

Classifying Human Long-term Memory: Evidence from Converging Dissociations

Lars Nyberg and Endel Tulving

*Rotman Research Institute of Baycrest Centre, University of Toronto,
Ontario, Canada*

This paper reviews the support for multiple human long-term memory systems that is provided by experimental findings of dissociations reported in the literature. Four putative systems are examined: episodic, semantic, perceptual representation (PRS) and procedural memory. The four systems are contrasted for four different forms of dissociations (functional, developmental, pharmacological and brain damage). At least one example of 23 of the 24 different types of dissociations is described. It is argued that this evidence from converging dissociations provides support for the existence of multiple long-term memory systems. The studies reviewed provide some hints about the critical neural substrates of different systems. This neuro-anatomical information was compared and found to be consistent with the results of available functional neuroimaging studies.

INTRODUCTION

An issue of fundamental importance in memory research has to do with the classification of memories. The traditionally accepted view of the unitary nature of memory, held until a couple of decades ago, was initially disturbed by the appearance of dichotomies, such as primary versus secondary, episodic versus semantic, and declarative versus procedural memory. Out of these dichotomies are now emerging more comprehensive

Requests for reprints should be addressed to Lars Nyberg, Department of Psychology, Umeå University, S-901 87 Umeå, Sweden. E-mail: Lars.Nyberg@psy.umu.se.

This work was conducted while L.N. was spending a post-doctoral year at the Rotman Research Institute, supported by a scholarship from the Swedish Council for Research in the Humanities and Social Sciences. E.T.'s research supported by the Natural Sciences and Engineering Research Council of Canada.

classificatory schemes of memory systems, subsystems, or memory tests (Johnson & Hirst, 1993; Markowitsch, in press; Moscovith, 1992; Tulving, 1987, 1991; Weiskrantz, 1987). A historical sketch of these developments and a summary of the current state of affairs in both human and animal memory is given in Schacter and Tulving (1994).

TASK COMPARISONS AND DISSOCIATIONS

The classification enterprise is still in an early stage of development, and hence necessarily shrouded in uncertainty about many features of its conduct. Among those who have accepted the basic premise of multiple memories, no consensus exists as to the exact objectives of the undertaking, the nature of relevant evidence, the rules for translating empirical observations into theoretical statements, and the general strategies and specific tactics that are to be followed in the search for "the" organisation of memory.

There is good agreement, however, that certain kinds of findings, provided by the *task-comparison methodology* (Richardson-Klavehn & Bjork, 1988), do constitute evidence relevant to the classification problem. These are findings of *dissociations* between task performances. Two tasks are said to be dissociated if their performances are not positively correlated. Such dissociations between task performances have for a long time played an important role in attempts to demonstrate the existence of neurologically distinct functional systems (Shallice, 1979, 1988; Teuber, 1955; Weiskrantz, 1968).

It is not necessary to assume a one-to-one mapping of tasks to systems in order to make use of task-comparison data for memory classification. In fact, it is generally agreed that such an assumption would be difficult to justify (e.g. Toth, Reingold, & Jacoby, 1994). What is necessary, however, is to have some knowledge of, or to be able to make reasonable assumptions about, the extent to which different systems contribute differentially to the performance of different tasks. To the extent that the tasks that are compared can be assumed to vary from each other with respect to their dependence on different putative memory systems, the observed task dissociations can be taken as evidence of the distinctiveness of these systems.

CONVERGING DISSOCIATIONS

The finding of dissociations as such is not logically inconsistent with a unitary view of memory (Dunn & Kirsner, 1988; Neely, 1989; Roediger,

Rajaram, & Srinivas, 1990). Therefore, the postulation of different memory systems is based on other criteria as well as dissociations (Schacter & Tulving, 1994; Sherry & Schacter, 1987; Tulving, 1984). For dissociations to be regarded as supportive of multiple memory systems, it is necessary that dissociations of different kinds *converge* on one and the same set of postulated systems. If task performances can be dissociated on the basis of multiple task comparisons of different kinds, the multiple-systems view may provide a more parsimonious explanation of the empirical facts than would a unitary-memory view (Schacter & Tulving, 1994).

