Memory Systems, Processing Modes, and Components: Functional Neuroimaging Evidence

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Abstract

In the 1980s and 1990s, there was a major theoretical debate in the memory domain regarding the multiple memory systems and processing modes frameworks. The components of processing framework argued for a middle ground: Instead of neatly divided memory systems or processing modes, this framework proposed the existence of numerous processing components that are recruited in different combinations by memory tasks and yield complex patterns of associations and dissociations. Because behavioral evidence was not sufficient to decide among these three frameworks, the debate was largely abandoned. However, functional neuroimaging evidence accumulated during the last two decades resolves the stalemate, because this evidence is more consistent with the components framework than with the other two frameworks. For example, functional neuroimaging evidence shows that brain regions attributed to one memory system can contribute to tasks associated with other memory systems and that brain regions attributed to the same processing mode (perceptual or conceptual) can be dissociated from each other. Functional neuroimaging evidence suggests that memory processes are supported by transient interactions between a few regions called *process-specific alliances*. These conceptual developments are an example of how functional neuroimaging can contribute to theoretical debates in cognitive psychology.

Philosophers and cognitive neuropsychologists have questioned whether functional neuroimaging has contributed (Coltheart, 2006) or will ever contribute (Fodor, 1999; Harley, 2004; Van Orden & Paap, 1997) to cognitive theory. We believe that functional neuroimaging data, just like lesion data in previous decades, can gradually strengthen or weaken a cognitive theory over competing ones and inspire new theories (Cooper & Shallice, 2011; Henson, 2005, 2006). In this article, we focus on the debate begun in the 1980s among proponents of memory systems, processing modes, and component process frameworks.

Memory Systems, Processing Modes, and Component Process Frameworks

During the heyday of implicit memory research in the 1980s and 90s, one of the most pressing theoretical issues was how to explain dissociations due to brain damage or experimental manipulations between *explicit memory tasks*, such as recall and recognition, which require awareness of memory at retrieval (and likely at encoding), and *implicit memory tasks*, such as motor skill learning and priming, in which memory can be retrieved without awareness but is inferred by changes in performance.

The theories proposed to explain explicit–implicit memory dissociations were typically based on one of three different frameworks. We use the term *framework* to refer to broad assumptions underlying specific theories. Unlike theories, frameworks are too abstract to be falsifiable; their success or failure can be evaluated only indirectly via the success or failure of the theories they support.

According to the *memory systems framework*, explicit and implicit memory task are dissociable because they depend on different memory systems. The most popular theory within this framework is the *declarative–nondeclarative theory*, which postulates that explicit memory tasks are mediated by a declarative memory system, which itself consists of two dissociable types, episodic and semantic, in which conscious awareness of having retrieved a memory is a prime component. By contrast, implicit memory tasks are mediated by several nondeclarative memory systems (Squire, 1992; Tulving & Schacter, 1990), such as procedural or perceptual systems, which do not depend on conscious awareness of the memory that is retrieved.

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According to the *processing modes framework*, dissociations reflect differential engagement of different types of processing. The dominant theory within this framework is the *conceptual–perceptual theory* (Blaxton, 1989; Roediger & McDermott, 1993; Roediger, Weldon, & Challis, 1989), which postulates that dissociations between explicit and implicit tasks occur because the former emphasize conceptual processing and the latter emphasize perceptual processing. If explicit and implicit tasks are both conceptual or both perceptual associations rather than dissociations should be found.

Finally, the *component process framework* (Moscovitch, 1992; Witherspoon & Moscovitch, 1989) proposes that, instead of a handful of memory systems or a couple of processing modes, there are dozens of different *processing components*. These components are associated with different brain regions and are recruited in different combinations by memory tasks, yielding complex patterns of associations and dissociations. Some components may be specific to tasks traditionally associated with one memory system, but other components are shared by tasks attributed to different memory systems. Also, components may be shared by memory and nonmemory tasks, such as those involving attention and perception. Thus, the processing components framework is not limited to memory; it is a general approach for conceptualizing mind–brain organization during task performance. The component process framework underlies *region-specific theories* that cut across systems and processing modes. For example, within the component process framework, the hippocampus may be defined as a region that mediates relational memory, regardless of whether the task is explicit or implicit or whether it is perceptual or conceptual (Olsen, Moses, Riggs, & Ryan, 2012).

By the early 1990s, a theoretical stalemate was reached between memory system and processing mode frameworks (Roediger & McDermott, 1993). By the late 1990s, evidence, particularly that emerging from the nascent neuroimaging literature, began favoring the components framework (Roediger, Buckner, & McDermott, 1999)—a process that has continued in the intervening years.

Functional Neuroimaging Evidence and the Three Frameworks

The sections below provide a few examples of how the three theories fit with functional neuroimaging evidence. These examples illustrate what we believe is the trend in the field; a formal evaluation of these theories would require a comprehensive meta-analysis of functional neuroimaging evidence, which is beyond the scope of this short theoretical article.

