness and with intention to recall. Notably, other forms of memory are not associated with awareness. While one may not be aware that one has learned, the influence of prior experience will be apparent from task performance. Initially, researchers referred to all forms of unconscious memory as implicit (or procedural), but today these forms of memory are separated into distinct systems.

The number of memory systems is a matter of ongoing debate, but there is relative agreement on the separability of the six systems listed in Table 1. These systems are differentiated in terms of their function and in terms of their neural substrate. It should be noted that these neural substrates are not necessarily the locations in which memory representations are stored but are areas thought to be critical to the normal functioning of the system.

**Background**

The shift from the single- to the multiple-system view occurred during the early 1980's through the influence of several lines of research. One important influence was studies of anterograde amnesia, as work on these patients performed in the 1960s and 70s came to be reinterpreted in a multiple systems framework. The core results from this literature can be appreciated by considering the patient known by his initials, HM, who is perhaps the most-studied amnesic patient.

HM underwent bilateral removal of much of the medial temporal lobe to relieve intractable epilepsy. After surgery, HM had a devastating loss of ability to learn new material (as measured by recall or recognition—what are now called explicit memory tests). This loss is so complete that he has learned almost no new information since the surgery in 1953. Despite what must be thousands of learning trials over many years, HM has never learned the route from the dining room to his bedroom in the nursing home where he lives nor to recognize the faces of nursing staff whom he has seen daily for years (Corkin, 1984).

In contrast to this dramatic loss of explicit memory, it has become clear that other forms of memory are intact in HM. HM shows normal working memory; he can retain information across a delay of 30 s as well as neurologically intact subjects (Corkin, 1984). In studying HM and other amnesic patients, it also became clear that memory is not always associated with intention to remember nor with awareness that one has learned. The influence of prior training or study may be apparent through task performance rather than through a report of what is consciously remembered. Examples of such tasks include motor skill learning and repetition priming tasks. In a priming task, the subject is asked to identify or complete a word or picture, and subjects do so more quickly or accurately if the stimulus was viewed a short time ago. HM shows normal motor skill learning and normal priming effects (Corkin, 1984). A straightforward interpretation of this pattern of performance is that explicit memory has been devastated in HM, but his ability on the other types of memory tests is unimpaired because these tests tap other memory systems that are undamaged.

Much of the evidence supporting the multiple-system view of memory comes from patients with focal lesions like HM. The multiple-system view has been adopted, in part, because it appears that individual memory systems can be selectively disrupted while leaving other memory systems undisturbed. The conclusion that the damaged structure mediates the lost memory function is not straightforward, however, because the lesion may disrupt fibers of passage, alternative brain structures may be recruited to compensate for damaged tissue, or the subject may have learned to adopt different strategies to complete a task that normally relies on the damaged structure. Such concerns are to some extent assuaged when studies using functional imaging methods (Positron Emission Tomography or functional Magnetic Resonance Imaging) implicate the same brain structures in a memory system that lesion studies implicate. Functional imaging studies have their own problems of interpretation, but they do not overlap with the problems of lesion studies. In imaging studies one may see activation in a parallel system that is not crucial to the function of interest. There are also theoretical and practical difficulties in using the subtraction technique that is typically used to establish neural areas of activation. A combination of lesion and imaging studies provide converging evidence for all of the memory systems described here.

**Separate Memory Systems**

Explicit memory is associated with a conscious awareness that one is remembering and is usually tested by directly querying the individual, as in a typical recognition or recall test. Such memory relies on a set of structures in the medial temporal lobe, particularly the hippocampus, entorhinal and perirhinal cortex, and diencephalon (Squire, 1992). Lesions to these structures produce explicit memory deficits in humans and nonhuman primates (although defining explicit memory in nonhuman animals is a matter of some controversy because the definition usually includes reference to the subject's awareness), and functional imaging studies show activation in these structures during encoding and recall of explicit memories (Squire et al., 1992).

A useful distinction in thinking about explicit memories is that between episodic and semantic memories.
Episodic memories are those that are associated with a particular time and place, and also a sense on the part of the person remembering that “this happened to me.” Hence, the memory of a recent vacation would be an episodic memory. Semantic memory, on the other hand, does not have these qualities; for example, knowing that George Washington was the first president of the United States would be a semantic memory. A typical memory experiment tests episodic memory, because a subject is queried about a particular instance of a stimulus; by asking if the word “president” was on the studied word list, the experimenter asks whether that word is associated with a particular time and place. On the other hand, the question “Who was the first president of the United States?” taps semantic memory because the knowledge that allows one to answer the question is not associated with a particular time or place.

