Declarative and Nondeclarative Memory: Multiple Brain Systems Supporting Learning and Memory

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Abstract

■ The topic of multiple forms of memory is considered from a biological point of view. Fact-and-event (declarative, explicit) memory is contrasted with a collection of nonconscious (nondeclarative, implicit) memory abilities including skills and habits, priming, and simple conditioning. Recent evidence is reviewed indicating that declarative and nondeclarative forms of memory have different operating characteristics and depend on separate brain systems. A brain-systems framework for understanding memory phenomena is developed in light of lesion studies involving rats, monkeys, and humans, as well as recent studies with normal humans using the divided visual field technique, event-related potentials, and positron emission tomography (PET). ■

INTRODUCTION

The recognition that there are multiple forms of memory developed beginning in the early 1980s, and now only 10 years later a substantial body of experimental data and theoretical material has accumulated. As with any new idea, one can point to historical precedents and frank anticipations (for reviews see Hintzman, 1990; Polster, Schacter, & Nadel, 1991; Roediger, 1990; Schacter, 1987; Squire, 1987; Tulving, 1985; Weiskrantz, 1987). Yet, in the early 1980s one can also identify a few experimental findings that were especially influential in establishing the idea that memory is not a single mental faculty (Cohen & Squire, 1980; Graf, Squire, & Mandler, 1984; Jacoby & Witherspoon, 1982; Malamut, Saunders, & Mishkin, 1984; Tulving, Schacter, & Stark, 1982; Warrington & Weiskrantz, 1982). In the short time since these experiments were carried out, the topic of multiple forms of memory has become a major theme of memory research. Recent work has focused especially on three fundamental issues: What are the various kinds of memory? What are their characteristics? How is each kind of memory implemented in the organization of brain systems? Following some introductory remarks about terminology, each of these issues will be discussed in turn.

TERMINOLOGY

Declarative Memory

Although a variety of terms have been used, one finds striking consistency among them. One kind of memory provides the basis for conscious recollections of facts and events. This is the kind of memory that is usually meant when the terms "memory" and "remembering" are used in ordinary language. Fact-and-event memory refers to memory for words, scenes, faces, and stories, and it is assessed by conventional tests of recall and recognition. This kind of memory was termed "declarative" to signify that it can be brought to mind and that its content can be "declared" (Cohen & Squire, 1980; Cohen, 1984; for its earlier use in psychology, see Anderson, 1976). Other similar terms include explicit memory and relational memory. Declarative memory identifies a biologically real category of memory abilities. Severely amnesic patients fail tasks of recall and recognition (declarative memory), while succeeding as well as normal subjects at many other kinds of memory tasks (see below). Thus, declarative memory depends on the integrity of brain structures and connections in the medial temporal lobe and the diencephalon that have been associated with memory functions and that, when dam-

aged, cause amnesia. At the same time, it should be emphasized that declarative memory is not just a story based on what amnesic patients can and cannot learn. That is, the concept of declarative memory is not locked into circularity around the performance of amnesic patients. For example, it is notable that the operating characteristics of declarative memory also distinguish this form of memory from other forms (see Characteristics of Declarative and Nondeclarative Memory, below). It is important that distinctions between kinds of memory not rest on dissociations alone and that they can be supported by independent sources of evidence (cf. Sherry & Schacter, 1987; Schacter, 1992). In this way, one can go beyond simply dissociating one component of cognition from another and begin to understand how functions are actually related to each other and how they are organized in the brain.

Nondeclarative Memory

Declarative memory can be contrasted with a collection of nonconscious memory abilities, all of which are intact in otherwise severely amnesic patients. The term *procedural* memory was originally used to contrast with *declarative* memory (Winograd, 1975; Cohen & Squire, 1980). Whereas the term *procedural* appropriately describes a wide variety of skill-based kinds of learning, certain memory phenomena have also come to light that are clearly not declarative but that are also not well accommodated by the term *procedural*. Subsequently, we suggested the broader and more neutral term *nondeclarative* to identify a heterogeneous group of learning abilities that are defined not by any positive feature so much as by the fact that they are not declarative (Squire & Zola-Morgan, 1988). Thus, the memory abilities that are not declarative are not of a single type and are not subserved by a single brain system. Whereas declarative memory refers to a biologically meaningful category of memory, which is dependent on a specific brain system, nondeclarative memory embraces several kinds of memory and depends on multiple brain systems. The term implicit memory (Reber, 1967; Schacter, 1987) has a meaning similar to nondeclarative memory.

KINDS OF MEMORY: A SUMMARY OF RECENT DATA

Studies with amnesic patients have provided particularly compelling evidence about the kinds of learning that are declarative and nondeclarative. Amnesic patients fail tasks of recall and recognition (tasks that are thought to depend on declarative memory), so that a finding of fully normal performance in this patient group constitutes strong evidence that a task does not depend materially on the strategies of declarative memory. Although this section focuses on findings from amnesic patients, other important information has come from demonstrations of

functional dissociations in normal subjects and also from studies of rats and monkeys with surgical damage to the brain structures that, when damaged in humans, cause amnesia.

Nondeclarative memory includes information that is acquired during skill learning (motor skills, perceptual skills, and cognitive skills), habit formation, simple classical conditioning including some kinds of emotional learning, the phenomenon of priming, and other knowledge that is expressed through performance rather than recollection. Experience can cumulate in behavioral change but without affording conscious access to any previous learning episodes or to any memory content. To be sure, many skill learning and conditioning paradigms give rise to both declarative and nondeclarative knowledge (Mackintosh, 1985; Willingham, Nissen, & Bullemer, 1989). However, the two kinds of knowledge can arise independently. Some tasks tap primarily what has been acquired declaratively; some tap nondeclarative knowledge; still other tasks measure the contribution of both declarative and nondeclarative knowledge. Figure 1 illustrates a classification scheme for declarative and nondeclarative memory.