The aim of this review is to examine the support for multiple long-term memory systems from converging dissociations. We present a summary of findings from task comparisons that speak to the hypothesised existence of four major human memory systems: episodic, semantic, perceptual representation (PRS) and procedural. These four systems form the major part of the five-fold classification system described by Schacter and Tulving (1994; see also Tulving, 1991; Weiskrantz, 1987).

The episodic memory system enables people to recollect personally experienced events; the semantic memory system is involved in the acquisition and retention of general knowledge of the world; the PRS facilitates identification of perceptual objects; and the procedural memory system is concerned with the acquisition and expression of motor, perceptual and cognitive skills, and simple conditioning.

Tasks which we assume primarily reflect the influence of procedural memory include mirror reading, serial reaction time and rotor-pursuit. The PRS tasks include primed stem completion, primed fragment completion and primed identification of degraded words. The operations of semantic memory are assumed to be reflected in word fluency, vocabulary, and primed and unprimed category association. Tasks to which episodic memory is assumed to contribute prominently include free recall, cued recall and recognition.

It should be pointed out that although we consider dissociations yielded by task comparisons as partial evidence for multiple memory systems, this approach does not rival an explanation of dissociations in terms of different memory processes (Roediger, Weldon, & Challis, 1989; Roediger et al., 1990). Memory systems differ from one another with respect to their rules of operation and component processes (Schacter & Tulving, 1994; Sherry & Schacter, 1987; Tulving, 1984, 1985). Hence, the systems view is compatible with the idea that dissociations reflect different processes, but the systems view goes beyond the processing view by postulating a structure of memory that helps to understand process differences.

KINDS OF DISSOCIATION

Task comparisons may assume different forms, each generating a different kind of dissociation. In this paper, we will be concerned with four kinds of comparisons, and hence dissociations, namely those involving (1) different values of independent variables (functional dissociations), (2) stages of ontological development (developmental dissociations), (3) drug-induced brain states (pharmacological dissociations) and (4) the presence or absence of brain damage (brain-damage dissociations).

Functional dissociations are observed in experiments in which a single group of subjects is given two different tasks whose performance varies as a function of the independent variable. For instance, Graf and Mandler (1984) observed that explicit completion of word stems with previously studied words was enhanced by deeper levels of processing at study, whereas implicit stem completion, attributable to priming, was unaffected by level of processing. This lack of correlation between the two measures as a function of the level of processing defines a functional dissociation between the two task performances.

Developmental dissociations are observed in experiments in which the performance of (at least) two groups of subjects differing in age is compared on (at least) two tasks. For instance, Naito (1990) tested 7-, 9- and 12-year-old children as well as young adults for primed word-fragment completion and for explicit recall of semantically encoded words. The priming effects were indistinguishable across all age groups, whereas recall exhibited a pronounced increase with the age of the subjects.

Pharmacological dissociations are similar to developmental ones in that they also involve more than a single group of subjects, or the same group on separate test occasions. Performance comparisons on two or more tasks while the subjects are under the influence of different drugs, frequently including placebo controls, provide the data of interest. For instance, Curran and Gorenstein (1993) found that two benzodiazepine drugs, lorazepam and oxazepam, when compared with placebo, reduced performance in free recall, while only one of them, lorazepam, reduced the amount of priming measured in a word-stem completion task.

Brain-damage dissociations may be found in experiments involving (at least) two groups of subjects differing in the kind or extent of brain damage, including controls with none, whose performance is compared on (at least) two tasks. For instance, in a study reported by Warrington and Weiskrantz (1974), it was observed that "yes/no" recognition performance was greatly inferior in a group of amnesic subjects, when compared with that of a group of controls, while the two groups performed in an identical fashion on what we would now refer to as a primed stem-completion task. The lack of correlation between the two measures of

memory across the two groups defines a pathological dissociation between the two task performances, and allows the inference that different memory systems exist which contribute differentially to the two tasks.

