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On the Evolution of a Functional Approach to Memory

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Abstract

In an analysis of memory systems, Sherry and Schacter (1987) emphasized the importance of functional and evolutionary considerations for characterizing mechanisms of memory. The present article considers four different yet closely related topics from more recent research in which similar considerations have played a prominent role in shaping both experiment and theory: the seven sins of memory, mechanisms underlying memory misattribution errors, the role of memory in imagining future experiences, and the relation between associative inference and memory errors. These lines of research illustrate the usefulness of attempting to integrate functional and mechanistic considerations, in line with the general approach articulated by Sherry and Schacter (1987).

During the 1980s, a debate raged among memory researchers in cognitive psychology and neuropsychology regarding whether memory is best conceived as reflecting the operation of a unitary system or multiple, dissociable systems (for perspectives on the debate, see Cabeza & Moscovitch, 2013; Roediger, 1990; Schacter, 1992; Schacter & Tulving, 1994; Squire, Knowlton, & Musen, 1993; Tulving, 1985). Most researchers involved in the debate focused on how to interpret evidence of dissociations among cognitive measures of memory in healthy individuals and in amnesic patients with medial temporal lobe damage. For example, when an experimental variable exerts different effects on the performance of Task X and Task Y, or when amnesic patients perform normally on Task X and poorly on Task Y, do these dissociations justify the postulation of distinct memory systems underlying each task?

In the midst of this debate I began having a series of productive conversations with David Sherry, whose research on memory for food locations in birds was already familiar to me (e.g., Sherry, 1984). We discussed the possible contribution of evolutionary and functional perspectives on memory to addressing the contentious issues at stake in cognitive and neuropsychological debates about multiple memory systems, which up to then had focused almost exclusively on attempting to identify underlying mechanisms in light of experimental results. Those conversations eventually resulted in a *Psychological Review* article that laid out our ideas on how evolutionary and functional perspectives could help to inform the multiple memory systems debate (Sherry & Schacter, 1987). The centerpiece of the article was the idea that we called *functional incompatibility*: “when an adaptation that serves one function cannot, because of its specialized nature, effectively serve other functions (1987, p. 439)”. We viewed functional incompatibility as a critical concept that was missing from the

ongoing multiple memory systems debate: “The reason, we will argue, that the evolutionary outcome has been multiple memory systems rather than a single system capable of serving many functions is that the memory system that effectively solves some environmental problems may be unworkable as the solution to others (1987, p. 443).” Sherry generated striking examples of functional incompatibility from the literatures on song learning, food caching, and related domains in non-human animals that clearly illustrated the operation of functional incompatibility, and that motivated our application of the concept to human memory and the debate over memory systems. We argued that multiple memory systems should be invoked only when a case could be made for functional incompatibility among systems proposed to underlie performance of dissociable tasks.

The 1987 paper impacted the subsequent debate over memory systems in various ways, as evidenced by over 1,200 citations to the paper according to Google Scholar. Interestingly, a near-identical concept was incorporated into the highly influential complementary learning systems model of multiple memory systems (McClelland, McNaughton, & O’Reilly, 1995), but without any reference to the Sherry & Schacter (1987) paper. This oversight was later recognized by O’Reilly, Bhattacharya, Howard, and Ketz (2014) in a retrospective paper on the complementary learning systems approach: “Unbeknownst to us at the time, Sherry and Schacter (1987) had advanced a very similar idea based on functional tradeoffs leading to an evolutionary pressure to develop multiple memory systems (p. 1230).” Nonetheless, the combined impact of the two papers has resulted in the general idea of functional incompatibility becoming familiar to researchers in a variety of domains, including cognitive and behavioral neuroscience, computational modelling, cognitive psychology, and animal learning.

Although the concept of functional incompatibility articulated in the Sherry and Schacter (1987) paper subsequently guided my own thinking about multiple memory systems, our more general emphasis on the importance of functional and evolutionary considerations in memory theories had a broader influence on my approach to conceptualizing the nature of memory. In the present paper, I attempt to illustrate this influence by briefly summarizing ideas and findings concerning four related topics to which I have devoted much attention during the past two decades, and where my approach has been heavily impacted by functional and evolutionary considerations: the seven sins of memory, mechanisms underlying memory misattribution errors, the role of memory in imagining future experiences, and the relation between associative inference and memory errors.