Skills and Habits

Amnesic patients can acquire a variety of skills at an entirely normal rate. These include motor skills (Brooks & Baddeley, 1976), perceptuomotor skills (Nissen & Bullemer, 1987), perceptual skills (Cohen & Squire, 1980), and cognitive skills (Squire & Frambach, 1990). Studies with speeded reading tasks, among other methods, show that acquired skills can reflect highly specific information about the items that were encountered (Moscovitch, Winocur, & McLachlan, 1986; Musen, Shimamura, & Squire, 1990; Fig. 2A). Moreover, the skills can be based on novel material (Musen & Squire, 1991; Fig. 2B).

Skill-based learning is also intact in monkeys with large medial temporal lobe lesions who fail tasks of object
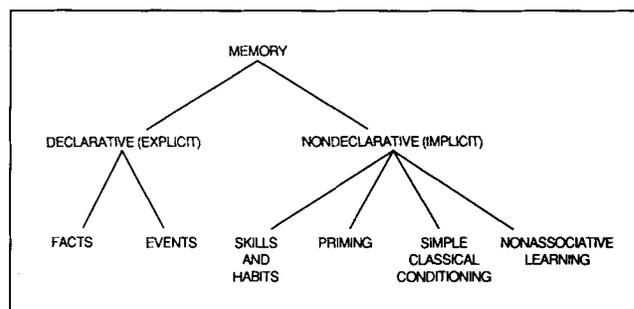

Figure 1. Classification of memory. Declarative (explicit) memory refers to conscious recollections of facts and events. Nondeclarative (implicit) memory refers to a heterogeneous collection of abilities whereby experience alters behavior nonconsciously without providing access to any memory content. (From Squire & Zola-Morgan, 1991.)
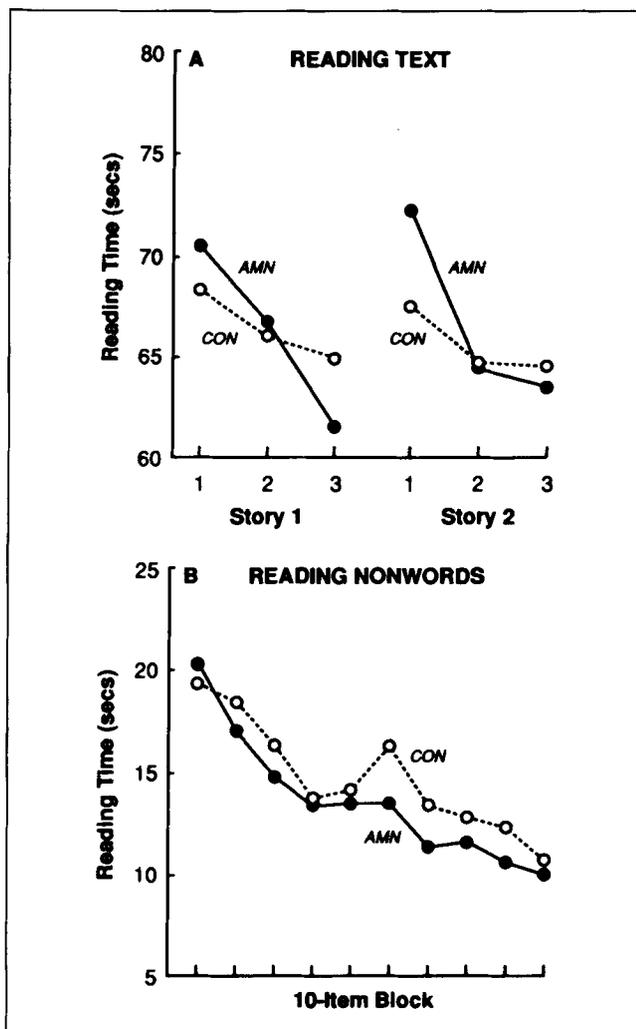
Figure 2. Intact learning by amnesic patients as measured by improved reading times. In both cases, other experiments demonstrated that the learning persisted across a 10-min delay. (**A**) Text-specific reading skill. Subjects read aloud a story three times in succession, followed immediately by three readings of a second story. (**B**) Acquisition of a reading skill for novel material. Subjects read aloud a 100-item list consisting of 5 nonwords repeated 20 times each. Amnesic patients improved their reading speed at the same rate as normal subjects. AMN, amnesic patients; CON, control subjects. (From Musen, Shimamura, & Squire, 1990; Musen & Squire, 1991.)

recognition memory (Zola-Morgan & Squire, 1984). For example, monkeys with medial temporal lobe lesions succeeded at acquiring an associative habit, i.e., the 24-hr concurrent discrimination task, in which the same 20 object pairs are presented once each day and one object in each pair is always correct (Malamut et al., 1984). Similarly, rats with damage to the hippocampal system succeeded as well as control animals at a win–stay habit task in which specific arms of a radial maze were associated with reward, despite failing a win–shift task in the same apparatus (Packard, Hirsh, & White, 1989).

