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Category learning and the memory systems debate

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Abstract

A substantial and growing body of evidence from cognitive neuroscience supports the concept of multiple memory systems. However, the existence of multiple systems has been questioned by theorists who instead propose that dissociations can be accounted for within a single memory system. We present convergent evidence from neuroimaging and neuropsychological studies of category learning in favor of the existence of multiple memory systems for category learning and declarative knowledge. Whereas single-system theorists have argued that their approach is more parsimonious because it only postulates a single form of memory representation, we show that the multiple memory systems approach is superior in its ability to account for a broad range of data from psychology and neuroscience.

The concept of multiple memory systems (MMS) is perhaps one of the most successful ideas in cognitive neuroscience. Over the last 25 years, a broad range of research has established the notion that "memory" is not a unitary concept, but rather involves a set of distinct systems that are functionally and neurobiologically dissociable. Particular interest has focused on dissociating memory functions supported by the hippocampus and medial temporal lobe (MTL) structures (which comprise the *declarative* memory system) from systems supported by other cortical and subcortical structures (which comprise a set of *procedural* or *nondeclarative* memory systems). A wide set of studies in both humans and nonhuman animals has confirmed this notion and provided substantial evidence regarding the functional characteristics of these systems.

Despite strong support within cognitive neuroscience for the MMS theory, some resistance to the concept remains. In particular, some cognitive psychologists have argued broadly against the notion of MMS in favor of a single memory system. The primary argument in favor of a single system has been one of parsimony: Namely, that the dissociations thought to compel multiple systems can be produced by computational models that do not involve multiple systems, and thus that the more parsimonious single-system view is preferable. In addition, these researchers have on occasion argued against the validity of particular empirical dissociations.

Parsimony requires that one explain the data as simply as possible; thus, all things being equal, a theory that explains the data through a single mechanism is preferable to one that explains the same data using multiple mechanisms. We will argue here that although single-systems models may be able to explain a limited set of human behavioral data, there is a broad range of neuroscientific data that are not addressed by the single

system model and that compels the MMS concept. We will focus on studies of probabilistic category learning, which have provided a great deal of evidence regarding the organization and function of memory systems; other papers in this issue (Smith, Reber) discuss the topic with regard to other domains of category learning. We will conclude that by limiting its scope to human behavioral data, the single system approach is unable to account for a range of data that are naturally accounted for under the MMS view, and thus that parsimony requires adoption of the MMS theory.

Neuropsychological dissociations

Early studies of intact procedural learning in amnesia focused on the learning of motor skills (e.g., Brooks and Baddeley, 1976; Corkin, 1968), perceptual skills (e.g., mirror reading: Cohen and Squire, 1980; Martone et al., 1984), and cognitive skills (e.g., Tower of Hanoi: Cohen et al., 1985). In each of these cases, dissociations were found between skill learning and explicit memory for the study episode. However, these tasks did not generally make strong contact with models of learning and memory from cognitive psychology. In the 1990's, a set of studies introduced the study of category learning as a method to investigate the nature of memory impairments in amnesia. Because category learning has been extensively studied in the cognitive psychology literature, these studies provided a more direct link to cognitive models, and thus drew greater attention from researchers studying basic cognitive processes.

Two tasks were introduced by Knowlton, Squire, and colleagues to study category learning in amnesia. One of these, perceptual categorization using dot patterns (Knowlton and Squire, 1993), is discussed in the papers by Smith and Reber in this issue, and will not be discussed in detail here. Another paradigm, the probabilistic

classification learning task (PCT), was introduced by Knowlton, Squire, and Gluck (1994). In this task, which was based on previous work by Gluck and Bower (1988a; 1988b), subjects are presented with multi-featured stimuli and must learn to classify those stimuli into one of two categories based on trial-by-trial feedback. This feedback is probabilistic, such that subjects cannot rely on simply remembering the outcome from the previous encounter with each stimulus; rather, they must integrate information over many trials to form a representation of the optimal stimulus-response associations. In a common version of this task, known as the "weather prediction" task, the cover story involves predicting the weather based upon a set of geometric features presented on four individual cards, which are presented in all possible combinations.

