Book review

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Giving evolution its due in memory systems research

Elisabeth Murray, Steven Wise and Kim Graham. *The Evolution of Memory Systems*. Oxford, UK: Oxford University Press, 2017, 512 pp., $90.00, ISBN 9780199686438.

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In 1957, Milner and Scoville published their seminal work with the amnesic patient H.M. Unable to encode or recall experiences in memory following a bilateral medial temporal lobectomy; H.M.'s impairments became the basis for how we conceptualise memory systems today. The impact of Milner and Scoville's findings cannot be understated for cognitive neuroscience, particularly for memory research. In virtually every introductory cognitive psychology course, these findings are presented to emphasise the inextricable relationship between the medial temporal lobes (MTL) and explicit memory, and they formed the starting point for research programmes in countless psychology and neuroscience labs globally. Yet, work in the tradition of H.M. may have overstated the importance of the MTL, making this region the crown seat of memory—with the hippocampus the ultimate jewel. In our pursuit of explaining memory functions in the MTL, we have largely ignored the evolutionary context that shapes the memory systems humans have inherited. Perhaps, due partially to the field's myopic focus on the MTL, we have lost track of a fundamental question: *why did memory evolve?* Only by reconstructing the evolutionary history of memory systems in the brain can we fully understand the ultimate cause of its existence and thereby its function.

So, why does memory exist?

This is the question that launches Elisabeth Murray, Steven Wise, and Kim Graham's new book *The Evolution of Memory Systems* into a provocative discussion on reconciling the role of phylogeny with our framework of memory systems. The authors reconstruct the evolutionary context in which different parts of the brain evolved in mammals, ultimately refuting the prevailing notion that the individual brain regions in the MTL function in a similar, cooperative manner—as a unitary system that operates in service of only one type of memory. They instead propose a new framework altogether, the *evolution accretion model of memory*, comprising seven distinct memory systems that rely on a vast network of brain regions, including those other than the MTL. Given the advent of novel imaging technologies allowing for research into complex brain network interactions, their new proposed framework provides a long-overdue overhaul of traditional memory accounts.

What does the evolution accretion model tell us?

As a response to the fundamental question of why memory exists, the authors describe four main tenets of their evolution accretion model of memory. First, they hold that the memory systems humans are endowed with arose as our ancestors successively adapted to new ways of life. In essence, memory is like a "toolbox," where each system is a tool that has been adapted to the specific needs of a previous ancestor. In early humans, one tool that emerged is self-representation, allowing us to feel and remember complex emotions in response to experiences, to introspect, and to represent facts about one's self. Second, given that these memory systems arose due to varying pressures on our ancestors, they recruited different cortical areas contributing to specialised representations. The authors suggest that *all* cortical regions are involved in memory processes, not just select MTL regions. Notably, they remind us that the hippocampus—today, embedded within the MTL—actually originated in the allocortex of early mammals, before the MTL had even evolved. Third, Murray and colleagues hold that these cortical areas are not exclusive to memory, and have perceptual functions. Most strikingly, the authors confront the prevailing perception-memory division, wherein the function of the MTL is thought to be restricted to memory whereas perception depends on the sensory areas of cortex. Recent neuroimaging studies discussed by Murray and colleagues have demonstrated that MTL structures show differential patterns of activation even on simple visual discrimination tasks, suggesting that the MTL also contributes to perceptual functions. In addition, lesion studies from both the human and animal literature show that damage to the MTL leaves some memory functions intact while also causing some perceptual deficits. Taken together, evidence from neuroimaging and neuropsychological studies challenge the current framework of explicit memory (predicated on studies of patient H.M.) that the MTL acts solely in service of memory. The fourth tenet of the model concludes that explicit memory emerged in the course of hominin evolution from the interaction of specialised representational systems, including representations of the self. In short, the authors move beyond immediate human-animal differences, such as verbal and non-verbal communication, and instead focus specifically on how unique evolutionary pressures among humans have shaped seven distinct memory systems that recruit a range of diffuse cortical networks.

How has the evolution of memory served us?

The critical proposal that Murray and colleagues present is with regards to the evolution of explicit memory, as part of the fourth tenet of their model. The prevailing view holds that there is a singular explicit memory system that evolved in rodents, monkeys, and humans, and can be studied under the assumption that all these species share this system. Instead, the authors clearly illustrate how explicit memory arises from the interaction of four main representational systems (the social-subjective system, the extended hippocampal-navigation system, the feature system, and the goal system). Key to this proposal is the role of the social-subjective system in creating representations of the self, which arose from distinctive selective pressures from the complex social system of hominins that were not faced by other species and their ancestors. From this, the authors argue that a critical feature of explicit memory unique to humans is the ability to re-experience or re-live encoded events. Specifically, Murray and colleagues' proposal describes how this hallmark of explicit memory surfaces through the interaction of the social-subjective system, which contributes to a representation of the self, and the hippocampal-navigation system, which contributes to the binding of event features. In other words, the representation of the self is embedded within the other representational systems, a phenomenon that is absent in other animals because they lack the evolved hominin social-subjective system. Together, the interactions of these systems "give rise to the perception of participating in—and having participated in—the events of one's life" (p. 395). Simply put, we can vividly replay past events in our minds, even attributing meaning to these personal memories—thanks to evolution.

How do we move forward?

In reading Murray and colleagues' book, readers are compelled to move past a memory framework that dichotomises cortical regions into *memory* and *non-memory* functions. There are several critical implications of this reconceptualization for memory research, such as for clinical patient studies and comparative species studies. First, the authors remind us that even patient H.M., hailed as the human example of purely isolated memory impairment, also showed marked difficulties in tasks that we now consider perceptually based. In future research, we need to better our understanding of how cortical networks (or functionally connected cortical regions whose coordinated activity has been shown in recent years to be related to episodic memory, such as the default mode network) might break down in patients, instead of just focusing on discrete cortical regions. Second, by considering how memory systems came online through evolution, we may be able to reconcile the long-standing debate about whether explicit memory is *uniquely* human. To this point, the authors leave us with a simple—but profound—idea: a rodent's representation of the self will surely be different from a human's self-representation at many levels, so other cognitive processes—namely memory—that rely on this self-representation will undoubtedly be different, too. Importantly, Murray, Wise, and Graham urge us to question the way in which we have conceptualised explicit memory in other species by providing clear and convincing evidence that this cognitive process in humans is not just a more complex version of what other species have. Instead, it is a fundamentally different phenomenon that arises from the interaction of adapted representations in the human MTL and cortical systems. As research moves forward, we must revisit the fundamental question, *how did memory evolve and what does evolution tell us about why it exists?*

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