Recently, there has been interest in the possibility that more complex kinds of learning, such as probability learning or artificial grammar learning, might also de-

pend on nondeclarative memory. In the artificial grammar learning paradigm (Reber, 1967), subjects first inspect a group of letter strings that adhere to a finite-state rule system. Subjects are then able to classify new letter strings as either "grammatical" or "nongrammatical" at well above chance levels. There has been disagreement as to whether successful classification learning reflects implicit (nonconscious) memory or partially developed, imperfect explicit (conscious) memory. Amnesic patients provide a way to decide between these two views. In a recent experiment, amnesic patients were able to classify grammatical and nongrammatical letter strings as well as normal subjects despite impaired recognition memory for the items they had encountered (Knowlton, Ramus, & Squire, 1992, Fig. 3).

These results argue for the operation of two kinds of memory in artificial grammar learning. One kind of memory stores declarative information about the specific items that are presented. The second kind of memory stores information nondeclaratively, either by abstracting information from the items in the form of rules, or by assembling information from the items as a collection of associations between item features and the grammatical category. Memory for the specific items is not important in the second kind of learning. Rather, the information that is invariant across many trials is important. In this sense, artificial grammar learning resembles skill learning, habit formation, and conditioning.

Priming

Priming refers to the improved facility for detecting or processing a perceptual object based on recent experience (Shimamura, 1986; Tulving & Schacter, 1990). Contrary to the suggestion from early studies that priming is based on modifying preexisting memory representations (Diamond & Rozin, 1984; Cermak, Talbot, Chandler, & Wolbarst, 1985), priming can involve the acquisition of new information. The important finding is that amnesic patients exhibit fully intact repetition priming effects, whether the test materials are words, familiar objects, or entirely novel material such as nonwords, novel objects, or line patterns (Gabrieli, Milberg, Keane, & Corkin, 1990; Haist, Musen, & Squire, 1991; Schacter, Cooper, Tharan, & Rubens, 1991; Musen & Squire, 1992a). In one study, perceptual identification of briefly presented words and nonwords was enhanced in amnesic patients and control subjects to a similar extent following a single presentation of the test items (Haist et al., 1991; Fig. 4A). The priming effect for nonwords did not appear to be based on the priming of words that were phonologically or orthographically similar to the nonwords, i.e., the priming effect for nonwords was not based on neighborhood effects involving real words. Accordingly, it appears that priming can involve the creation of novel representations and does not reflect simply the activation of preexisting representations. These priming effects can
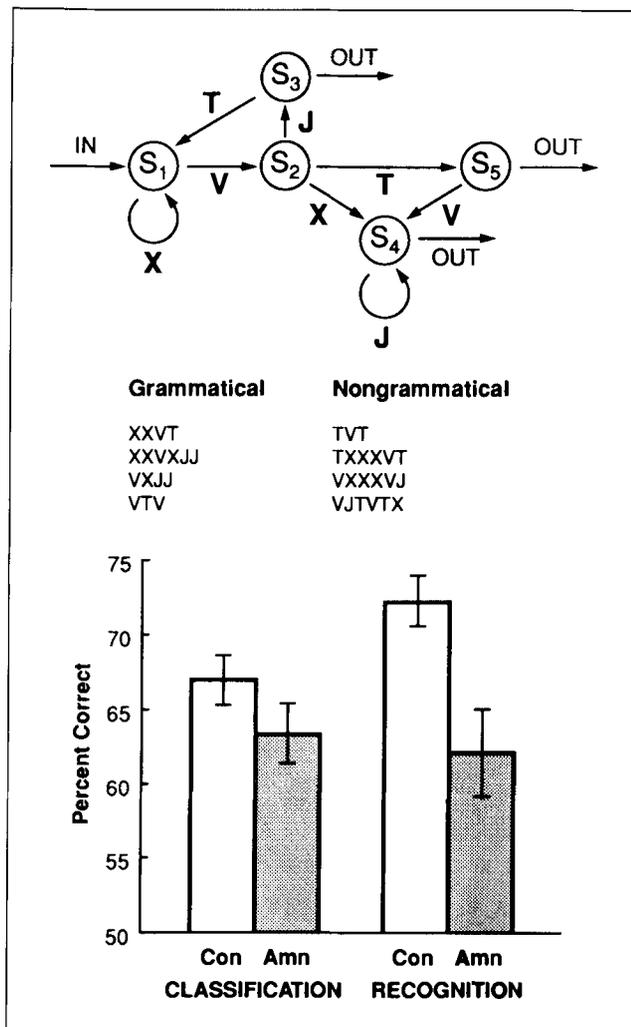
Figure 3. Normal artificial grammar learning by amnesic patients. Top. A finite-state rule system for generating "grammatical" letter strings. Below the diagram are examples of "grammatical" letter strings, which can be generated by this rule system, and nongrammatical letter strings, which violate the rule system at one letter position. Bottom. Percent correct classification judgments and recognition memory judgments by amnesic patients ($n = 13$) and control subjects ($n = 14$). After studying a list of 23 grammatical letter strings twice each, subjects saw 46 new items (half grammatical and half nongrammatical) and attempted to classify each letter string; or they saw 23 old items and 23 new (nongrammatical) items and decided which ones had been presented. Brackets show standard error of the mean. AMN, amnesic patients; CON, control subjects. (From Knowlton, Ramus, & Squire, 1992.)
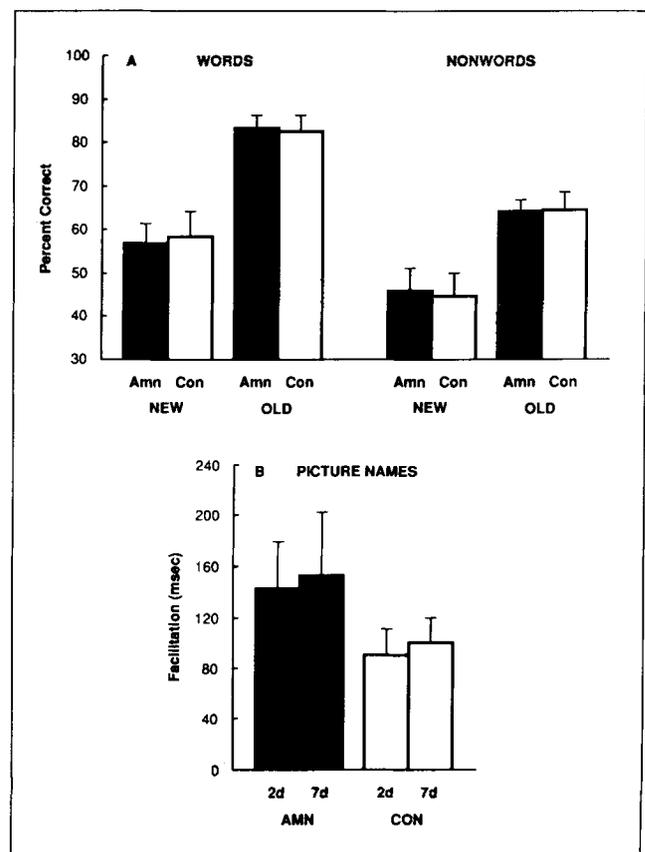