Performance of amnesic patients on the PCT was first examined by Knowlton et al. (1994). Across multiple versions of the PCT, amnesic patients exhibited learning that was not statistically different from age-matched controls, whereas they were impaired on tests of declarative knowledge about the learning situation. These data provided the first suggestion of a dissociation between PCT learning and declarative memory in amnesia. Two subsequent studies from the same group (Knowlton et al., 1996a; Reber et al., 1996) replicated these findings, showing that amnesics were not significantly impaired relative to controls, though their performance was numerically lower than controls. By contrast, a recent study by Hopkins et al. (2004) found impairments of PCT learning in a group of anoxic amnesics. It is likely that the difference in impairment between these groups relates to the populations in each study. The amnesics in the studies of Knowlton and Squire and colleagues were relatively old, such that the age-matched controls were likely to suffer from some degree of normal age-related declarative memory loss. By contrast,

the amnesics in the Hopkins et al. study were relatively young. Given the evidence

presented below that normal young adults may use declarative memory strategies to learn

the PCT, it is possible that the difference between these studies may reflect the greater

advantage in declarative memory function held by the young controls in the Hopkins et

al. study.

Whereas the studies of amnesics showed that learning could proceed (at least to some

degree) without support from the MTL, studies of patients with basal ganglia disorders

(Parkinson's disease [PD] and Huntington's disease [HD]) have shown clearly that the

basal ganglia are necessary for learning in the PCT. Knowlton et al. (1996) demonstrated

a double dissociation between classification learning and declarative memory: Amnesic

patients show normal PCT learning but impaired declarative memory, while PD patients

show the opposite pattern. The deficit for PCT learning in PD patients has been replicated

by Shohamy et al. (2004), and a parallel deficit in HD patients was observed by

Knowlton et al. (1996b). Thus, it appears that different forms of damage to the basal

ganglia lead to a similar deficit in PCT learning.

Why are the basal ganglia necessary for learning the PCT, whereas they are not

necessary for other forms of category learning such as dot-pattern classification or

artificial grammar learning (Reber and Squire, 1999)? One potential explanation is that

the basal ganglia are involved in learning on the basis of feedback, which is necessary in

the PCT but not in the other tasks mentioned above. This question was examined by

Shohamy et al. (2004), who compared PD patients learning two versions of the PCT: A

standard feedback-based version of the task, and an observational version where the

participant was not required to select responses but simply observed the stimulus-

outcome associations. The PD patients were impaired at learning the feedback-based version of the task, but were significantly better at learning the task under observational conditions, and did not differ from controls in that condition. Consistent with these results, PD patients are impaired at learning of artificial grammars when they must learn them based on trial-by-trial feedback (Smith and McDowall, 2006). These results are strongly consistent with the neurobiology of the basal ganglia and the dopamine system, which provides a prediction error signal that drives reinforcement learning. PD is associated with dysfunction in the DA system (in both medicated and unmedicated states), so it is not surprising that they are unable to learn from feedback given the lack of a functioning reinforcement learning system.

In summary, the neuropsychological data provide strong evidence for a deficit in PCT learning associated with basal ganglia disorders, and some evidence for spared (but perhaps not fully normal) learning of the PCT in amnesic patients.

Behavioral dissociations

If classification learning does not require declarative memory, then it should be possible to dissociate the two in normal subjects by manipulations that affect declarative but not procedural memory systems. In a recent study (Foerde et al., in press), we examined whether the presence of a secondary task during learning would affect declarative memory more than category learning. Participants learned the PCT either alone or while additionally performing a secondary tonecounting task. Inclusion of probe blocks, where those learning under dual task conditions were able to perform under single task conditions, showed that although ongoing tonecounting impaired PCT performance, it did not impair learning: Under single task conditions PCT performance was equivalent

regardless of the conditions of learning. In contrast, measures of declarative knowledge about cue-outcome associations were significantly reduced after learning under dual task conditions. These results showed that in healthy, young adults multiple sources of information can contribute to performance, but that these contributions may be separated due to differential sensitivity to interference. Additional analyses separated some participants into more and less aware according to declarative knowledge measures. Although subjects with more declarative knowledge performed better than those without, even those classified as unaware still exhibited significant learning on the PCT. Thus, category learning can be dissociated behaviorally from declarative memory.