Memory system framework: Declarative– nondeclarative theory

Though starting within a purely cognitive framework, memory system theories were translated into neuropsychological terms to capitalize on lesion evidence that purportedly supported them. According to *declarative–nondeclarative theory*, dissociations at a functional cognitive level had counterparts at a neuropsychological level, leading to the conclusion that explicit memory tasks that tap episodic memory depend on medial temporal lobe (MTL) and prefrontal cortex (PFC) regions whereas implicit memory tasks, such as priming and skill learning, are dependent on other brain regions (Squire, Knowlton, & Musen, 1993; Tulving, 1991). Although many functional neuroimaging findings fit well with these ideas (e.g., Gabrieli, 1998), it quickly became apparent that the neuroimaging data did not support the dissociations on which memory systems theory depended. Dissociations were found as much within explicit and implicit tests of memory as between them, and associations across tests also proliferated. Thus, the PFC regions associated with the declarative memory system are also activated by variety of implicit memory tasks (e.g., Badre & Wagner, 2007; Fletcher & Henson, 2001). In addition, MTL regions associated with declarative (episodic) memory can contribute to implicit memory (for reviews, see Dew & Cabeza, 2011; Henke, 2010). For example, the hippocampus is activated by old items consciously perceived as new (e.g., Daselaar, Fleck, Prince, & Cabeza, 2006), by subliminally processed items (e.g., Henke, Mondadori, et al., 2003), and by saccade-related implicit memory effects (Hannula & Ranganath, 2009). Finally, there is evidence that another MTL region, the perirhinal cortex, contributes to conceptual priming (Voss, Hauner, & Paller, 2009; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010), as well as to visual discrimination with no memory components (e.g., Barense, Henson, Lee, & Graham, 2010; O'Neil, Cate, & Kohler, 2009; but see Squire & Wixted, 2011). Although MTL activity during an implicit memory task could reflect a contamination by explicit strategies, if one uses this argument without independent evidence of contamination, the declarative–nondeclarative theory becomes difficult to falsify.

Also, visual perceptual priming is assumed to depend on visual cortex (for a review, see Grill-Spector, Henson, & Martin, 2006; Tulving & Schacter, 1990), but this region is also associated with declarative memory retrieval in both episodic and semantic domains (for reviews, see Binder & Desai, 2011; Danker & Anderson, 2010; Kim, 2011). It has been suggested that perceptual priming attenuates visual cortex activity whereas declarative memory enhances it (Henson, 2003). However, visual priming can sometimes enhance visual cortex activity (Henson, Shallice, & Dolan, 2000; Slotnick & Schacter, 2004) and declarative memory can reduce it (Poppenk, Moscovitch, & McIntosh, 2012). Likewise, conceptual priming has been linked to activity in the left anterior ventrolateral PFC (Blaxton et al., 1996; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000), but the same region is also activated during episodic and semantic memory tasks (for a review, see Badre & Wagner, 2007). Finally, skill learning memory has been linked to the basal ganglia (Knowlton, Mangels, & Squire, 1996), but basal ganglia activations have also been reported during episodic memory (Han, Huettel, Raposo,

Adcock, & Dobbins, 2010; Sadeh, Shohamy, Levy, Reggev, & Maril, 2011).

Processing mode framework: Conceptual–perceptual theory

Although the conceptual–perceptual theory did not originally include hypotheses about brain regions, if one adds auxiliary function-brain hypotheses (Roskies, 2009), the resulting view predicts that conceptual memory tasks should engage regions associated with semantic processing, whereas perceptual memory tasks should engage regions associated with sensory processing. Although these predictions fit well with many functional neuroimaging findings, these broad differences cannot explain dissociations on memory tests between regions associated with the same processing mode. For example, the left anterior ventrolateral PFC (VLPFC) and the left lateral temporal cortex (LLTC) are both associated with conceptual processing (Binder, Desai, Graves, & Conant, 2009), but their contributions to memory tasks has been dissociated. For instance, in the explicit memory domain, a study found that the left anterior VLPFC contributed to both semantic retrieval and episodic encoding, whereas the LLTC contributed to semantic retrieval but not to episodic encoding (Prince, Tsukiura, Daselaar, & Cabeza, 2007).

Likewise, even though the fusiform gyrus (FG) is broadly associated with visual perceptual processing, dissociations have been reported between the functions of the left and right FG. For example, the left FG shows object priming (repetition suppression) across different exemplars and views of the same object, whereas the right FG shows it only for identical objects (Koutstaal et al., 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Vuilleumier, Henson, Driver, & Dolan, 2002).