If the four putative memory systems represent distinguishable entities, it should be possible to demonstrate corresponding dissociations among them with respect to the manner in which their operations are affected by independent variables (functional), development, psychoactive drugs and brain damage. With four systems and four kinds of dissociation, we can specify 24 different classes of task comparison that are logically capable of yielding dissociations. The question we posed at the beginning of our inquiry was how many of the 24 potential dissociations are actually presented, at least by a single instance, in the literature.

EXAMPLES OF RELEVANT DISSOCIATIONS

To be included as an example of a functional dissociation, the study had to show a differential effect of an independent variable on the performance on two tasks supposed to reflect two distinct systems. To be included as an example of a developmental dissociation, the study had to include two different age groups and two measures assumed to reflect separate systems. To be included as an example of a pharmacological dissociation, the study had to include the administration of one drug and measures of two separate systems. Several studies included the administration of more than one drug, and all included a control group (placebo). To be included as an example of a study demonstrating a dissociation caused by irreversible brain damage, it had to include a single case or group of patients with irreversible brain damage, and measures of at least two separate systems. All reported studies also included controls.

Next, we present the results of our survey of the literature. For each dissociation, we provide a brief description of one representative study (summarised in Table 1) and give references to other relevant published studies.

Episodic/Semantic

Functional. Nyberg and Nilsson (1995) demonstrated a functional dissociation between episodic memory (free recall) and semantic memory (category association). Subjects studied simple sentences in imperative form (e.g. *roll the ball*) in three different study conditions: reading the sentences, enacting the action described by each sentence, and generating the noun in each sentence. In free recall, enactment at study resulted in a markedly higher performance than the other conditions, and generation

TABLE 1

Disassociations Between Procedural Memory, PRS, Semantic Memory and Episodic Memory as a Function of Experimental Manipulations, Chronological Age, Pharmacological Agencies and Brain Damage

<i>Dissociation</i>	<i>Study</i>	<i>Example of Tasks</i>
<i>Episodic vs semantic</i>		<i>Semantic</i>
Functional	Nyberg and Nilsson (1995)	Category association
Developmental	Mitchell (1989)	Picture naming, vocabulary
Pharmacological	Roy-Byrne et al. (1987)	Word fluency
Brain damage	Weingartner et al. (1983)	Word fluency, sentence completion
<i>Episodic vs PRS</i>		<i>PRS</i>
Functional	Mitchell and Brown (1988)	Picture naming
Developmental	DiGiulio et al. (1994)	Gollin figures, degraded words
Pharmacological	Danion et al. (1990)	Stem completion
Brain damage	Warrington and Weiskrantz (1970)	Stem completion, fragmented words
<i>Episodic vs procedural</i>		<i>Procedural</i>
Functional	Willingham et al. (1989)	Serial reaction task
Developmental	Howard and Howard (1989)	Serial reaction task
Pharmacological	Nissen et al. (1987)	Serial reaction task
Brain damage	Cohen and Squire (1980)	Mirror reading

<i>Semantic vs PRS</i>					
Functional	Srinivas and Roediger (1990)	<i>Semantic</i>	Category association	<i>PRS</i>	Fragment completion
Developmental	Jelicic et al. (1995)		Category association		Fragment completion
Pharmacological	Sellal et al. (1992)		Word fluency		Stem/picture completion
Brain damage	Grosse et al. (1990)		Sentence completion		Stem completion
<i>Semantic vs procedural</i>		<i>Semantic</i>		<i>Procedural</i>	
Functional	—	—		—	
Developmental	Cornell and Heth (1979)		Look left/right		Look left/right
Pharmacological	Knopman (1991)		Word fluency		Serial reaction task
Brain damage	Ostergaard (1987)		Vocabulary, fluency, lexical decisions		Gollin pictures, video games
<i>PRS vs procedural</i>		<i>PRS</i>		<i>Procedural</i>	
Functional	Schwartz and Hashtroudi (1991)		Primed partial-word identification		Unprimed partial-word identification
Developmental	Hashtroudi et al. (1991)		Primed partial-word identification		Unprimed partial-word identification
Pharmacological	Danion et al. (1992)		Stem completion		Tower of Toronto
Brain damage	Heindel et al. (1989)		Stem completion		Pursuit rotor task