Neuroimaging

Although studies of patients with brain damage may provide evidence regarding the necessity of particular brain systems for particular cognitive functions, they can only provide limited insight into the neural architecture of normal behavior. In particular, if memory systems are not completely independent then their function in the normal individual will differ. Neuroimaging methods such as functional magnetic resonance imaging (fMRI) can fill this gap, by elucidating the dynamics of neural activity in normal individuals while they learn (Poldrack, 2000). In the case of PCT learning, we have used fMRI in a series of studies (Aron et al., 2006; Aron et al., 2004; Foerde et al., 2006; Poldrack et al., 2001; Poldrack et al., 1999a) to examine the brain systems that are engaged during the PCT. These studies have shown a remarkably consistent pattern of cortical and subcortical activation across studies.

To highlight the consistent pattern of PCT-related activation across multiple studies, we performed a meta-analysis including data across 4 fMRI studies of the PCT (Aron et

al., 2006; Aron et al., 2004; Foerde et al., 2006; Poldrack et al., 2001). The results of this analysis are shown in Figure 1; this figure shows regions that were significantly active in all four studies. These results show that corticostriatal circuits as well as midbrain dopaminergic regions are engaged during PCT learning, consistent with the aforementioned neuropsychological results that highlight the importance of these circuits. We have also examined the test-retest reliability of activation in the PCT over a one-year interval (Aron et al., 2006), and found that activation in both cortical and subcortical regions was highly reliable over time.

As discussed above, behavioral dissociations have supported the idea that multiple sources of information may contribute to PCT performance and have shown that a secondary task can manipulate these contributions. In a recent study (Foerde et al., 2006), we examined whether learning under dual-task conditions would modulate the relative contribution of declarative and procedural memory systems to PCT performance, using fMRI. Participants learned two different PCTs, one under single task conditions and one under dual task conditions. During learning of the tasks, the pattern of activity was consistent with previous studies, with additional activity in auditory and prefrontal cortices during the dual task PCT. After acquisition of the two classification tasks a probe task was given. The probe consisted of items from both the PCT learned under single and dual task conditions. All items were presented under single task conditions and without feedback, so that no test-phase learning could occur. Performance was not significantly different when accuracy for items learned under either single-task or dual-task conditions was compared. However, analyses of correlations between brain activity and measures of accuracy showed very different patterns depending upon how the task was learned:

classification accuracy for items learned under single task conditions was correlated with activity in the MTL, whereas accuracy for items learned under dual task conditions was correlated with activity in the striatum. Declarative knowledge for single task items was significantly better than that for dual task items and better declarative knowledge about single task cue-outcome associations was associated with greater MTL activity during classification. Such a relationship was not found for declarative knowledge about items learned under dual task conditions. Learning under conditions that interfere with declarative knowledge thus resulted in performance tied to the striatum, consistent with results from amnesic patients, whereas single task learning in normal young adults resulted in performance tied to MTL regions generally associated with declarative memory.

Single systems approaches

Although the foregoing data seem to compel the notion of multiple memory systems, a number of theorists have posited that dissociations between memory phenomena can be accounted for using a single memory system. Their main argument has relied on the use of simple computational models to show that the behavioral data demonstrating dissociations can be fit equally well by models that posit just a single memory mechanism. For example, Nosofsky and Zaki (1998) showed that the dissociation between perceptual category learning and recognition memory observed by Knowlton and Squire (1993) could be accounted for by a model in which both category learning and recognition rely on a single system, and amnesics and normal subjects differed by a single memory strength parameter. Similarly, Kinder and Shanks (2003) showed that dissociations between repetition priming and recognition memory could be accounted for

within a single-system model. In each case, the ability of the model to account for the dissociations relies upon the fact that the declarative memory task is more sensitive than the nondeclarative task.

Although amnesics do appear to show a statistically significant but small average deficit in some nondeclarative memory tasks (Zaki, 2004), there are several examples of numerically normal or superior nondeclarative memory in amnesics in the face of severely impaired declarative memory. The best example is patient E.P., who shows completely normal category learning in the dot pattern paradigm in the face of no explicit memory (Squire and Knowlton, 1995). The models outlined above are unable to account for such a dissociation using a single memory strength parameter; because these models assume that category learning is simply less sensitive to memory dysfunction than recognition memory (an assumption that is likely incorrect; Smith, submitted), complete absence of recognition memory requires that there be at least a small deficit in category learning. In the face of these results, Palmeri and colleagues (Palmeri and Flanery, 1999) have argued that the intact performance of amnesics on the dot pattern categorization task may reflect learning that occurs during the test phase rather than reflecting memory for the study episode. In support of this argument, they showed that normal subjects showed above-chance performance on the category learning task when presented a "subliminal" study phase in which no stimuli were actually presented.