The Seven Sins of Memory

Psychologists and neuroscientists have long known that memory is subject to forgetting and distortion. In an attempt to organize our knowledge of memory’s misdeeds, I proposed that they could be classified into seven basic categories, which by analogy to the classical seven deadly sins, I called the seven sins of memory (Schacter, 1999, 2001). Three “sins of omission” refer to different kinds of forgetting: *transience* (decreasing accessibility of information over time), *absent-mindedness* (breakdown at the interface of attention and memory), and *blocking* (temporary inaccessibility of information that is stored in memory). Three “sins of commission” refer to different kinds of memory distortions: *misattribution*

(attributing a memory or idea to the wrong source), *suggestibility* (implanted memories that result from suggestion or misinformation), and *bias* (retrospective distortions produced by current knowledge, beliefs, and feeling). The seventh sin, also one of commission, is *persistence* (intrusive or pathological remembering of events).

The memory sins can have serious negative consequences. For example, misattribution and suggestibility are often involved in wrongful convictions of innocent individuals who are later exonerated of crimes they did not commit (Garrett, 2011). Persistence of traumatic memories has been implicated in crippling psychological disorders such as depression and post-traumatic stress disorder (e.g., Herz, Bar-Haim, Holmes, & Censor, 2020). And in a recently updated edition of *The Seven Sins of Memory* (Schacter, in press), I discussed a lethal form of absent-minded forgetting in which well-intentioned parents, completing a drive on a hot day in which their infant is in a rear car seat, forget that the infant is in the car, and unknowingly leave the infant to die in the oven-like vehicle. Such cases typically involve a confluence of circumstances that favor absent-minded forgetting, such as a change in routine, absorption with urgent matters unrelated to the child, reliance on automatic behavior, and an absence of retrieval cues at the moment they are needed (for vivid illustrations of such cases, see Weingarten, 2009).

Given the potentially serious consequences of the memory sins, my initial engagement with them led me to consider a question that harked back to the functional and evolutionary perspectives developed by Sherry and Schacter (1987): Why would evolution produce such a flawed and potentially dangerous system? Are the seven sins simply the result of evolutionary inefficiencies or missteps, system glitches that serve only to undermine the operation of memory? Grappling with these kinds of questions led me to a very different perspective on the seven sins, namely that they are more profitably viewed as the products of processes that contribute critically to the adaptive functioning of memory (Schacter, 2001, Chapter 8). For example, although the sin of persistence often produces debilitating intrusive memories of negative or traumatic experiences, it is crucial for an organism to be able remember robustly potentially harmful or life-threatening events – persistence is a price we pay for this otherwise adaptive feature of memory. Informed by my prior discussions of evolutionary theory with David Sherry and our claims in the Sherry and Schacter (1987) paper, I was careful to make distinctions among the various ways in which evolution might have produced such an outcome: through an *adaptation* (i.e., a feature that arose through the operation of natural selection because it increased reproductive fitness), *exaptation* (i.e., an adaptation that has been co-opted to perform a function other than the one for which it was initially selected; Gould, 1991), or *spandrel* (i.e., a type of exaptation that is an unintended by-product of a particular feature; Gould & Lewontin, 1979). Indeed, in this discussion I drew on Sherry's elegant experimental work on sex differences in spatial memory in brown-headed cowbirds, which linked females' role in finding and remembering nest locations to their relatively larger hippocampus than male brown-headed cowbirds (Sherry, Forbes, Khurgel, & Ivy, 1993), as an example of an adaptation produced by natural selection. Nonetheless, acknowledging that it is often difficult to determine definitively which of these evolutionary accounts apply to each of the memory sins, I attempted to make the case for viewing transience and persistence as adaptations, and the other memory sins as either exaptations or spandrels (for detailed discussion, see Schacter, 2001, Chapter 8;

for other adaptive accounts of memory errors, see Anderson & Milson, 1989; Anderson & Schooler, 1991; Bjork & Bjork, 1988; Fawcett & Hulbert, 2020; Nørby, 2015; Howe, 2011; Schacter, Guerin, & St. Jacques, 2011). The key point is that viewing memory errors in light of evolutionary considerations allows us to see them as something other than flaws in the basic architecture of memory.