was found to lead to a higher performance than reading. In category association a similar generation effect was found, but enactment did not lead to a better performance than reading (see also Neely, 1989).

Developmental. Mitchell (1989) demonstrated a developmental dissociation between episodic and semantic memory. The performance of young (19–32 years) and old (63–80 years) subjects was compared. Episodic memory was measured by tests of recall and recognition, and the stimuli consisted of line-drawings. Age differences, favouring the young, were found for both types of tests. Semantic memory was measured by a range of tests, including picture-naming latencies, picture-naming errors and vocabulary. Only on one semantic test (vocabulary) was an age difference found—in favour of the older adults (see also Small, Hultsch, & Masson, 1995).

Pharmacological. Roy-Byrne et al. (1987) noted a pharmacological dissociation between episodic memory (free recall, recognition) and semantic memory (word fluency). Subjects aged 20–31 years were given oral diazepam (10 mg) and placebo 2 weeks apart. The results showed a significant drug effect on immediate recognition and intrusion corrected free recall scores, and no effect on the semantic memory tests (see also Knopman, 1991; Nissen, Knopman, & Schacter, 1987).

Brain Damage. Weingartner et al. (1983) demonstrated a dissociation between episodic memory (picture and word recall) and semantic memory (word fluency, sentence completion, sequencing activities, script generation). Patients with Korsakoff's syndrome were found to perform worse than memory-impaired controls on the episodic memory tasks. In contrast, their semantic memory performance was comparable to that of the controls (see also Shimamura & Squire, 1989; Tulving, Hayman, & MacDonald, 1991).

Episodic/PRS

Functional. Mitchell and Brown (1988) reported three experiments showing a functional dissociation between priming and episodic memory as a function of retention interval. Combining the results from the experiments showed a gradual decrease in episodic memory performance (measured by a picture-recognition test) over three measurement points (1 week, 4 weeks, 6 weeks). In contrast, priming (as measured by picture-naming facilitation) did not decrease over time (for a review, see Roediger & McDermott, 1993).

Developmental. DiGiulio, Seidenberg, O'Leary and Raz (1994) demonstrated a developmental dissociation between priming (Gollin figures, degraded words) and episodic memory (figure and word recall). The performance of 8- and 12-year-olds was compared. The results showed that the priming effects were of similar magnitude in the two age groups for both priming tasks, and that the older children outperformed the younger children on both recall tasks (for a review of ageing data, see La Voie & Light, 1994).

Pharmacological. Danion et al. (1990) demonstrated a pharmacological dissociation between priming (stem completion) and episodic memory (free recall). Subjects aged 20–27 years were given 6 mg per kg scopolamine hydrobromide intramuscularly, 0.3 mg per kg diazepam orally, 0.3 mg per kg trimipramine methanesulphonate intramuscularly, or placebo. The results showed a significant drug effect, as compared to the placebo group, of diazepam on free recall performance. The priming effect was unimpaired in all experimental groups (see also Danion et al., 1989; Knopman, 1991).

Brain Damage. Warrington and Weiskrantz (1970, experiment 2) demonstrated a dissociation between priming (stem completion, fragmented words) and episodic memory (recall, recognition). Amnesic patients (three Korsakoff's syndrome; one temporal lobectomy patient) were compared with matched controls. It was found that the amnesic patients performed as well as the controls on the priming tasks, and that the performance of the control subjects on the episodic tests was substantially better than that of the patients (see also Graf, Squire, & Mandler, 1984; Tulving et al., 1991).