The test-learning hypothesis of Palmeri and Flanery (1999) predicts that patients with memory disorders should perform at equivalent above-chance levels of categorization at test regardless of whether they actually studied any category members. This prediction was tested and falsified by Bozoki, Grossman, and Smith (2006). Using an object-based

category learning task (Reed et al., 1999), Bozoki et al. examined performance in patients with memory disorders due to Alzheimer's disease (AD) and normal controls either with or without training on the category. Like Palmeri and Flanery, Bozoki et al. did find evidence for test-phase learning; however, even after correcting for test-phase learning using the no-study baseline, there was evidence for implicit category learning in the AD patients. In contrast, both AD patients and controls were at chance on a test of episodic recognition of studied items, further dissociating category learning from recognition. Thus, the test-learning hypothesis cannot fully explain the dissociation between category learning and recognition memory in amnesic patients.

Can single-systems models account for the data?

The modeling and empirical results presented by the single-system theorists have provoked important and useful debate within the field and have highlighted both the need for stronger experimental control over memory phenomena and the limitations of dissociation logic. We do not dispute the fact that single-system models can often account for particular dissociations, or that dissociations themselves do not compel multiple memory systems (cf. Poldrack et al., 1999b). However, we will argue here that although the single-system approach can account for a range of human behavioral data, the broader set of results from neuroscience can only be explained by recourse to the notion of multiple memory systems. It may seem unfair to the single-system theorist to be taken to task for failing to explain data (i.e., neuroscientific data) that their theories were not designed to explain. However, the fundamental claims of both single-system and MMS theories regard the question of whether there are multiple forms of representation in memory, and this is a question to which both behavioral data and

neuroscientific data are directly relevant. Thus, any theory in this realm should be judged

on its ability to account for the maximum amount of those data.

With regard to neuropsychological data, the modeling approach described above may

be able to account for single dissociations, but it cannot easily account for double

dissociations such as those observed between amnesics and Parkinson's disease patients

on the PCT (Knowlton et al., 1996a). The fact that amnesics show spared PCT learning

but impaired declarative memory, whereas PD patients show the opposite pattern, cannot

be straightforwardly accounted for using a single parameter within a single-system

model. Some single system theorists have claimed to be able to account for double

dissociations, primarily by positing deficits in perceptual or response systems that are

separate from the single memory system. For example, Nosofsky and Zaki (1998)

proposed that the learning deficit on the PCT in PD patients could reflect deficits outside

of the memory system, such as deficits in response selection. Similarly, Kinder and

Shanks (2003) explained the double dissociation between recognition memory and

perceptual repetition priming through a secondary deficit in the perceptual system, which

was separate from the memory system thought to support both forms of memory. The

fact that deficits in other systems are proposed to explain these dissociations undercuts

the claims of parsimony from the single-system camp; the phenomena are explained

through multiple mechanisms just as in the MMS view, with the only difference being

that those other systems are involved in perception or response selection rather than

memory.

In contrast to the notion that the deficit in PD on the PCT task lies outside of the

memory system, we have found that this deficit is directly related to the requirement to

learn on the basis of feedback: PD patients can learn the same information normally in an

observational learning paradigm (Shohamy et al., 2004). Thus, response selection on the

basis of learned information is normal in PD patients, but they cannot learn on the basis

of feedback. This deficit in feedback-based learning is consistent with the role of the

dopamine system (which is impaired in PD) in the coding of outcomes in relation to

behavior. For example, work by Frank and colleagues (Frank et al., 2004) has directly

tied the learning deficits in PD to phasic activity in the dopamine system, by showing that

unmedicated PD patients are impaired at learning from positive but not negative

feedback, whereas PD patients on L-DOPA show the opposite pattern. These data are

also consistent with results from neurophysiology showing that dopamine neurons fire in

proportion to reward prediction errors (e.g., Schultz et al., 1997), in combination with the

known involvement of dopamine in modulating neural plasticity at cortico-striatal

synapses (e.g., Reynolds and Wickens, 2002). The multiple memory systems view offers

a straightforward means by which to link these behavioral dissociations to knowledge

about the underlying neurobiology (Poldrack and Carr, in preparation). From the

standpoint of a single system view, there is no way to account for the relation between

neurobiology and behavioral dissociations, since that account proposes that all memory

phenomena rely upon a single mechanism.