Setting aside these distinctions regarding the precise nature of the evolutionary mechanisms that could produce “adaptive sins”, in the subsequent sections I will illustrate how taking a broadly functional/adaptive perspective on memory errors can be linked to experimental evidence.

Memory Misattributions in Humans and Mice

One of the major paradigms for investigating misattribution errors in humans is the well-known Deese-Roediger-McDermott or “DRM” false recognition paradigm (Deese, 1959; Roediger & McDermott, 1995). Here, participants initially study lists of associated words (e.g., *candy, sour, sugar, bitter, good, taste, tooth, nice honey...*) and later make old/new recognition decisions about previously studied words (e.g., *taste*), unrelated new words (e.g., *point*), and most important, a semantically related and previously unstudied “critical lure” word (e.g., *sweet*). Numerous studies have shown that participants frequently claim with high confidence to “remember” having previously studied the critical lure word.

Although various interpretations of the precise basis of this memory illusion have been advanced (for a review of theory and data, see Gallo, 2010), one general interpretation is that high levels of false recognition in the DRM paradigm reflect the retention of semantic/associative information about list items, often referred to as semantic gist. In everyday life, it is often critical to remember the central meaning or gist of past experiences rather than retaining all the specific details, and the same semantic/associative processes that underlie this ability may be responsible for false memories in the DRM paradigm. Thus, false memories in the DRM paradigm may be byproducts of the operation of normally adaptive semantic/associative processes that are critical to such fundamental cognitive abilities as comprehension and generalization.

If DRM false memories do reflect the operation of adaptive semantic processes, then they should be linked to the operation of brain regions that play a role in semantic processing/representation. I collaborated with Martin Chadwick, Demis Hassabis, and their colleagues on an fMRI study that investigated this idea (Chadwick et al., 2016). The study focused on the temporal pole (TP), which is known as a “semantic hub” of the brain because it plays a critical role in processing and representing the meaning of and relations between concepts. Theoretical models of semantic cognition (e.g., Patterson, Nestor, & Rogers, 2007) maintain that concepts that are close in meaning are represented by more similar neural codes or patterns in the TP semantic hub than concepts that are more distant in meaning.

Based on this idea, Chadwick et al. predicted that DRM lists in which the neural representations of the nonstudied semantic lure words (e.g., *sweet*) and their associated study list items (e.g., *candy, sugar, tooth, taste*) in the left TP are highly similar would yield more false memories than DRM lists in which the neural representations of lure words are

less similar to their associated list items. This prediction exploited a well-known feature of DRM lists: some of the lists and their associated critical lures produce much higher levels of false memories than do others. In the scanner, participants viewed sets of four DRM list words and their associated critical lures, and their overlap was assessed with representational similarity analysis, which measures neural pattern similarity between pairs of stimuli as a basis for inferring representational similarity (see Chadwick et al., 2016, for details). Each set of words was associated with a different probability of a false memory for the lure item, as established previously in canonical data from other subjects (Roediger, Watson, McDermott, & Gallo, 2001; Stadler, Roediger, & McDermott, 1999). This approach yielded empirical support for the aforementioned prediction: the degree of pattern similarity between a lure and its associated list items in the left TP was significantly positively correlated with the likelihood of a false memory to that word in the canonical data ($r=+.40$). No other region in the brain showed such a relationship between neural pattern similarity and DRM false memories. These findings lend support to an adaptive view of DRM false memories because they indicate that the same left TP region that supports representation of semantic information and relations, a critical adaptive process, is linked to at least one type of memory error that results from the operation of that process.