Episodic/Procedural

Functional. Willingham, Nissen and Bullemer (1989, experiment 1) demonstrated a functional dissociation between procedural learning and episodic memory. Subjects performed a serial reaction time task in which a 10-trial sequence was presented 10 times (the task was repeated four times). On each trial, a light appeared in one of four positions and the subjects were instructed to press the response button directly below the position of the light as fast as possible. Following the fourth and final block, the subjects were asked whether they had noticed a sequence. If they had, their accuracy in indicating the sequence was measured. Based on their self-reports and accuracy in indicating the sequence, the subjects were classified as having no, some or complete explicit knowledge of the sequence. Subjects with no knowledge demonstrated substantial proce-

dural learning (as indicated by reaction times) and, after excluding anticipatory responses, subjects with no, some or complete explicit knowledge of the sequence demonstrated no significant differences in rate of learning. In contrast, the episodic memory performance of no-knowledge subjects (measured by having subjects predict the next stimulus position; generate task) was significantly lower than that of the subjects with some or complete explicit knowledge, and no different from that of a control group with no prior experience with the repeating sequence.

Developmental. Howard and Howard (1989) demonstrated a developmental dissociation between procedural memory (serial reaction time task) and episodic memory (generation task). Young (mean age 22.2 years) and old (mean age 71.2 years) subjects showed similar degrees of pattern learning on the serial reaction time task. On the episodic generation task, a reliable age difference was found (with young subjects outperforming old subjects).

Pharmacological. Nissen et al. (1987) demonstrated a pharmacological dissociation between procedural memory (serial reaction time task) and episodic memory (free recall). In a double-blind procedure, subjects aged 19–35 years received 0.43 mg scopolamine or 0.5 cc normal saline solution subcutaneously. The results showed no effect of scopolamine on learning on the serial reaction time task, but free recall performance was substantially impaired in the scopolamine group (see also Danion et al., 1992; Knopman, 1991).

Brain Damage. Cohen and Squire (1980) demonstrated a dissociation between procedural memory (mirror reading) and episodic memory (measured by recognition performance and facilitation by word repetition). A heterogeneous group of amnesic patients was compared with a group of matched controls. The results showed that the amnesic patients acquired the mirror-reading skill at a rate equivalent to that of the controls and retained it over a 3-month period. The controls outperformed the amnesic patients on the repeated words and on the recognition test (see also Corkin, 1968).

Semantic/PRS

Functional. Srinivas and Roediger (1990, experiment 1) demonstrated a functional dissociation between priming (fragment completion) and semantic memory (category association). Words that had been generated at study produced significantly higher priming on category association than did words that had been read. In contrast, priming on fragment

completion was significantly higher when the words had been read than when they had been generated at study (a study condition involving reading words in the context of a semantically related sentence was also included; in both tests, this study condition led to an intermediate level of priming) (see also Blaxton, 1989).

Developmental. Jelicic, Craik and Moscovitch (in press) demonstrated a developmental dissociation between priming (word-fragment completion) and semantic memory (category association). Young (21–37 years) and old (62–81 years) subjects were compared. The amount of priming on the word-fragment completion test was similar across groups, whereas the amount of conceptual priming on category association was significantly higher for the young subjects (see also Mitchell, 1989).

Pharmacological. Sellal et al. (1992) showed a pharmacological dissociation between priming (stem completion, picture completion) and semantic memory (word fluency). In a double-blind procedure, subjects aged 20–29 years received lorazepam (1.75 or 2.5 mg), diazepam (15 or 20 mg) and placebo. No significant drug effect was observed on the semantic memory test, but lorazepam (2.5 mg) impaired word-completion and picture-completion performance (see also Knopman, 1991).

