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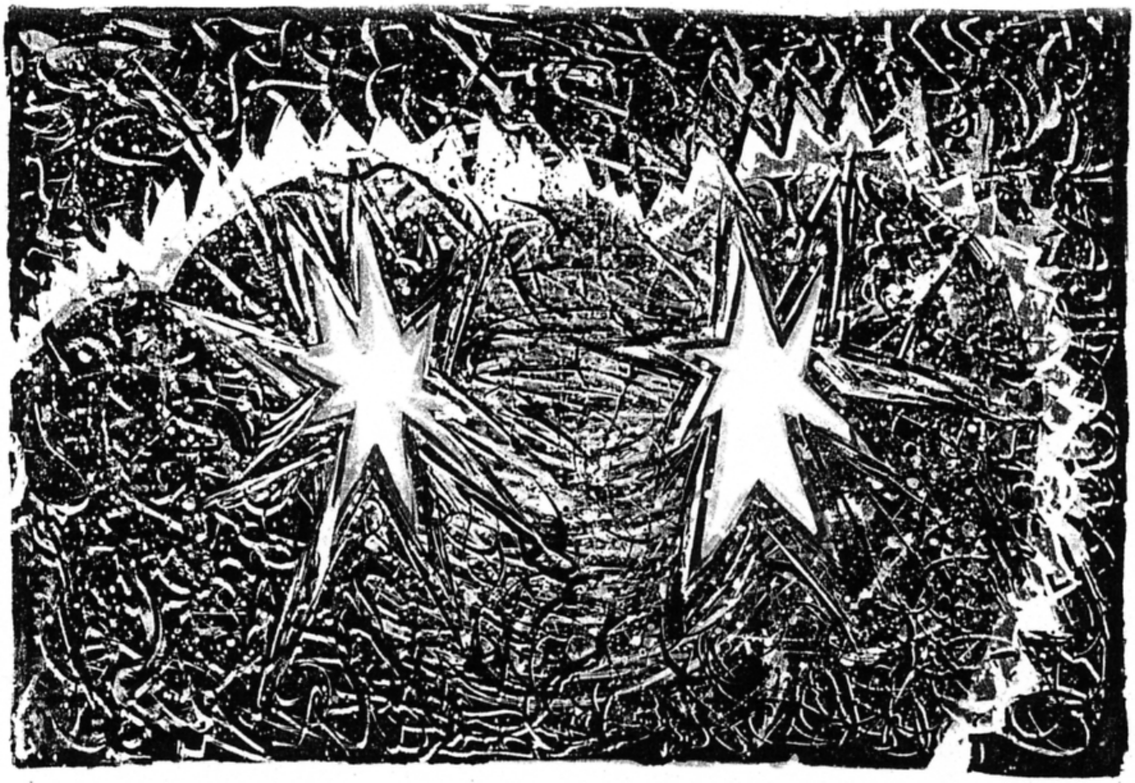

SCIENCE OF MEMORY: CONCEPTS

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Science of Memory: Concepts

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Memory systems

That there are functionally and biologically dissociable memory systems is today widely accepted by memory researchers and this concept deeply influences psychological, cognitive, and biological studies of memory. Advancing the study of memory systems requires the integration of behavioral observations with studies delineating cognitive and neural structures and as a result memory systems is a concept rooted by interlevel analysis. Those new to memory research might find it surprising that despite a rich historical record of philosophical musings, clinical observations, and experimental laboratory findings indicating that there were different "kinds" of memory, a clearly articulated description for many of the dissociable systems familiar today dates only from the mid-20th century. While the exact number of different memory systems remains contentious, one posssibility is that memory will follow the "rule of hand" proposed for the number of critical change variables observed in complex adaptive systems. If so, then there is likely to be a small set of memory systems, more than two but less than ten. Of course, the number of dissociable memory systems depends on how one defines "system." Reaching agreement on a final number is not what is conceptually important. Rather, the concept of memory systems is essential for building an organizational structure for interpreting the data converging across multiple levels of analysis. The search for dissociable memory systems generates experimentally answerable questions. Pursuit of such answers could reveal the nature of the cognitive operations and neural systems supporting behavior.

S.M.F.