Consider next a very different kind of false memory phenomenon documented in a recent study from the laboratory of Sheena Josselyn on which I was fortunate to collaborate (Lau et al., 2020). This study was based in part on previous research from Josselyn's lab and others (for reviews, see Josselyn & Frankland, 2018; Josselyn & Tonegawa, 2020) showing that at the time of an event, neurons compete for allocation to a memory trace or engram, and that the most highly excited neurons win this competition, thereby forming the engram that underpins memory for the event. These allocated "engram neurons" remain more excitable than neighboring, non-allocated neurons for roughly 6 hours after the event. Importantly, if a similar event occurs within this 6-hour period of heightened engram-neuron excitability, some of the same engram neurons that had been allocated to the first event will be co-allocated to the second event. This process of co-allocation serves the adaptive function of linking the two memories via common engram neurons. The question addressed by Lau et al. concerns whether this process of engram linking via co-allocation could also create memory distortions if elements of the two events are integrated and confused.

Lau et al. used a cued fear conditioning procedure in which mice exhibit a fear memory by freezing to a tone or a light that had previously been paired with shock. Behavioral data showed that mice also exhibited a "false fear memory" by freezing to a neutral stimulus – an auditory tone that had not been paired with shock – if they were exposed to this stimulus 3 hours after they had been conditioned to a tone of a different frequency that was paired with shock. A similar false fear memory was also observed to a neutral light stimulus 3 hours after fear conditioning to a tone, suggesting that simple stimulus generalization does not account for the phenomenon. Through their freezing behavior to both tone and light stimuli, mice in this experiment seemed to be misattributing aversive properties to these neutral stimuli based on their experience 3 hours earlier with a different stimulus. However, no such false fear memory was observed when the neutral stimulus was presented 24 hours after cued fear conditioning.

Neural data showed that, as in the earlier work on co-allocation, post-training excitability of engram neurons was implicated in the false fear memory: engram neurons showed heightened excitability in response to the neutral stimulus 3 hours after fear conditioning, but not 24 hours after conditioning. In addition, Lau et al. used optogenetic procedures to “silence” engram neurons 3 hours after fear conditioning, and found that this procedure reduced false fear memories. By contrast, optogenetically activating relevant engram neurons at the 24-hour delay increased the incidence of false fear memories.

Reviewing studies on memory allocation, Josselyn and Frankland (2018, p. 406) argued that “the allocation process allows information to be highly structured in the brain and may facilitate the adaptive transformation of memories for individual events into organized conceptual knowledge. Therefore, allocation may represent a general organizing principle for structuring memories and mnemonic information in the brain.” They went on to suggest that this adaptive allocation process might nonetheless also constitute a neural mechanism underlying certain kinds of memory distortions, where memories of one event are intermixed with another. The experiments by Lau et al. (2020) provide evidence that supports this view.

Remembering the Past and Imagining the Future

Most memory research has focused, not surprisingly, on understanding the processes that support recalling and recognizing previous experiences. During recent years, however, there has been increasing emphasis on understanding how memory is used to simulate and plan possible future events. Notably, one of the key issues that stimulated interest in this topic concerns whether non-human animals can engage in “mental time travel” into the past and future (cf., Clayton, Bussey, & Dickinson, 2003; Suddendorf & Corballis, 1997; Templer & Hampton, 2013; Tulving, 2005). This debate has sparked the development of new experimental procedures in attempts to provide evidence for mental time travel in non-humans (e.g., Boeckle & Clayton, 2017; Kabadayi & Osvath, 2017; for a critique, see Hampton, 2019), including a study in which David Sherry and colleagues contributed data suggesting that black-capped chickadees can anticipate future outcomes of their current foraging choices (Feeney, Roberts, & Sherry, 2011). Within the human literature, much of the current interest was stimulated by the documentation of striking cognitive and neural similarities when individuals remember the past and imagine the future. For example, fMRI studies have shown that the same core network of brain regions supports remembering past experiences, imagining future experiences, as well as other kinds of mental simulations, and various populations that exhibit memory impairments (e.g., amnesic patients, older adults) can also exhibit impairments when imagining future experiences or other hypothetical events (for reviews, see Benoit & Schacter, 2015; Schacter, Benoit, & Szpunar, 2017; Schacter et al., 2012; Mullally & Maguire, 2014; Vecchi & Gatti, 2020).