Brain Damage. Grosse, Wilson and Fox (1990) demonstrated a dissociation between priming (primed stem completion) and semantic memory (sentence completion). Alzheimer's disease (AD) patients and normal elderly control subjects were tested. The subjects completed sentence frames (e.g. "He hit the nail with a _____") and the stems of the best fit words (e.g. "Hammer") were later included in the stem-completion test. The AD patients performed worse than the controls on the sentence-completion task, but performance on the stem-completion task did not differ between the groups (see also Tulving et al., 1991).

Semantic/Procedural

Functional. No relevant dissociation was found.

Developmental. Cornell and Heth (1979, experiment 2) demonstrated a developmental dissociation between procedural and semantic memory. Infants aged 4, 8, 12 and 16 months were tested. During the acquisition phase of the experiment, a set of visual patterns was shown to the infants. When the infants oriented to the image, the pattern was turned off and two side screens were turned on. On one of the side screens a novel pattern was shown; the other side screen showed the same image again. In

the "place" condition, measuring semantic memory, the novel pattern was always shown at the same place (e.g. on the eastern screen). On half of the trials, the infants faced north and on the other half south. Thus, to look at the novel stimulus the infants had to look to the right on some trials and to the left on other trials. In the "response" condition, measuring procedural memory, the novel pattern was always shown on the same side of the infant (e.g. on their right side). Following the 24 acquisition trials there was a 5-min retention interval, after which the infants' retention was tested. In the place condition, there was a significant age effect; whereas the older infants looked at the novel stimulus on 75% of the trials, the youngest infants performed at chance level (50%). In the response condition, there was no age effect, and the performance level in all groups was well above chance (83–100%).

Pharmacological. Knopman (1991, experiment 2) demonstrated a pharmacological dissociation between procedural memory (performance on a verbal serial reaction time task) and semantic memory (word fluency). Young subjects were given 2.5 mg lorazepam or placebo orally (in a double-blind fashion). Testing began 2 h post-administration and showed that lorazepam impaired learning on the verbal serial reaction time task. Semantic memory performance did not differ reliably between the groups (see also Danion et al., 1992).

Brain Damage. Ostergaard (1987) demonstrated a dissociation between semantic memory and skill learning in a case study of a young boy who, at the age of 10 years and 4 months, developed encephalopathy during treatment of diabetic ketoacidosis. A computed tomography scan showed bilateral lesions in the medial temporal region. When tested with a large battery of memory tests it was found that the patient, relative to controls, showed impaired semantic memory performance (as measured by reading vocabulary, verbal fluency, lexical decisions and semantic classification). It was also found that he had the ability to learn and retain skills (identification on the Gollin incomplete pictures test) and his procedural learning seemed to be entirely normal (as indicated by a comparison of his ability to learn a computer video game versus matched controls).

PRS/Procedural

Functional. Schwartz and Hashtroudi (1991) reported four experiments which showed that priming effects were unrelated to skill learning. In their third experiment, they examined whether pre-experimental skill enhanced priming effects and skill learning. Based on the assumption that

subjects are exposed more often to high-frequency than to low-frequency words and therefore more skilled in identifying high-frequency words (e.g. Jacoby & Dallas, 1981), pre-experimental skill was operationalised as normative word frequency. A partial-word identification task, administered nine times in succession with a 10-min interval between trials, was used as a measure of priming and skill learning. The results showed a functional dissociation between test performance as a function of word frequency: Skill learning was greater for high-frequency than for low-frequency words, whereas the amount of priming was not affected by word frequency. Also, for both high- and low-frequency words, the correlation between skill learning and priming was non-significant.