The conceptual–perceptual theory is not incompatible with multiple forms of conceptual processing or multiple forms of perceptual processing. However, if these forms of processing are specified to explain the activity of individual brain regions, then the conceptual–perceptual theory is decomposed into many region-specific theories, which fit better with the component process framework, as is the case, for example, when the hippocampus is theorized to process relational information regardless of the domain in which it is applied.

Component process framework: Region-specific theories

Instead of investigating taxonomies of memory systems or processing modes, most functional neuroimaging researchers in the memory domain have implicitly assumed a component process framework and have focused on developing and refining theories about specific brain regions. These region-specific theories can explain not only the involvement of these regions in memory tasks but also their contributions to other cognitive domains. Although there are dozens of these region-specific theories, only a few examples for MTL, PFC, and parietal subregions are described below.

MTL subregions. Whereas the declarative–nondeclarative theory links MTL subregions to explicit memory, region-specific theories can explain their involvement in implicit memory tasks. For example, the theory that the hippocampus is involved in processing flexible relational memory representations (Eichenbaum, Otto, & Cohen, 1994) can account for hippocampal activations during implicit memory tasks with a relational component (Hannula & Ranganath, 2009; Henke, 2010; Olsen et al., 2012). Likewise, theories of perirhinal function that link this region to the integration of perceptual features (Bussey, Saksida, & Murray, 2005) can explain perirhinal activations during perceptual tasks with no memory components (Barense et al., 2010; O'Neil et al., 2009; Staresina, Duncan, & Davachi, 2011).

PFC subregions. Declarative–nondeclarative theory linked the PFC primarily with explicit memory (Squire et al., 1993), but theories of specific PFC subregions can explain their involvement in implicit memory tasks. For example, the theory that the left anterior VLPFC mediates controls access to semantic representations can explain the involvement of this region not only during semantic and episodic memory tasks but also during conceptual priming tasks (Badre & Wagner, 2007). This theory can also explain why this region is activated in controlled conceptual processing tasks but not in more automatic forms of conceptual processing, which may activate the left temporal cortex.

Parietal subregions. An important limitation of declarative–nondeclarative and conceptual–perceptual theories is that they do not account for some of the most frequent activations during memory tasks, such as those in the ventral parietal cortex (VPC) during episodic memory retrieval. In contrast, these activations can be explained by region-specific theories, such as the hypothesis that the VPC mediates bottom-up attention (Cabeza, Ciaramelli, & Moscovitch, 2012; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Cabeza et al., 2011; Ciaramelli, Grady, & Moscovitch, 2008). It is important to note that this hypothesis can explain the involvement of the VPC not only in episodic retrieval but also during perceptual and motor reorienting, language and number processing, and theory of mind tasks (Cabeza et al., 2012). Although our bottom-up attention hypothesis has been challenged in the literature (Hutchinson, Uncapher, & Wagner, 2009; Nelson, McDermott, & Petersen, 2012), the component process approach is assumed by all.

Region-specific theories make predictions that are as strong and falsifiable as those made by declarative–nondeclarative and conceptual–perceptual theories. For example, the declarative–nondeclarative theory predicts that the hippocampus should be activated for explicit memory tasks but not for implicit memory tasks (both relational and nonrelational), whereas the component process theory, in conjunction with relational memory theory, predicts that this region should be activated for relational memory tasks but not for nonrelational memory tasks (both declarative and nondeclarative).

It could be argued that multiple regions-specific theories are less parsimonious than a broad theory such as the declarative–nondeclarative theory. However, parsimony cannot redeem theories that do not fit well with the data; as the quote attributed to Einstein says, "everything should be kept as simple as possible, but no simpler." Broad theories based on memory systems and processing mode frameworks seem to be too simple to account for available functional neuroimaging data, whereas region-specific theories may be less parsimonious, but they have the potential of explaining both memory and nonmemory data.

Interactions Among Components: Process-Specific Alliances

Although the main message of this article is that functional neuroimaging evidence is more consistent with the components framework than with memory systems and processing modes frameworks, it is worth noting that this evidence also suggests the need for updating the components framework. In particular, functional neuroimaging studies using functional connectivity methods have clearly shown that the way an individual brain region contributes to a cognitive task depends on its interactions with other brain regions. Thus, the component framework, which posited such interactions (Moscovitch, 1992, 1994), must be expanded with specific assumptions about component interactions, which we do here by introducing *process-specific alliances* (PSAs).

A PSA is a small group of brain regions working together to achieve a cognitive process. This small "team" is rapidly assembled in response to task demands and is rapidly disassembled when no longer needed. Thus, we view PSAs as flexible, temporary, and opportunistic. These characteristics distinguish PSAs from large-scale networks that are assumed to be relatively stable across tasks and persist during periods of rest (e.g., Doucet et al., 2011; Wig, Schlaggar, & Petersen, 2011; Yeo et al., 2011). The links among nodes or components in large-scale networks, however, may bias but not determine the components that form different PSAs.