In attempting to conceptualize these striking similarities, Schacter and Addis (2007) put forth the *constructive episodic simulation hypothesis*. Extending earlier ideas from Tulving (2002) that emphasized a role for episodic memory in thinking about the future, Schacter and Addis (2007) adopted a functional perspective and argued that episodic retrieval plays a key role in imagining or simulating possible future scenarios by supporting the flexible recombination of elements of stored episodes to construct possible future episodes. We

contended that this capacity for flexible recombination – that is, weaving together elements of different past experiences that are relevant to an upcoming event – is adaptive for constructing future simulations because the future is rarely identical to the past, so we need to be able to simulate *novel* events based on past experiences. However, we also suggested that a system that supports this kind of flexible episodic recombination has a potential cost in the form of memory errors that can occur when elements of past experiences are miscombined (for related ideas, see Dudai & Carruthers, 2005; Suddendorf & Corballis, 2007; for an update on the constructive episodic simulation hypothesis, see Schacter & Addis, 2020).

During the past decade and more, evidence has mounted that episodic simulation does indeed serve adaptive functions. This evidence has been reviewed elsewhere (Bulley, Henry, & Suddendorf, 2016; Schacter, 2012; Schacter et al., 2017), and I will only briefly mention a couple of examples here. One of the most extensively documented adaptive aspects of episodic simulation comes from the study of intertemporal choice, where people choose between rewards that differ in both size and the amount of time one has to wait until the reward is delivered. Studies of intertemporal choice have documented the phenomenon of temporal discounting – people typically devalue a reward as a function of how long they have to wait to receive it, which can lead to shortsighted or impulsive decisions to choose a smaller but more immediate reward over a larger but delayed one (da Matta, Gonclaves, & Bizarro, 2012). Importantly, a number of studies have shown that simulating the future experience associated with a delayed but larger reward can lead to more patient or farsighted decisions to select the larger delayed reward (e.g., Benoit, Gilbert, & Burgess, 2011; Bulley & Gullo, 2017; Mok et al., 2020; Peters & Büchel, 2010; for review and discussion, see Bulley et al., 2016; Bulley & Schacter, 2020). Moreover, a growing number of studies have shown that engaging in episodic future simulations can promote farsighted intertemporal choices in populations and conditions in which tendencies toward impulsive intertemporal decisions are associated with significant health problems, including alcohol dependence (Snider, LaConte, & Bickel, 2016), obesity (O’Neill, Daniel, & Epstein, 2016), high risk for type 2 diabetes (Stein et al., 2020), and poverty (O’Donnell et al., 2019).

Episodic simulation has also proven adaptive in the domain of prospective memory – remembering an intention to carry out a future action. Several studies have shown that simulating performance of a future action can increase the likelihood of remembering to carry out that action at a later time (e.g., Altgassen et al., 2015; Brewer & Marsh, 2010; Neroni, Gamboz, & Brandimonte, 2014). In an fMRI study, Spreng, Madore, and Schacter (2018) examined the neural underpinnings of this benefit and provided evidence that interactions between the default mode network (which has been linked to episodic simulation in numerous studies; e.g., Benoit & Schacter, 2015; Buckner, Andrews-Hanna, & Schacter, 2008; Buckner & DiNicola, 2019) and an executive control network are linked to the episodic simulation boost on prospective memory performance.

The foregoing and related lines of evidence (Schacter, 2012; Schacter et al., 2017) support an adaptive perspective on episodic simulation. As noted earlier, an important contention of the constructive episodic simulation hypothesis is that some of the same processes that

enable adaptive simulation functions can also produce memory errors. Recent research has also begun to provide empirical support for this idea.