Developmental. Hashtroudi, Chrosniak and Schwartz (1992, experiment 2) demonstrated a developmental dissociation between skill learning and priming. On three consecutive days, old (65–75 years) and young (17–25 years) subjects were given three trials of a partial-word identification task (a total of nine trials). The task of the subjects was to identify the words. Priming was measured as an increased ability to identify repeated words; skill learning was measured as an improvement in performance on non-repeated words. The results showed similar levels of priming for young and old adults and priming increased across trials for both groups. However, whereas young subjects showed skill learning, the older adults' performance on non-repeated words did not increase across trials. When the older adults were given additional perceptual information (the words were 37% degraded instead of 50%), significant skill learning was also seen among this group (experiment 2a). Based on this finding, it was suggested that perceptual components related to the acquisition of the skill were deficient—not procedural memory *per se*.

Pharmacological. Danion et al. (1992) demonstrated a pharmacological dissociation between procedural memory (Tower of Toronto puzzle) and priming (stem completion). Their subjects (mean age 23 years) received 12.5 or 25 mg chlorpromazine, 2.5 mg lorazepam or a placebo orally. The priming effect was significantly lower for subjects receiving lorazepam than for the placebo group (chlorpromazine did not impair priming). In contrast, lorazepam did not impair skill learning (see also Knopman, 1991).

Brain Damage. Heindel et al. (1989) demonstrated a double dissociation between procedural memory (pursuit rotor motor learning) and priming (stem completion). Patients with Huntington's disease were found to be impaired on the motor learning task, but not on the stem-completion task. Patients suffering from dementia of the Alzheimer type showed

TABLE 2
Summary of Converging Dissociations

Dissociation	Support from Different Types of Dissociations			
	Functional	Developmental	Pharmacological	Brain Damage
Episodic vs semantic	Yes	Yes	Yes	Yes
Episodic vs PRS	Yes	Yes	Yes	Yes
Episodic vs procedural	Yes	Yes	Yes	Yes
Semantic vs PRS	Yes	Yes	Yes	Yes
Semantic vs procedural	No	Yes	Yes	Yes
PRS vs procedural	Yes	?	Yes	Yes

the opposite pattern; they performed normally on the motor task but showed poorer stem completion performance (the performance levels were compared with those of age-matched control groups) (see also Heindel, Butters, & Salmon, 1988; Salmon, Shimamura, Butters, & Smith, 1988).

BRAIN MAPS OF MEMORY SYSTEMS

This highly selective review of the literature focused on task-comparison dissociations seen to be addressing the issue of multiple human long-term memory systems. We have listed and briefly described experimental findings in 23 categories that demonstrate functional, developmental, pharmacological and brain-damage dissociations among task performances that can be argued to be differentially sensitive to the operation of four major human memory systems: episodic, semantic, PRS and procedural (for a summary, see Table 2). Indeed, the support for some dissociations is stronger than that for others in the sense that it is based on several studies using several different measures and different kinds of materials. The support for a developmental dissociation between PRS and procedural memory may be singled out as particularly weak (indicated by a "?" in Table 2). This is because the results suggested that perceptual components related to the acquisition of the skill, rather than procedural memory *per se*, were impaired.¹ Nevertheless, these "converging dissocia-

¹It may be noted that a failure to demonstrate a developmental dissociation between PRS and procedural memory is in line with the idea that both of these memory systems are developed early in life and remain relatively intact in old age (Tulving, 1983; Tulving & Schacter, 1990).

tions" constitute one important category of criteria that have to be satisfied for the postulation of different memory systems (Schacter & Tulving, 1994; see also Roediger et al., 1990).

The studies included in this review serve first and foremost to demonstrate the existence of dissociations. However, they can also be seen as providing hints about the nature of the systems (cf. the "property lists" of Schacter & Tulving, 1994), as well as contributing to the neuroanatomical localisation of memory functions. Thus, they suggest that the two declarative systems (episodic and semantic) seem to depend critically on the integrity of medial temporal-lobe structures (cf. Gabrieli, Cohen, & Corkin, 1988; Squire & Knowlton, 1995). This is indicated by the fact that damage to this region, caused by a direct lesion or neuronal degeneration in Alzheimer's disease (Goldman & Coté, 1985; Hyman, Van Hoesen, Damasio, & Barnes, 1984), leads to impaired performance, and also by the negative effect of diazepam on episodic memory (Sellal et al., 1992, suggested that diazepam may primarily be distributed in the temporo-parietal regions). Furthermore, the impairment of episodic memory in old age (cf. Creasey & Rapoport, 1985) and in Korsakoff's disease (cf. Shimamura, Jernigan, & Squire, 1988) suggests that frontal-lobe structures are critical for episodic memory.