An example of a PSA in the episodic memory domain is the VLPFC–hippocampus alliance assumed to mediate the encoding of new information into episodic memory (Simons & Spiers, 2003). During this process, the VLPFC is assumed to process and organize incoming information, which is stored in the hippocampus (Moscovitch, 1992). Thus, each component of a PSA has its own function, but together they mediate a more complex operation. An example of a PSA in the emotion domain is the VLPFC–amygdala alliance mediating emotion regulation (Ochsner & Gross, 2005): The amygdala responds relatively automatically to emotional stimuli, but the VLPFC can dampen this activity to prevent the alteration of behavioral goals.

As illustrated by these examples, the same brain region (e.g., VLPFC) may be a part of many PSAs. Although the same brain region is likely to mediate a similar function in different PSAs (e.g., a control function for VLPFC), the way this function is applied varies depending on the PSA (e.g., control of memory vs. control of emotion). This idea could explain how the same brain region may contribute to very different memory tasks, such as explicit and implicit memory tasks. For example, one may assume that the hippocampus contributes relational memory processing to both explicit and implicit memory task, but that this process is accessible to consciousness and under voluntary control only when the hippocampus interacts with certain PFC regions for explicit memory tasks and not when it interacts with other brain regions (e.g., motor or sensory cortices) for implicit memory tasks. In other words, although the explicit–implicit distinction cannot be easily applied to individual components, future work will show whether it may be applied to PSAs themselves.

Implications for Cognitive Theory

The question remains whether the component process framework has influenced cognitive theory and experimentation. The finding that the hippocampus is activated during tests of implicit memory (e.g., Schacter, Wig, & Stevens, 2007) has led to cognitive studies showing that recollection influences priming (e.g., Sheldon & Moscovitch, 2010), perception (e.g., Hannula & Ranganath, 2009; Ryan, Althoff, Whitlow, & Cohen, 2000), and semantic memory (e.g., Westmacott & Moscovitch, 2003). Conversely, findings that the hippocampus is activated during subliminal encoding and retrieval (e.g., Henke, Treyer, et al., 2003; Reber, Luechinger, Boesiger, & Henke, 2012) have led to cognitive studies showing that nonconscious encoding and retrieval influences episodic memory (e.g., Voss, Baym, & Paller, 2008). These findings, which get at the heart of cognitive memory theories, suggest that recollection, the core of episodic memory, is a two stage process: nonconscious activation of memories leading to the conscious awareness of the activated memories (see also Tulving, 1983).

The functional neuroimaging evidence, and the component process views it supports, have also eroded the boundaries between episodic memory, working memory (Cowan, 2001; Jonides et al., 2008; Postle, 2006), and perception (Graham, Barense, & Lee, 2010; Lee, Yeung, & Barense, 2012; Peterson & Skow-Grant, 2003). Though such developments had already begun in the cognitive domain, findings that common memory structures in the MTL were activated during nonepisodic memory tasks helped support and extend these cognitive models against their competitors (e.g., Baddeley, 2012; Squire & Wixted, 2011).

Within episodic memory itself, evidence from neuroimaging threatens to challenge the commonly held assumption that laboratory tests of episodic memory, based on single stimuli, capture the essence of autobiographical memories derived from the world outside the laboratory. The overlap in brain activation during retrieval in the two types of tasks is not as extensive as one would have predicted if the laboratory events are meant to model autobiographical episodes (Cabeza & St

Jacques, 2007; Gilboa, 2004; McDermott, Szpunar, & Christ, 2009). These findings can now stimulate the search for crucial rather than incidental components of episodic memory.

Finally, the observation that common components, such as the hippocampus, are activated both when recalling the past and planning for the future has had a profound influence not only on the type of cognitive experiments that are conducted but on our ideas about the very nature of episodic memory and its ultimate function (Addis & Schacter, 2012; Schacter, Addis, & Buckner, 2007). Deriving support from neuroimaging evidence, cognitive memory theory has began to slip the bonds that tethered it only to the study of memory per se and emancipated it to pursue its fortune in other domains, as Bartlett (1932) anticipated.

Conclusion

The components processing framework is not antithetical to other approaches—it accommodates them within its own framework. It emphasizes that to understand cognition and the functional neuroanatomy that underlies any given cognitive act, it is necessary to identify the separate components that mediate it and appreciate the nature of their interaction. Though admittedly "fuzzy" because there is no adherence to a fixed system in any domain, the components approach provides a framework for research on memory and other functions. By first fractionating a task into its components and attempting to understand how these components operate as PSAs, one can apply this knowledge to other tasks where such components are needed. Components and PSAs provide the building blocks for theories of memory. In general, the component process approach is largely accepted in functional neuroimaging, though it still has its competitors in network models, and it is a good example of how functional neuroimaging has contributed to cognitive theory.

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