One line of research from my laboratory that supports this view has used brief training in retrieving episodic details of recent events – what we have called an episodic specificity induction (ESI) – to examine downstream effects on a variety of tasks, including future imagining. The ESI is a modification of the well-established procedure Cognitive Interview (Fisher and Geiselman, 1992), which encourages people to focus on specific details of past experiences during retrieval attempts, and that has proven useful for increasing detailed episodic recall in eyewitnesses (for review, see Memon, Meissner, & Fraser 2010). In our ESI experiments, participants initially watch a brief video of people engaging in everyday activities, and then either 1) receive the ESI, which requires responding to questions that probe their memory for episodic details regarding people, objects, and actions in the video, or 2) received a control induction that requires providing their general impressions of the video without recalling specific details. We have found that following an ESI versus this control induction, participants imagine future experiences with richer episodic detail (Madore, Gaesser, & Schacter, 2014), and also show enhanced performance on related tasks that draw on episodic retrieval and recombination, including means-end problem solving (e.g., Jing, Madore, & Schacter, 2016) and divergent creative thinking (e.g., Madore, Addis, & Schacter, 2015; for a review, see Schacter & Madore, 2016). However, along with these beneficial effects we have also found that the ESI can increase memory errors. In experiments in which participants studied DRM lists, administering the ESI after list encoding and just prior to a recall test produced a significant increase in false recall, while having no effect on true recall (Thakral, Madore, Devitt, & Schacter, 2019).

In related research, Dewhurst, Anderson, Grace, and van Esch (2016) instructed participants to encode words on a DRM list by thinking about each word in reference to a future event, past event, or by rating its pleasantness. For example, in the future condition, participants imagined a future holiday and rated how relevant each list item would be to planning the holiday. Dewhurst et al. found that following the future encoding condition, both false recall and recognition of nonstudied lure words increased compared with the other encoding conditions. This increase was specific to false memories: the encoding manipulations did not affect true recall or true recognition of studied words. Dewhurst, Anderson, Grace, and Howe (2019) reported similar findings in an experimental paradigm where participants encoded schema-related words (e.g., for a holiday scenario, *sunblock* and *air tickets*) and schema-unrelated words (e.g., *hammer* and *telescope*) with respect to future events or past events, or in an atemporal encoding condition where they simply visualized the words without any reference to future or past. On a subsequent recognition test, participants made more false alarms to schema-related lures (e.g., *currency*) following the future condition than the other encoding conditions.

According to the constructive episodic simulation hypothesis, it is the capacity for flexibly recombining elements of past experiences that is both adaptive for simulations of future events and also a contributor to memory errors. These ideas fit well with Dewhurst et al.'s (2016) account of increased false (but not true) memories following future-oriented encoding: “the greater flexibility of future thinking may have enabled participants to think

creatively about the possibility of encountering studied items in a hypothetical future event, thereby increasing the possibility of activating the critical lure (p. 1083).” More generally, once again we can see that adopting a functional perspective inspired by evolutionary thinking has proven fruitful for empirical studies.

Associative Inference, Flexible Recombination, and Memory Errors

To explore further the conceptually important link between flexible recombination processes and memory errors, in recent experiments we have examined episodic recombination processes that support another adaptive function: associative inference, where people combine information from different events to make novel connections about related elements of those events. For example, if you observe an unfamiliar man walking a little boy to school one morning and then the next morning observe an unfamiliar woman of similar age walking the same boy to the same school, you can infer a relationship between the man and woman via their common link to the boy. Carpenter and Schacter (2017) devised an experimental paradigm based in part on prior associative inference work from Zeithamova and Preston (2010) to test whether recombination processes that are used to make associative inferences can also lead to memory errors in which elements of the two associated events are confused.

In the Carpenter and Schacter (2017) experiments, participants viewed scenes comprised of a person, an object, and a background setting. Critically, pairs of scenes were linked by a common element. For example, one scene showed a man holding a toy in a living room with a white couch, and the related scene showed a boy holding the same toy in a different living room with a brown couch. Participants were told to try to remember details of each scene and also to infer connections between people in different scenes who were linked to one another via a common object, such as the toy in the foregoing example. The next day, participants were tested for contextual details of half of the scenes *before* they were given an associative inference test in which they indicated whether, for example, the man and the boy were related, and were tested for contextual details of the other half of the scenes *after* the associative inference test.