Turning to the non-declarative systems, we note that priming was negatively affected by lorazepam. This drug may primarily be restricted to the occipital regions (Sellal et al., 1992),² indicating that occipital brain structures are critical for the visual subsystem of the PRS (cf. Gabrieli et al., 1995). In this context, it is worth pointing out that Heindel et al. (1989) found impaired priming in Alzheimer's disease, whereas Grosse et al. (1990) did not. Grosse and co-workers' study included a study task that ensured conceptual processing of the target words, suggesting that activation of a defective semantic network in Alzheimer patients may be a prerequisite for them to show normal priming on completion tests (cf. Salmon & Heindel, 1994). On more "pure" perceptual priming tasks, conceptual processing of the target words does not seem to be necessary for Alzheimer patients to show intact priming (Meiran & Jelicic, 1995). The basal ganglia are clearly implicated in the operations of the procedural memory system, as indicated by impaired procedural-memory performance (Heindel et al., 1989) in patients suffering from Huntington's disease, in which there is structural damage to the neostriatum (Saint-Cyr, Taylor, & Lang, 1988).

²The effect of lorazepam on procedural memory in the Knopman (1991) study appears inconsistent with this view. However, Knopman showed that lorazepam only affected a cognitive procedural task, not a motor version of the same task, suggesting that a perceptual component was involved.

These pieces of evidence of the neuronal underpinnings of the different memory systems agree reasonably well with the results of a number of recent positron emission tomography (PET) studies. The medial temporal brain regions have been found to be involved in both episodic-memory (e.g. Kapur et al., 1995; Schacter et al., 1996; Squire et al., 1992) as well as semantic-memory (Frith, Friston, Liddle, & Frackowiak, 1991) retrieval. Frontal-lobe structures have been found to be critical for *both* episodic and semantic memory, but different frontal regions seem to be important for the two systems. Specifically, frontal regions in the left hemisphere seem to be more involved in semantic than episodic memory, whereas the right frontal regions are involved more in episodic than semantic memory (for reviews, see Nyberg, Cabeza, & Tulving, in press b; Tulving et al., 1994). Interestingly, the PET data also suggest that the cerebellum plays an important role in both episodic (Andreasen et al., 1995; Nyberg et al., in press a) and semantic (Bäckman et al., in press; Buckner et al., 1995) memory. The occipital brain regions have been found to be implicated in (visual) perceptual priming in recent PET studies (Bäckman et al., in press; Buckner et al., 1995), more so in the right than in the left hemisphere (cf. Gabrieli et al., 1995; Marsolek, Kosslyn, & Squire, 1992). Finally, a strong involvement of midbrain structures in procedural memory has been confirmed by several PET studies (Blaxton et al., in press; Jenkins et al., 1994; Seitz & Roland, 1992).

CONCLUSION

In conclusion, our survey of existing dissociation evidence can be regarded as encouraging. The studies that we have reviewed, yielding the dissociations that fit into the proposed classificatory scheme of the four long-term memory systems, do not, of course, *prove* the existence of these systems any more than would any other relatively isolated pieces of evidence. Nevertheless, the survey suggests that converging dissociations from experimental, developmental and pharmacological studies, together with studies of brain-damaged patients, can play an important role in shaping our ideas about classifying memories. When combined with the rapidly accelerating flow of relevant functional neuroimaging data, the dissociative evidence that we already have, and that will be generated in the future, will provide a firm foundation for the important enterprise of identifying the organisation of memory.

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