The imaging results of Foerde et al. (2006) are highly convergent with the

aforementioned double dissociation between amnesic and PD patients on the PCT, by

showing that a manipulation that reduces later declarative memory also reduces the

involvement of the MTL in performance, while at the same time increasing the

involvement of the striatum. These imaging results are also in line with the results of the

studies in rodents by Packard and colleagues (Packard, 1999; Packard and McGaugh, 1996) , which have shown that the degree of involvement of declarative versus habit memory systems can be modulated by manipulating the relative activity of hippocampus and striatum. The fact that the imaging studies have isolated exactly those regions predicted on the basis of neuropsychological and animal results is easily explained on the multiple-system view, and because the dissociation in the Foerde et al. study involved correlations with learning, it is difficult to argue that these effects reflect non-mnemonic systems, as has been argued to explain neuropsychological dissociations. Similar imaging dissociations observed by Reber and colleagues in the context of perceptual categorization (see Reber, this issue) prove equally difficult for the single-system theorist to explain.

Finally, the clear dissociations between declarative memory and habit systems in animal models pose serious difficulties for the single-system theorist. Manipulations of the basal ganglia and hippocampus in animals result in double dissociations between tasks (such as the win-stay and win-shift maze tasks: Packard et al., 1989) that are strongly parallel to the dissociations observed in humans. Further, manipulations of these areas can either enhance or reduce the engagement of different memory strategies (e.g., Packard, 1999), whose characteristics are similar to those of different memory phenomena that rely upon the same brain regions in humans. Under the MMS approach these parallels between animal and human memory systems reflect a conserved neurocomputational architecture that underlies learning and memory across species. Single-systems theories have been limited to accounting for human behavioral data and

thus cannot explain how animal lesion results could be integrated with human behavioral and imaging data.

The single-system theorist might respond that, although the data from neuroimaging and animal studies are interesting from a biological point of view, they are not directly relevant to questions about the *psychological* organization of learning. It is certainly possible that there could be fractionated neural systems underlying a single unified cognitive process, such that neural dissociations do not imply psychological dissociations (Van Orden and Paap, 1997). Although there are no data to our knowledge that would support this view, in the end the single versus multiple systems approaches must be evaluated on the basis of both their explanatory power and their productivity, in terms of generating new and interesting results. We would argue that the MMS view has continued to provoke new and interesting results across human and animal research, whereas the single system view has largely focused on protecting its central assumptions and attacking results from the MMS approach rather than inspiring novel findings. It is this kind of productivity that we believe argues strongly in favor of the MMS approach in comparison to the single-systems approach.

Proliferation of memory systems or parameters?

Opponents of MMS views have often posed a *reductio ad absurdum* in which memory systems proliferate to the point where every single dissociation is explained by a different memory system; this argument has appeared in the debate over systems versus processing theories of amnesia in the 1990s (e.g., Roediger et al., 1990) and the more recent debate over single versus multiple system models of category learning (e.g., Palmeri and Flanery, 2002). Further, it is suggested that the single-system approach is

less susceptible to this problem; for example, Palmeri and Flanery (2002) claimed that "In general, whereas the proliferation of multiple systems can be a natural consequence of a simplistic neuropsychological interpretation of behavioral dissociations and double dissociations, computational modeling approaches are far more conservative in positing separate systems".

We agree with Palmeri and Flanery that a very simplistic view of neuropsychological dissociations could lead, in principle, to a proliferation of memory systems. However, we would note that the proliferation of memory systems that this would predict has not actually come to pass: The overall scheme of memory systems laid out by Squire (Squire, 1992) has remained largely constant, with only minor additions in the last fifteen years. Instead of positing a new memory system on the basis of every dissociation, the MMS approach requires converging evidence from human behavioral and patient work, animal studies, and (more recently) neuroimaging in order to propose a new memory system that is to be taken seriously.