Carpenter and Schacter (2017) found that after making correct associative inferences, participants were more likely to commit memory errors that resulted from miscombining contextual details from related scenes (e.g., mistakenly recalling that the man was in a room with a brown couch) than after making incorrect inferences. No such difference was found when the test for contextual details was given before the associative inference test. This basic pattern was replicated across four experiments that varied details of the experimental parameters. The finding that increased memory errors for successful associative inferences occurred only when the memory test for contextual details was given after the inference test is critical because Carpenter and Schacter (2017) hypothesized that the associative inference test engages flexible recombination processes that link the two scenes and support making the correct inference – yet can also lead to memory errors.

Carpenter and Schacter (2018) documented a similar effect using a version of the associative inference paradigm just described in which participants tried to remember value details – i.e., whether an individual was designated as “high value” or “low value” – instead of

contextual scene details. After making correct associative inferences, participants were more likely to commit memory errors in which they misremembered which individual had been designated “high value” and which had been designated “low value” than after making incorrect associative inferences. Because no such difference was found when the test for value details was given *before* the associative inference test, once again the pattern of errors implicates flexible recombination processes that were engaged during the associative inference test as a key driver of the memory errors.

In a recent fMRI study, Carpenter, Thakral, Preston, and Schacter (in press) adapted Carpenter and Schacter’s (2017) associative inference/contextual scene details paradigm to investigate the possible role of the hippocampus and other regions in contextual memory errors following successful associative inference, as documented by Carpenter and Schacter (2017). Carpenter et al. (2021) found that after successful vs. unsuccessful inferences, neural patterns in the anterior hippocampus (and several other regions of interest) were more similar to the neural pattern previously elicited by the related yet incorrect contextual detail. For example, after successfully inferring that a man they had seen in a living room with a white couch was linked to a boy in a living room with a brown couch because the man and boy were each holding the same toy, a mistaken memory that the man had appeared in a living room with a brown couch was accompanied by a neural pattern elicited by the brown couch in an earlier testing session. Because the anterior hippocampus was also linked to successful associative inference (replicating previous work; e.g., Zeithamova & Preston, 2010), these findings provide evidence suggesting that the same brain region that supports the adaptive process of associative inference via episodic recombination also contributes to a memory error that is linked to the operation of that process.

Concluding Comments

Towards the end of our analysis of the role of functional incompatibility in the analysis of memory systems, Sherry and I noted that students of memory often focused on the analysis of mechanism without commensurate consideration of function and argued that, just as an analysis of mechanism can inform functional considerations, “awareness of functional considerations can help form and refine hypotheses about memory processes and systems” (Sherry & Schacter, 1987, p. 450). Sherry went on to develop even more elaborated views of the relationship between mechanistic or causal analysis and functional analysis in understanding animal behavior (e.g., Sherry, 2005), and as noted earlier, his experimental work nicely illustrates the integration of these pursuits (e.g., Sherry et al., 1993).

The research and theorizing that I have discussed in this article is in some ways quite different from the research and theorizing that drove the memory systems debate of the 1980s and the ideas developed by Sherry and Schacter (1987). The work discussed here has focused on explicit or declarative memory, mainly episodic memory, and the hypotheses under investigation do not involve claims about multiple memory systems. In contrast to the idea of functional incompatibility that was central to Sherry and Schacter (1987), much of the work I have reviewed here has focused more on functional *compatibilities*. For example, the central idea of the constructive episodic simulation hypothesis is that the flexibility of

episodic memory is compatible with, and makes it suitable for, activities such as simulating future experiences by recombining elements of past experiences. Moreover, the same kind of flexibility is compatible with supporting associative inferences via episodic recombination. But, as we have seen, the capacity for flexible episodic recombination that supports these adaptive functions can result in memory errors. My research program in recent years has focused more on documenting associations among processes in different domains than dissociating different memory systems. Nonetheless, this work has been strongly influenced by a critical emphasis highlighted in my collaboration with David Sherry: the importance of taking into account the functions performed by memory systems when developing and testing hypotheses about the underlying mechanisms. Future studies focused on the relation between mechanism and function will no doubt continue to help deepen and broaden our understanding of memory and cognition.

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