Declarative memory is representational, and what is learned is expressed through recollection. Declarative memory provides a way to model the external world, and in this sense is either true or false. It is the kind of memory that is referred to when the term 'memory' is used in everyday language. Procedural memory is expressed through performance rather than recollection, and it is neither true nor false. Procedural memory reflects the various ways that we have learned to interact with the world. Performance changes as the result of experience, and in this sense deserves the term memory, but performance changes without requiring any conscious memory content or in many cases even awareness that memory is being used.

Soon after this distinction was proposed, new interest was directed towards a different task that amnesic patients could sometimes perform well. In the 1970s, it had been reported that, when word stems were given as cues for previously presented words, patients often produced as many previously presented words as their controls. This was a demonstration of what would later be called priming. However, it took some time to appreciate the crucial role of task instructions, and the significance of these findings was initially overlooked. It turned out that amnesic patients perform well only with nonmemory instructions (use this word stem to form the first word that comes to mind). With conventional memory instructions (use this word stem as a cue to help you remember a study word), amnesic patients do more poorly than controls (Graf *et al.* 1984).

Evidence for the special status of priming also came from studies of normal subjects (Tulving *et al.* 1982). These authors wrote '... we are tempted to think that [these priming effects] reflect the operation of some other, as yet little understood, memory system' (p. 341). Thus, priming came to be viewed as a distinct form of memory, separate from what is impaired in amnesia (Tulving and Schacter 1990; Schacter and Buckner 1998). Perhaps the strongest evidence that priming is independent of declarative memory came with the later demonstration that both perceptual and conceptual priming can be fully intact in severely amnesic patients, even though the patients perform at chance on conventional tests of recognition memory constructed from the same test items (Hamann and Squire 1997; Levy *et al.* 2004).

Due to these and other discoveries, it became unwieldy after the mid-1980s to fit the accumulating facts into a two-part dichotomy, such as one based on declarative and procedural knowledge. In addition to skill learning and priming, other kinds of memory abilities were identified and linked to particular brain systems. The cerebellum was discovered to be essential for simple eye-blink classical conditioning. The neostriatum was identified as important for the gradual, feedback-guided learning that results in habit memory.

Other kinds of learning that involve the attachment of positive or negative valence to a stimulus, as in fear conditioning, were found to depend on the amygdala. Given this variety of memory tasks and brain structures, the mid-1980s saw a shift in perspective towards a framework that accommodated multiple (i.e. more than two) memory systems (Tulving 1985; Squire 1987). The term 'nondeclarative' was introduced with the idea that declarative memory refers to one memory system and that 'nondeclarative memory' is an umbrella term referring to additional memory systems (Squire and Zola-Morgan 1988). Figure 58.1 illustrates a taxonomy that incorporates these ideas (for the earliest version of this diagram, see Squire 1987). Note that one can subdivide declarative memory into two separate types (Tulving 1983), one involved with factual knowledge (semantic memory) and one involved with knowledge about specific events (episodic memory).

The notion of multiple memory systems is now widely accepted (Schacter *et al.* 2000; Eichenbaum and Cohen 2001; Squire *et al.* 2004), even if uncertainty remains about exactly how many memory systems there are. One is struck by the fact that the term 'memory system' did not come into comfortable use until it was possible to place the concept, and related experimental work,