In contrast, it appears that the single system theorists may suffer from a "parameter proliferation" problem. The fit of any model can be improved by including additional free parameters, and this is indeed how single-system theorists have chosen to account for double dissociations. For example, as discussed above, Nosofsky and Zaki (1998) explained the Knowlton et al. (1996) double dissociation by adding a response scaling parameter to their model; this was not meant as a serious theory of the deficit in PD, but rather to show that the pattern of data in PD could be explained by a parameter that is unrelated to the strength of the memory mechanism. Similarly, Kinder and Shanks (2003) modeled a double dissociation between repetition priming and recognition memory by

varying a parameter related to perceptual degradation. Whereas there are multiple

constraints from neuropsychology and neurobiology on the systems that are proposed by

MMS theorists, the single-system theorist can apparently add parameters to account for

dissociations without external constraints (such as the relevant neurobiology). This

provides substantial flexibility to account for data; however, the neural plausibility of

these parameters must be taken into account in assessing the resulting claims.

Neural models and the single-system approach

The models proposed by single-system theorists to account for memory dissociations

have generally been simple mathematical or computational models that do not attempt to

model the known neural circuitry underlying the behaviors being modeled. In contrast,

there is a growing move towards models that are directly informed by the

neurocomputational architecture of the relevant neural systems identified by cognitive

neuroscientists, taking advantage of the recent explosion in computational neuroscience.

For example, several computational models of declarative memory have been developed

based on details of the neurobiology of cortico-hippocampal interactions and the

computational structure of the medial temporal lobe (e.g., Gluck and Myers, 1993;

Norman and O'Reilly, 2003). In the domain of nondeclarative memory, Frank and

colleagues (Frank et al., 2004) have described a model of procedural learning based on

the features of cortico-striatal and dopamine systems. An examination of these models

makes clear that there is substantial structure within the neural systems that support

various forms of learning, and that taking this structure into account provides a better

account of human learning compared to models that ignore neurobiology. For example,

Norman and O'Reilly (2003) showed how a set of behavioral phenomena that have

proven difficult for single-system models of declarative memory (e.g., the lack of a list strength effect in recognition memory) arise naturally from models that are based on the known computational structure of the medial temporal lobe. We would argue that it is simply not possible to maintain a single-system approach to learning and memory if one takes neurobiology seriously. We envision that the continued development of neurocomputational models of learning will provide even further impetus for MMS approaches.

Challenges for MMS theories

The foregoing should not be taken to suggest that MMS theories do not suffer from their own problems and challenges. One serious challenge is that interpretation of dissociations often relies upon the assumption that individual tasks are relatively pure measures of a particular memory system. However, it has long been appreciated that memory tests rarely are sensitive to just a single memory mechanism. Although some approaches, such as Jacoby's (1991)process dissociation procedure, have been proposed to allow more direct estimation of the underlying systems, this issue remains deeply problematic for the MMS approach. There is hope that neuroimaging may provide a means by which to better understand the contribution of different memory systems to performance. In the work by Foerde et al. (2006) described above, fMRI provided converging data to suggest that learning under single versus dual-task conditions differently relied upon basal ganglia and hippocampal memory systems. Although it is important to realize the limitations in inferring cognitive processes from activation (Poldrack, 2006), neuroimaging data can clearly contribute to better understanding the functional architecture of cognitive tasks.

Another important challenge for MMS theories is the increasing realization that memory systems are interactive rather than independent (Packard et al., 1989; Poldrack and Packard, 2003). Dissociations between memory systems led initially to the concept of functionally and neurally independent systems underlying different memory capacities. However, it is now clear that hippocampal and striatal memory systems may compete to drive performance (Packard, 1999), and that the relative engagement of these memory systems is negatively related in humans (Poldrack et al., 2001). Because such interactions rely upon intact function in each system, it is difficult to study them in patients, but neuroimaging can allow measurement of these systems in normal individuals. An important remaining challenge for MMS theories is to better understand the neurobiological mechanisms by which these interactions occur (cf. Poldrack and Rodriguez, 2004).