Patients with anterograde amnesia can retrieve semantic memories learned prior to the onset of amnesia, but they cannot acquire new semantic memories, which implies that the medial temporal lobe and diencephalon are crucial to the formation of semantic memories. One interpretation of this finding is that all memories are initially episodic and come to be semantic memories as time and place tags become confused through repeated exposure to the information at different times and in different places.

Working memory (sometimes called short-term memory), like explicit memory, is associated with awareness, but it is different in that it is short-lived. It is often conceptualized as a system that maintains the activity of a perceptual representation (e.g., visual, phonological, etc.), keeping it “on-line,” and it is tested by asking subjects to remember information across a very brief delay, i.e., 30 s or less. Working memory is dissociable from explicit memory; for example, patients with severe explicit memory deficits show normal working memory capabilities, and patients with frontal or parietal lobe lesions are impaired in working-memory tasks but show normal explicit memory (Warrington et al., 1971). A series of single-cell recording studies in the monkey by Goldman-Rakic and colleagues showing that some cells in the prefrontal cortex are active only during the brief delay in a working-memory task has been seminal in establishing the role of this cortical area to working memory (Goldman-Rakic, 1995). Functional imaging studies confirm the role of prefrontal and parietal cortex in working memory in humans (D’Esposito et al., 1995).

One interpretation of these findings is that the frontal lobe maintains the activation of perceptual representations in more posterior cortical areas.

Working memory may hold perceptual representations on-line, but a different process tunes perceptual representations on the basis of experience. Some evidence of such change may be found in priming tasks, in which experience with a word or picture influences later processing of the same or a similar stimulus. For example, as part of a list of words, a patient might read the word STAMP. Later, the patient would be asked to perform a word identification task in which a word is flashed very briefly on a computer monitor, and the patient must try to identify it. The patient will be better able to identify words read an hour ago than novel words. It is hypothesized that the representations supporting word identification are tuned toward identifying that word. This word identification task is just one priming paradigm. There are in fact a number of different priming tasks, all of which share certain characteristics: subjects study materials and sometime later are presented with a task that makes use of the same or related materials; the performance of the task is biased or enhanced by the prior study.

Lesion studies show that priming is based in neocortex. Patients with occipital lobe damage are impaired on priming tasks but not on explicit or working-memory tasks (Tulving and Schacter, 1990), and patients with temporal or frontal lobe damage may show impairment on some priming tasks. Patients with anterograde amnesia (such as HM) show normal priming with words and pictures and with novel stimuli such as pronounceable nonwords and pictures of nonsensical objects. Functional imaging studies also indicate that these cortical areas are crucial to priming (Squire et al., 1992).

Motor skill learning refers to making movements more quickly and accurately with practice, and this process appears distributed among a number of motor cortical areas as well as the striatum. Patients with striatal abnormalities (e.g., Huntington’s disease, Parkinson’s disease) are impaired on many motor skills (Willingham et al., 1996). They are also impaired, though sometimes to a lesser extent, on other sorts of memory, including explicit and working memory, although they show normal priming effects. The deficits in explicit and working memory may be due to cortical degeneration associated with Huntington’s and Parkinson’s diseases, or it may be that striatal abnormalities serve to deafferent frontol and temporal cortical areas that support these memory systems. Functional imaging studies show activation associated with motor skill learning in a number of different areas but most often in the striatum, supplementary...
motor area, premotor cortex, and primary motor cortex (Grafton et al., 1992).

In classical conditioning tasks, subjects are exposed to repeated pairings of a neutral perceptual cue (e.g., a tone) and a stimulus (e.g., a puff of air to the eye) that leads to a predictable response (an eye blink). Subjects learn the relationship between the neutral cue and the appropriate response. The neural mechanisms of such learning have been described in considerable detail in the rabbit, and it is clear that the cerebellum and closely related brain stem structures are critical to learning in this task (Thompson, 1988). Amnesic patients show normal classical conditioning, although they are impaired on trace conditioning, where a brief delay (500 ms) is introduced between the conditioned and unconditioned stimulus. Humans with cerebellar lesions show deficits in eye-blink conditioning, but they also show a host of other cognitive deficits, including problem-solving tasks and motor skill learning (Fiez, 1996). Functional imaging studies show cerebellar activation associated with classical conditioning in humans, but it should be noted that cerebellar activation is associated with performance on many other tasks. There seems to be little doubt of the cerebellum’s importance to eye-blink conditioning, but further work may show that a broader description of cerebellar learning is possible.