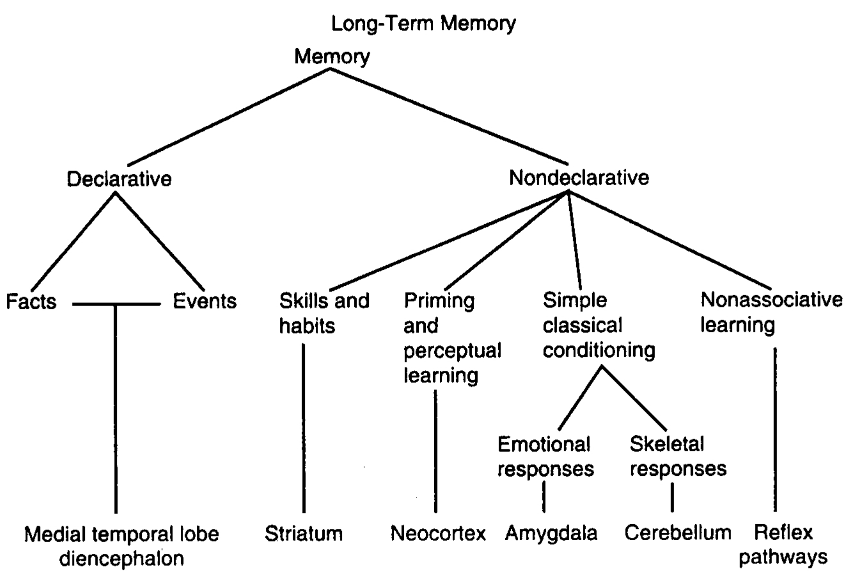

Fig. 58.1 A taxonomy of mammalian long-term memory systems. The taxonomy lists the brain structures thought to be especially important for each form of declarative and nondeclarative memory. In addition to its central role in emotional learning, the amygdala is able to modulate the strength of both declarative and nondeclarative memory.

within a biological framework. The term 'system' has its own tradition within biology (the digestive system, the respiratory system, the nervous system). Even within the nervous system itself, it has been possible for many decades to speak of brain systems as groupings of related structures with defined inputs and outputs, sometimes with identified functional significance (e.g. the cholinergic system, the visual system). The usefulness of the term 'memory system' appears to depend considerably on the extent to which a particular kind of memory can be related to a specific brain system. A memory system is best viewed as a brain system with a significant, though not necessarily exclusive, role in memory function. Emerging biological information has made discussions of memory systems more specific and has helped to define their properties.

History shows that as biological information becomes available about structure and mechanism, explanation becomes more concrete and less dependent on terminology. Terminology is important in psychological science because the concepts tend to be abstract and difficult to pin down. However, terminology is less important when a concept or a function has been related to mechanism. The term 'heredity' may be a little fuzzy, but DNA is not. Whereas one might debate exactly what heredity means, there is no similar argument about DNA. In the case of DNA, one could call it something else. Similarly, in the context of memory systems, 'habit memory' is not easy to define, but there is less difficulty with the 'neostriatum', which has been linked to habit memory (Mishkin *et al.* 1984). The discovery that there are kinds of learning supported by the neostriatum provides considerable clarification and simplification. One can expect to move towards a sharper and more accurate definition of 'habit memory' by considering what kinds of learning, and what kinds of tasks, depend on the neostriatum. Biology provides leverage on the issue of classification and definition.

It is difficult to specify exactly how many memory systems there are. Figure 58.1 lists seven kinds of memory: fact memory, event memory, procedural memory, priming and perceptual learning, emotional learning, conditioning of skeletal responses and nonassociative learning. One can add working memory. That would make eight, but there are a number of uncertain cases. For example, various kinds of nonassociative learning have been demonstrated, even in invertebrates (i.e. habituation and sensitization). These do not constitute memory systems as much as different reflex pathways by which a multiplicity of different stimuli can lead to either diminished or augmented responding. In addition, one could separate priming and perceptual learning, but the difference between priming and perceptual learning seems no more fundamental than the difference, for example, between perceptual and conceptual priming. The point is that there are many kinds of priming and perceptual learning. Fact memory and event memory might merit classification as distinct memory systems, though one could instead take the perspective that these two forms of declarative memory are both products of the medial temporal lobe's interaction with neocortex, and that event memory is different only because it depends on the resources of the frontal lobe to a greater extent than fact memory (Squire 1987). From the perspective of biology, one can identify five basic brain systems that support long-term memory: the medial temporal lobe system, which supports declarative memory; the neostriatum, which supports procedural learning; regions and networks within neocortex, which support varieties of priming and perceptual learning; the amygdala, which supports emotional learning; and the cerebellum, which supports the conditioning of skeletal responses. All these systems can be distinguished in terms of the kinds of information they process, the principles by which they operate, and the brain structures and connections that support them.

At this stage, it is more important and useful to work away at the biology of the various kinds of memory than to debate how many kinds there are. Consider that one does not debate much about how many systems are found in a working automobile. We already know all the parts and how they work. As more is learned about how the brain works, one can expect epistemological questions about what a memory system is and how many there are to become less interesting. In the meantime, it seems reasonable to look for broad principles that can be used to construct a few large categories. Accordingly, one should have in mind on the order of 5–10 memory systems but not, for example, 100. The central idea is that there exist a few major categories, and a few major brain systems, which support the various capacities for experience-dependent behavioral plasticity.

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