Figure 4. Intact repetition priming in amnesic patients. (A) Percent identification of briefly presented words and nonwords. Old items were presented once prior to the perceptual identification test. The advantage of identifying old items over new items indicates priming. (B) Facilitation of picture naming at 2 and 7 days after a single presentation. Priming was measured in each case by subtracting the time needed to name 50 new pictures from the time needed to name 50 old pictures. Brackets show standard errors of the mean. AMN, amnesic patients; CON, control subjects. (From Haist, Musen, & Squire, 1991; Cave & Squire, 1992.)

be highly specific in the sense that the magnitude of priming is often diminished by altering the perceptual features of test material (Schacter, 1990; Cave & Squire, 1992).

Priming not only improves the ability to identify stimuli but also alters judgments and preferences that involve the same stimuli. In a recent study, amnesic patients exhibited the same tendency as normal subjects to judge proper names as famous, if the names had recently been presented (Squire & McKee, 1992). This facilitatory effect,

which was originally studied in normal subjects (Jacoby, Woloshyn, & Kelley, 1989; Neeley & Payne, 1983), was as large for nonfamous names (e.g., Fritz Bernowski) as for famous names (e.g., Leon Jaworski). Specifically, the probability of identifying a famous name as famous increased from 53 to 65% as a result of a recent encounter with the name, and the probability of identifying a nonfamous name as famous increased from 12 to 23%.

In some circumstances, priming effects can last a very long time. For example, in normal subjects the response time to name pictures of common objects is reduced for several weeks after a single, brief presentation of the pictures (Mitchell & Brown, 1988). Amnesic patients exhibit this facilitatory effect at full strength (Cave & Squire, 1992). In the first of two experiments, amnesic patients exhibited intact priming of picture naming even 7 days after the pictures had been presented (Fig. 4B). In the second experiment, priming in both normal subjects and amnesic patients was shown to depend on highly specific

visual information as well as on less visual, more conceptual information. Thus, new pictures were named in 1129 msec, old pictures were named in 996 msec, and pictures that changed from one example to another example of the same item (e.g., two kinds of dogs) were named in 1051 msec. In contrast to these effects, recognition memory was severely impaired in the amnesic patients, whether assessed by choice accuracy or response time. These results provide the first evidence of long-lasting priming in amnesic patients following a single encounter, which occurs as strongly in the patients as in normal subjects. Nondeclarative memory can apparently support even long-lasting changes in performance following a single encounter.

Declarative Memory: Recall, Recognition, and Conscious Feelings of Familiarity

Recall and recognition are ordinarily considered to provide two different ways to measure declarative memory. One view has been that recall and recognition are closely linked functions and are similarly impaired in amnesia. An alternative view, based on studies of normal subjects, is that recognition is supported in part by priming, i.e., by the fluency with which a subject processes the recognition cue (Mandler, 1980; Jacoby, 1983). By this view, recall depends on declarative memory, and recognition depends on both declarative and nondeclarative memory. A test of these two views was recently carried out with amnesic patients (Haist, Shimamura, & Squire, 1992). Free recall, forced-choice recognition, and confidence ratings for the recognition judgments, which presumably assess conscious feelings of familiarity, were tested parametrically. On 12 separate occasions, 20 different words were studied, and memory was then tested at one of several retention intervals ranging from 15 sec to 8 weeks. Free recall was tested six times, and forced-choice recognition (together with confidence ratings) was also tested six times. If recognition judgments are significantly supported by a nondeclarative process like priming that is intact in amnesia, then recognition memory should be disproportionately spared in amnesia in comparison to recall. However, this effect was not observed (Fig. 5).