In an emotional-conditioning paradigm, a neutral stimulus (e.g., a light) is paired with a consequence (e.g., an electric shock) that generates an emotion (e.g., fear) such that the stimulus comes to be associated with the emotion. There is compelling evidence that the amygdala is crucial to this learning. This evidence comes primarily from rats undergoing fear conditioning (LeDoux, 1995; Maren and Fanselow, 1996) and is supported by lesion studies in humans, including a dissociation in a patient with bilateral amygdala damage who showed no fear conditioning but showed normal recall of the events during the training session (a measure of explicit memory). An amnesic patient with hippocampal damage showed the opposite pattern of task performance (Bechara et al., 1995).

Further Distinctions

The theoretical fractionation of memory has in fact not stopped with the six systems described in Table 1. A number of researchers have proposed further breakdowns of some of these systems.

As described earlier, two varieties of explicit memory have been described: episodic and semantic. Some recent neuroimaging evidence points to a special role for right dorsolateral prefrontal cortex in episodic memory retrieval (Tulving et al., 1994), and there have been case studies of selective loss of autobiographical memory (Hodges and McCarthy, 1995). These patients show a paucity of recall of information from their life history.

There is also evidence regarding the cortical organization of information in semantic memory. Information about objects appears to be organized by attribute. That is, the areas of the cortex that mediate knowledge about objects each subserve an object attribute, rather than the representations of all of the attributes of a particular object being located physically near one another. This idea seemed reasonable based on case studies reported in the last 30 years of patients with focal lesions who lost the ability to identify a particular attribute of objects. For example, a cortical lesion might result in a selective deficit in identifying the color of objects. Recent neuroimaging evidence provides more direct support for the idea in the normal brain and further shows that the attribute knowledge is stored near the location where perception takes place. Object color appears to be subserved by the ventral temporal lobe, just anterior to the area involved in color perception. Knowledge of actions associated with objects is subserved by an area in the middle temporal gyrus, just anterior to an area involved in the perception of motion (Martin et al., 1995).

As one might suspect, working memory in different sensory modalities appears to have different neural bases. Thus, working memory for auditory and for visual material appears to rely on different cortical areas (Goldman-Rakic, 1995). Within the visual modality, compelling single-cell recording data and neuroimaging data support a distinction between working memory for objects and for their spatial locations.

There is also good evidence from lesion studies for a distinction between different varieties of priming. The occipital cortex appears to support priming based on the visual features of the stimulus. A potential locus of priming tasks based on the semantic content of the stimulus is the frontal or temporal lobes (Tulving and Schacter, 1990).

Motor skill learning has also been further fractionated. Willingham et al. (1996) have suggested that motor skill learning is supported by a striatal system for learning skills that rely on producing the same movement repetitively and a posterior parietal–premotor cortical system for learning new mappings between stimuli and the appropriate motor response.

The Future of a Systems Analysis

There has been considerable success in identifying memory systems that are anatomically distinct. Two directions of continued research seem timely. First, it has been assumed that these separate systems will have important differences in their operating characteristics, but these differences have yet to be carefully specified. Anatomic separability would seem to imply computational distinctiveness. A next step in a systems analysis of memory could be a more thorough program to delineate the processes and representations used by each system.

A second target for future work in this area might be some consideration of how these separate systems interact. It is likely that there is overlap in these separate systems. For example, it seems improbable that there are two separate and complete lexicons, one to support priming and the other to support explicit memory. Aside from such instances of overlap, there must be instances where the processing in one system influences processing in another. For example, it has been known for at least 20 years that the content and durability of explicit memory depend on the action of working memory at the time a memory is encoded. Explicit memory can also influence performance of motor skills, as subjects adopt different strategies based on explicit memories of prior performance. It is true that different memory systems are independent in that they can operate normally in the face of damage to other systems, but that
does not mean that they do not influence one another under normal circumstances, i.e., in the intact brain.

Selected Reading