Conclusions

The study of category learning using a cognitive neuroscience approach has provided substantial insights into the cognitive and neural systems that support multiple forms of learning, yet some theorists continue to insist on the viability of a single memory system. We have argued here that, contrary to the claims of single system theorists, the single system approach lacks parsimony because it fails to successfully explain a large body of data from neuropsychological, neuroimaging, and animal neuroscience studies. This convergence of data demonstrates the power of category learning as a tool for understanding memory system organization and function.

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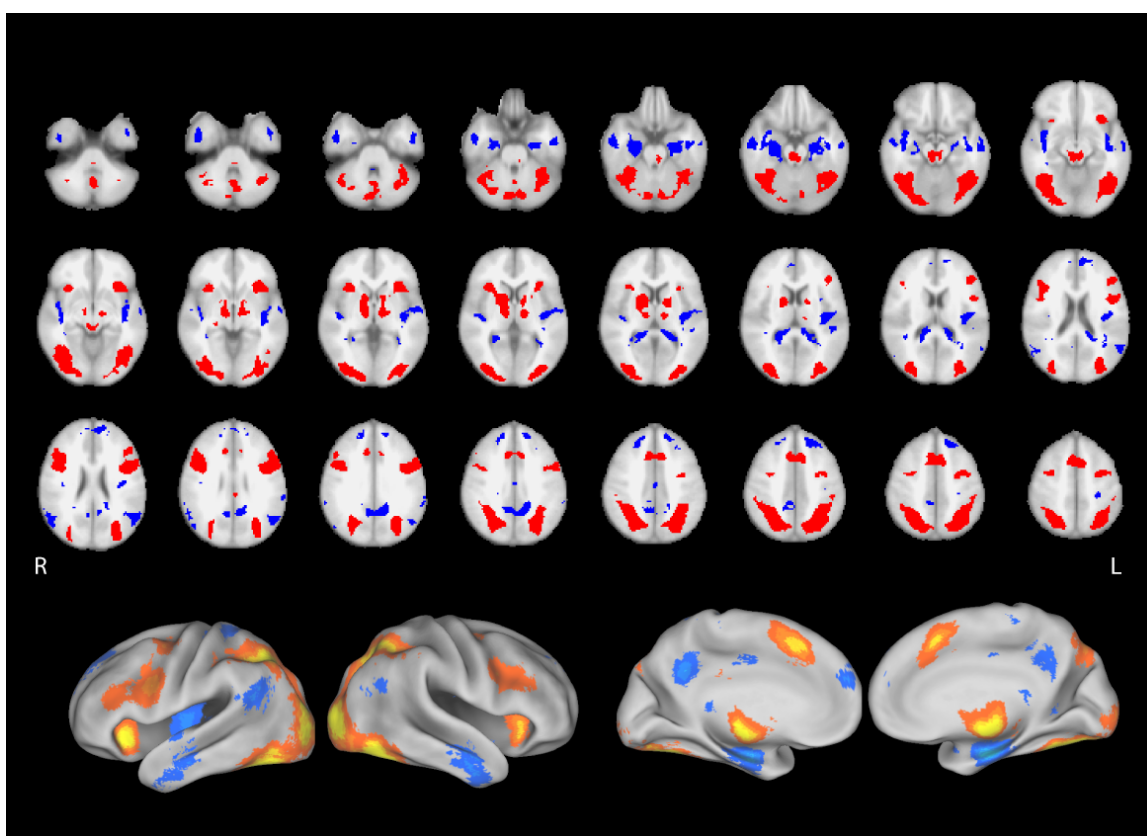Squire, L.R., Knowlton, B.J., 1995. Learning about categories in the absence of memory. Proceedings of the National Academy of Sciences (U. S. A.) 92, 12470-12474.

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Figure 1. Meta-analysis of imaging results from fMRI studies of probabilistic classification learning (Aron et al., 2006; Aron et al., 2004; Foerde et al., 2006; Poldrack et al., 2001). Regions highlighted in color were significantly active (z > 1.96) in each of the four studies; regions in red were significantly more active for classification learning versus baseline, regions in blue were significantly less active for classification versus baseline. Cortical surface renderings were created using multifudicual mapping to a population-average landmark- and surface-based (PALS) atlas using CARET software (Van Essen, 2005)

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