The crucial finding was that the recognition judgments of amnesic patients and the confidence ratings attached to these judgments were about the same at every retention interval as would have been predicted from the recall scores. These results do not rule out the possibility that priming or other nonconscious processes might sometimes contribute to recognition performance (see Johnston, Hawley, & Elliott, 1991). However, the results do not support the idea that recognition typically draws support from such processes. The results also do not support the suggestion that amnesic patients will make correct recognition choices but then claim they are guessing (Weiskrantz, 1988). Recall, recognition, and as-
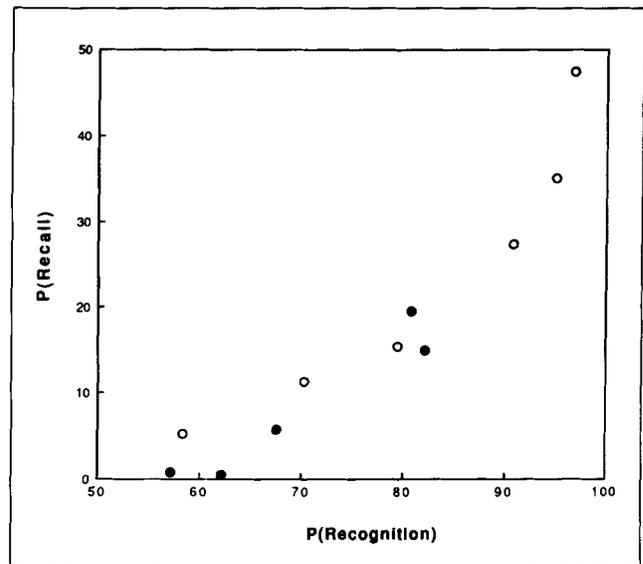

Figure 5. State-trace plot showing the probability of recall as a function of the probability of recognition. Average scores are plotted for 12 amnesic patients (filled circles) and for 19 control subjects (open circles) at 11 different retention intervals ranging from 15 sec to 8 weeks. Recall and recognition were tested at the same (variable) retention interval in all 11 cases. The points appear to align themselves along a single monotonically increasing function, indicating that recall and recognition scores can be expressed as a quantitative change along a single dimension. These results do not support the view that recognition memory is supported significantly by nondeclarative memory. (From Haist, Shimamura, & Squire, 1992.)

sociated feelings of familiarity are related functions of declarative memory and are equivalently dependent on the brain system damaged in amnesia.

Two earlier studies of amnesic patients came to a different conclusion about recall and recognition based on comparisons at a single performance level (Hirst, Johnson, Phelps, Risse, & Volpe, 1986; Hirst, Johnson, Phelps, & Volpe, 1988). We were unsuccessful at replicating the second of these two studies using the identical experimental design (Haist et al., 1992; Experiment 2). Although it is unclear what accounts for the different findings, one possibility is that there are important differences in the patient populations such as the prevalence of frontal lobe pathology. Frontal lobe pathology occurs in some etiologies of amnesia and produces characteristic cognitive impairment in addition to amnesia itself (cf. Shimamura, Janowsky, & Squire, 1991). For example, damage to the frontal lobe can affect recall performance more than recognition (Jetter, Poser, Freeman, & Markowitsch, 1986), perhaps because of deficient search strategies that are more critical for recall.

Learning Novel Associations

The varieties of learning that can be acquired normally by amnesic patients might lead one to suppose that nondeclarative memory can support any kind of learning

that can be accomplished by declarative memory. However, consider the case of acquiring new associations rapidly. Normal subjects can quickly memorize new word pairs declaratively. The hippocampal formation and related structures are specialized for forming conjunctions rapidly between arbitrarily different stimuli. By contrast, nondeclarative memory appears poorly suited for such learning. Nondeclarative memory can support the gradual and cumulative acquisition of new associations, as in classical conditioning, but does not seem well adapted for acquiring novel associations rapidly. This issue has been explored in two different paradigms. The first involves the priming of new associations, which is a robust phenomenon in normal subjects (Graf & Schacter, 1985). Specifically, word-stem completion priming is greater when the word stem presented at test is paired with a previously associated word than when the word stem is paired with a new word (e.g., study BELL–CRADLE, test BELL–CRA vs. test LAND–CRA). Subsequently, it was found that amnesic patients do not exhibit this effect reliably (Shimamura & Squire, 1989; Mayes & Gooding, 1989; Cermak, Bleich, & Blackford, 1988; Schacter & Graf, 1986), probably because at one crucial step the phenomenon depends critically on declarative memory (see Shimamura & Squire, 1989).

The second paradigm in which the learning of new associations has been explored involves measures of reading speed (Moscovitch et al., 1986; Musen & Squire, 1992b) or perceptual identification (Musen & Squire, 1992b). In this case, word pairs are presented for study and then memory is tested by presenting the same word pairs, different word pairs, or old words in new pairings. Old word pairs would be expected to be read more rapidly (or identified more accurately) than new word pairs. In addition, if new associations are formed between the two members of each word pair, then presenting the members of a pair in combination with other old words should break the association. If new associations are formed, recombined word pairs should be treated more like new word pairs than like old word pairs. Evidence for learning of new associations in a single trial was reported in an initial study involving young, elderly, and memory-impaired subjects (Moscovitch et al., 1986), but the effect was a small one and it was not clear that it was detectable in the memory-impaired group itself. Subsequently, in three separate experiments involving a reading speed measure, this effect was not observed in either normal subjects or amnesic patients unless multiple learning trials were provided (Musen & Squire, 1992b). In a fourth experiment, a small effect was observed using a perceptual identification method, but only when the results for amnesic patients and control subjects were combined.

In summary, amnesic patients do not readily form new associations between unrelated stimuli. Although such an effect might yet be observed under optimal circumstances, it would appear that nondeclarative memory is not specialized for such learning. In contrast, declarative memory is adapted precisely for such learning, i.e., for the rapid acquisition of relational information involving multiple stimuli.

CHARACTERISTICS OF DECLARATIVE AND NONDECLARATIVE MEMORY

To what extent can declarative and nondeclarative memory be identified and characterized independently of evidence from functional dissociations in normal subjects and independently of the evidence concerning what amnesic patients can and cannot learn? Declarative memory is fast, accessible to conscious recollection, and is flexible, i.e., available to multiple response systems. Nondeclarative memory is nonconscious, and it is less flexible, i.e., it provides limited access to response systems not involved in the original learning. Attempts to account for multiple kinds of memory within a transfer-appropriate processing framework (cf. Blaxton, 1989; Roediger, 1990) usefully capture this feature of nondeclarative memory. The transfer-appropriate processing approach emphasizes that memory retrieval is successful to the extent that the processing requirements of the study task are similar to the processing requirements of the retrieval task.

Three important experiments in rats and monkeys have demonstrated striking differences in the flexibility of declarative and nondeclarative kinds of memory (Eichenbaum, Mathews, & Cohen, 1989; Eichenbaum, Stewart, & Morris, 1990; Saunders & Weiskrantz, 1989). There is a straightforward connection between the constructs of declarative and nondeclarative memory, which are grounded in studies with humans, and the kinds of memory studied in rats and monkeys: in both cases, one kind of memory depends on the integrity of the hippocampus and related structures and another kind does not. The studies with experimental animals have as their starting point the finding that animals with hippocampal damage will sometimes learn tasks successfully, albeit at a much slower rate than normal. Subsequent transfer tests then demonstrate that normal animals and the animals with damage to the hippocampal system have acquired different kinds of knowledge. The normal animals have acquired a flexible representation that can be expressed in new ways. For example, in one study of discrimination learning involving two pairs of stimuli (AB and CD), a high level of performance persisted in the normal animals when the correct stimuli (A and C) were paired with different incorrect stimuli (i.e., AD and BC). In contrast, the animals with hippocampal system damage had apparently acquired conditional associations and could not express their knowledge outside the context in which the knowledge was originally acquired. Performance fell to chance levels when the stimuli were recombined (Eichenbaum et al., 1989). Other evidence from humans also suggests that nondeclarative memory

can be inflexible and hyperspecific (Tulving & Schacter, 1990). These studies show that declarative and nondeclarative memory have different characteristics.

MEMORY AND BRAIN SYSTEMS

It has sometimes been suggested that the distinction between kinds of memory is best understood as reflecting the different processes that are required to access a common underlying engram (Blaxton, 1989; Jacoby, 1988; Masson, 1989; Roediger, 1990). In support of this idea, it could be pointed out that the different kinds of memory (i.e., declarative and nondeclarative memory) can appear to be rather similar to each other. For example, the same word can be produced as verbal output, either as a result of priming or as a result of cued recall, and in both cases the effect can be rather specific to the training conditions. Thus, the memories that are formed in each case can seem to substitute for one another as viewed from a behavioral endpoint. However, the view presented here is that these forms of memory are different in terms of what kind of learning occurs in each case, in terms of what is achieved as stored knowledge, and in terms of the brain systems that are involved. When discussion of the issues is limited to priming, the matter can seem difficult to settle (see Schacter, 1990, 1992, for a consideration of the so-called processes-systems debate that focuses on how to account for priming phenomena). However, when the discussion is broadened to include skill learning, habit learning, and conditioning, a brain-systems view of multiple memories is more consistent with the biological and psychological facts than a processing view.

What is known about the brain systems important for declarative and nondeclarative learning? The evidence is clearest in the case of classical conditioning of reflexes involving the skeletal musculature (Thompson, 1986). In this case, pathways and connections within the cerebellum are part of the essential circuitry that supports the memory. The hippocampus is not essential. Relevant evidence also comes from tasks in which monkeys learn about visually presented objects. The ability to remember a newly presented visual object, so that it can be selected in a later recognition memory test, depends on an interaction between, on the one hand, the visual areas in neocortex (especially area TE in inferotemporal cortex) that are important for perception, and, on the other hand, the limbic–diencephalic regions that are essential for transforming perceptions into declarative memories (Mishkin, 1982; Squire & Zola-Morgan, 1991). By contrast, the ability to develop a habit involving the same visual object (e.g., when the object is one of the stimuli in the previously mentioned 24-hr concurrent discrimination task) requires an interaction between visual areas in neocortex and the neostriatum (Wang, Aigner, & Mishkin, 1990). A similar distinction between memory and habit learning in terms of the importance of the hippocampal

system and the caudate nucleus, respectively, has also been elegantly demonstrated in rats (Packard, Hirsch, & White, 1989; Packard & McGaugh, 1992).

One could conceivably argue from these data that the neocortex holds the engram in both the memory and the habit tasks, and that the hippocampal system and the basal ganglia are simply two different routes by which the same information can be expressed in behavior. If so, one could suppose that the biological facts just summarized are consistent with a "processes" view of multiple memories. This scenario presumes that the information expressed in the memory tasks and in the habit tasks is in fact stored in neocortex from the first moment that learned behavior is evident. However, there is no evidence to support such an assumption, and some reason to think that it is incorrect. Single-cell recording in monkeys has identified plasticity in the temporal lobe in one-trial learning tasks, so it is clear that neurons can change their properties quickly in response to a change in the environment (cf. Fuster & Jervey, 1981; Miller, Li, & Desimone, 1991; Riches, Wilson, & Brown, 1991). However, it is not at all clear that this plasticity is related to long-term declarative memory. Instead, altered neuronal activity could reflect short-term (working) memory or priming.

It is consistent with a number of observations about the role of the medial temporal lobe in memory (for review, see Squire, 1992) to suppose that plasticity related to long-term declarative memory can occur rapidly in the hippocampal system. Plasticity in the neocortex related to long-term memory may then develop only slowly and not be detectable initially. Thus, in the case of the interaction between neocortex and the hippocampal system that supports declarative memory, the plasticity that records the memory may initially exist only within the hippocampal system itself. If these ideas are correct, it cannot be the case that a common engram in neocortex serves both declarative memory (through the hippocampal system) and nondeclarative memory (through the basal ganglia).

Recent studies also provide some clues about the neural basis of repetition priming and suggest that priming is also best understood as depending on a brain system different from the system supporting declarative memory. First, divided visual field studies show that more word-stem completion priming occurs when word stems are presented to the right cerebral hemisphere (in the left visual field) than to the left cerebral hemisphere (in the right visual field) (Marsolek, Kosslyn, & Squire, 1992). The right-hemisphere advantage occurred if and only if the study words and the test stems were in the same sensory modality and in the same typecase (Fig. 6A). Thus, word priming is sometimes based on form-specific mechanisms that are more effective in the right cerebral hemisphere than in the left.

By contrast, when cued-recall (i.e., explicit memory) instructions were given to the effect that subjects should
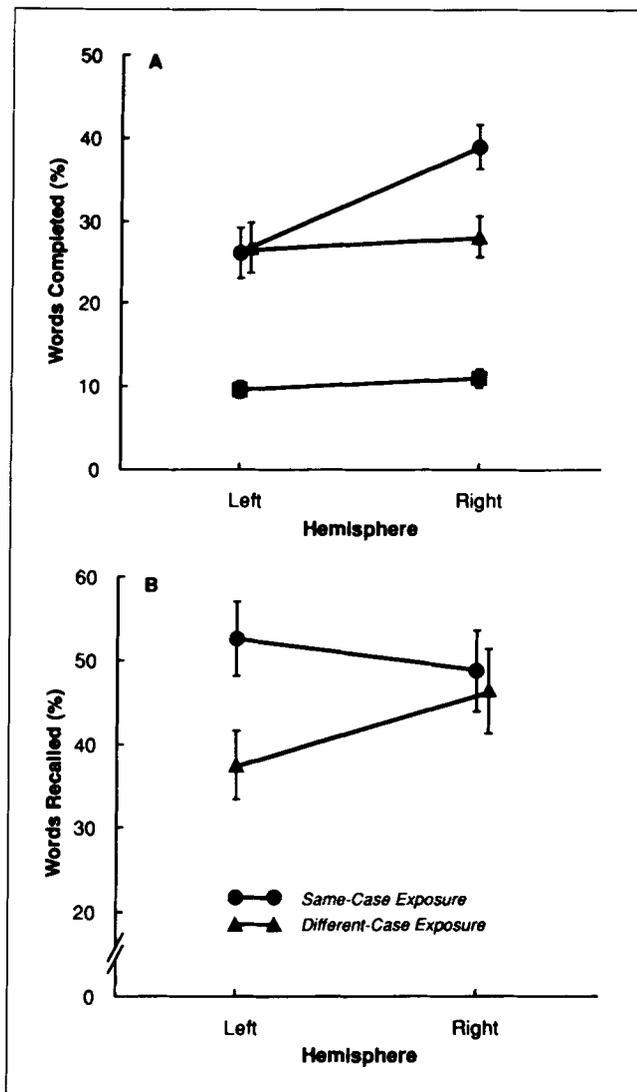
Figure 6. Normal subjects saw words in their central visual field (e.g., MOTEL or motel), and then saw word stems (e.g., MOT or mot) presented briefly in either the left or right visual field, i.e., so that the stems were initially received by the right or left cerebral hemispheres, respectively. Half the word stems were presented in the same lettercase as during study, and half were presented in the opposite lettercase. (**A**) Word-stem completion priming. Subjects were instructed to complete each stem to form the first word that comes to mind. Squares show baseline priming rates, e.g., the probability of completing MOT to form MOTEL when no words beginning with MOT were encountered during study. (**B**) Cued recall. Subjects were instructed to recall study words using the word stems as cues. Brackets show standard errors of the mean. (From Marsolek, Kosslyn, & Squire, 1992.)

try to recall the study words using word stems as cues, cued recall was slightly (though not significantly) better when the word stems were presented to the left hemisphere than to the right (Fig. 6B). Furthermore, in striking contrast to the results for word-stem completion priming, presenting study words and test stems in the same typecase improved performance only when the stems were presented to the left hemisphere.

These findings make the distinction between priming and declarative memory more specific and concrete. Indeed, the divided visual field experiments provide direct evidence about the locus of brain systems supporting declarative and nondeclarative memory. Whereas priming can sometimes be supported more effectively by the right hemisphere than the left, declarative memory need not depend on this same brain organization. Thus, word-stem completion priming and word-stem cued recall differ with respect to which cerebral hemisphere is most effective in supporting performance. This finding suggests that the same engram does not support performance in both cases. One could argue that memory for recently studied words is represented in a widely distributed network and that one component of this network in the right hemisphere is dominant in supporting priming, and that a different component in the left hemisphere is dominant in supporting cued recall. However, on this view it cannot be the case that priming and declarative memory depend on the same engram.

One could also suppose that different processes in the left and right hemispheres, important for cued recall and priming, respectively, are able to access a common engram. However, such an interpretation is in conflict with much biological data and with current perspectives about the locus of memory storage, which emphasize the close relationship between the locus of storage and the locus of the processing systems that are engaged during the perception, processing, and analysis of the material being learned (Mishkin, 1982; Squire, 1987). For example, split-brain studies show that the left and right hemispheres can store separate memories relating to different components or features of the same stimulus (Levy & Trevarthen, 1977).

A recent functional anatomical study using positron emission tomography (PET) provided direct evidence for the importance of right posterior, extrastriate cortex in word priming (Squire, Ojemann, Miezin, Petersen, Videen, & Raichle, 1992). In that experiment, both study words and test word stems were presented to center visual field and both were printed in uppercase letters. One finding was a significant reduction in cerebral blood flow in a region of right extrastriate cortex during word-stem completion priming. The reduction occurred in comparison to a baseline condition in which subjects also completed word stems but priming could not occur because none of the possible word completions had been presented for study. One way to understand the finding of reduced activity during priming is that, for a time after a perceptual stimulus has been presented, less neural activity is required to process the same stimulus. This observation thus suggests a neural account for the key psychological feature of priming—that less information is needed to perceive and identify a stimulus the second time it is presented. A second finding was activation of the right hippocampal region when subjects used the word stems as cues to recall the study words.

The activation was significantly greater during the cued recall condition than during priming. Reasons why activation was observed in the right, not in the left, hippocampal region in this case have been discussed elsewhere (Marsolek et al., 1992; Squire et al., 1992).

The PET study strongly endorses the brain systems view of multiple forms of memory. Word-stem completion priming can be supported significantly by early-stage, right posterior cortex that operates prior to the analysis of meaning and prior to the involvement of the hippocampal region and widespread cortical areas that must be engaged for an item to be remembered declaratively, i.e., in relation to the item's meaning and in relation to the context in which the item was presented. It remains possible that the posterior cortical locus identified in PET, which is important for form-specific, word-stem completion priming, is *one* of the critical sites that are bound together by the hippocampal system (Squire & Zola-Morgan, 1991) and which together comprise declarative memory for a whole event. However, this posterior cortical locus could not support much declarative knowledge on its own. Indeed, in earlier PET studies (Petersen, Fox, Posner, Mintun, & Raichle, 1988; Petersen, Fox, Snyder, & Raichle, 1990), precisely this region of right extrastriate cortex was found to be activated by the visual features of words, not their orthographic regularity. Words, nonwords, nonsense letter strings, and letter-like shapes were all effective at activating this locus.

Finally, recent studies of event-related potentials (ERPs) in normal subjects also point to different brain systems for declarative and nondeclarative memory (Paller, 1990; Paller & Kutas, 1992). ERPs related to declarative memory (word recall or recognition) had a different amplitude, latency, and scalp distribution than ERPs related to word-stem completion priming or perceptual identification priming. For example, in one study (Paller & Kutas, 1992), the ERP associated with recollection was largest at a latency of 500–800 msec, whereas the ERP associated with priming was largest at a latency of 400–500 msec. The ERP related to recollection was dominant at left anterior electrode placements. The ERP related to priming was dominant at posterior electrode placements. These findings demonstrate that declarative and nondeclarative memory are associated with different neural events at different brain loci.

It should be noted that a left hemispheric word form area has been proposed as a locus of word priming (Schacter, 1990; Tulving & Schacter, 1990). The PET findings and the divided visual field studies indicate directly that this cannot be a general explanation for repetition priming of words. More likely, left or right posterior cortex is important depending on whether repetition priming is largely form-specific or whether it is supported by more abstract mechanisms. For example, some priming is found across sensory modalities, albeit less than within modality, and across-modality priming cannot be form specific. Priming may occur in any of the multiple cortical areas known to be involved in visual processing. Which areas are most important in any particular case should depend on task demands, the characteristics of the test stimuli, and the similarity between study and test stimuli.

CONCLUSION

During the past few years, a considerable amount of new information has become available about different forms of memory. Data from amnesic patients, as well as from normal subjects and experimental animals, have expanded and redefined the category of nondeclarative memory. Nondeclarative memory is now understood to include highly specific perceptual skill learning, win–stay habit learning, artificial grammar learning, and priming of novel material. At the same time, studies of normal human subjects using new neuroimaging technology and event-related potentials, and studies of animals with selective lesions, have affirmed the biological reality of multiple memory systems. Organisms have available to them multiple ways of benefiting from experience and acquiring knowledge. In most situations, more than one memory system will be engaged. These memory systems have different operating characteristics, acquire different kinds of knowledge, and depend on different brain structures and connections for their operation.

A final comment is in order about "processing" views of multiple forms of memory. When any idea about the function of a complex device is stated very abstractly, it can be difficult to know what evidence would count for or against it, and even whether it can be properly tested. The discussion of multiple memories that has been cast in the language of processing functions is rather abstract, and also has been focused mostly on the phenomenon of priming. It is therefore not entirely clear that a processing approach and a brain-systems framework are mutually exclusive (also see Schacter, 1992). What is clear is that multiple forms of memory are supported by separate brain systems and have different characteristics. Although there is surely interaction between the systems, a feature that is emphasized within the processing approach (Jacoby, 1988), a brain-systems framework provides the most complete and satisfying account of memory. To understand the organization of a complex problem like memory, it will be essential to combine the strategies of cognitive psychology with those of neuroscience. "It is not usually advantageous to have one hand tied behind one's back when tackling a very difficult job" (Crick, 1988, p. 150).

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