

valuation and affect (mPFC). Their findings extend earlier work illustrating the role of the mPFC in mediating popularity [2], revealing that the mPFC likely has a more global role in indexing social evaluation processes.

Given that participants were scanned while only passively viewing other group members – rather than performing a task that required them to proactively think about social bonds within their network (such as choosing whether to cooperate with a given member) – it is particularly striking that the authors were able to identify neural systems that tracked information about each group member's social standing (i.e., their social status, distance, and ability to broker information). That we appear to do these computations spontaneously, rather than on a need-to-know basis, suggests that our brains are always preparing for social engagement with each individual, regardless of whether such engagement is needed.

These findings provide insight into a question that has been the topic of much theoretical debate in recent years: how do we encode another individual's social value? [3] The authors' finding that social status is indexed by the mPFC, a region that has a critical role in computing value across numerous decision-making contexts [3], indicates that the mPFC represents the social value of another individual even before deciding to trust, help, or cooperate with that person. However, it is unclear why this region would spontaneously represent these social values in situations where no choice is required. One possibility is that the mPFC response is laying the groundwork for a subsequent decision, signaling a potential opportunity for bolstering one's own social status by connecting with a high-status individual.

Indeed, in conjunction with classic evolution theory [4,5], Parkinson and colleagues' findings suggest that the brain is pre-emptively evaluating other individuals to strategically bias subsequent encounters [12].

One way to interrogate how this value signal is being operationalized would be to measure if there is an association between the integrity of the mPFC response and subsequent decisions to abuse trust, attenuate cooperative actions, or only offer help when there is something to be gained socially. If our brains are keeping track of group members' social status and distance, not only should prosocial acts be exhibited more readily towards a person of high status within the network, which should scale with the mPFC response (compared with those who exhibit lower interconnectedness and status), but these decisions should also be made more quickly and reflexively. Additionally, given the impact of empathy and theory of mind capacities on decisions to trust and be altruistic [6,7], prosocial behavior may be further biased by the interaction between an individual's empathic ability and each group members' social status, distance, and brokerage.

Intriguingly, these findings may also provide insight into the motivations behind punitive behavior, something that remains somewhat elusive [8–11]. One possibility is that doling out punishment is contingent on where the perpetrator stands within the social network. For example, the degree of punishment may parametrically scale with the perpetrator's social status and distance from the individual conferring the punishment. This would suggest that the utility of punishment depends, in part, on how well situated a perpetrator is within the social community.

Parkinson and colleagues [12] have successfully measured how the brain encodes real-world social connections, demonstrating that we track in real time not only where we stand among our peers, but also how our peers measure up against everyone else. This innovative work adds to a budding literature characterizing how we understand our social worlds, while also bringing to the forefront further questions about how we plan to interact with others who occupy our world.

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Forum

Retrieval as a Fast Route to Memory Consolidation

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Retrieval-mediated learning is a powerful way to make memories last, but its neurocognitive mechanisms remain unclear. We propose that retrieval acts as a rapid consolidation event, supporting the creation of adaptive hippocampal–neocortical representations via the 'online' reactivation of

associative information. We describe parallels between online retrieval and offline consolidation and offer testable predictions for future research.

Introduction

For over a century, psychologists have known that repeatedly and actively retrieving information from memory, as opposed to restudying the same information, strongly enhances long-term retention [1]. The benefits of retrieval-mediated learning (also known as the ‘testing effect’) hold across a wide variety of materials and testing formats and remain evident across much of the lifespan [1]. No mechanistic framework exists to date integrating these behavioral findings with the growing literature on the neural basis of learning and memory [1]. Here we attempt such an explanation.

In short, we propose that retrieval acts as a fast route to memory consolidation. Specifically, we propose that retrieval integrates the memory with stored neocortical knowledge and differentiates it from competing memories, thereby making the memory less hippocampus dependent and more readily accessible in the future. We explore theoretical links between retrieval and offline consolidation, describe some key evidence in support of a shared mechanism, draw parallels between this proposal and other forms of rapid consolidation, and outline predictions for future research (Box 1).

Retrieval as a Rapid Consolidation Event

Extensive evidence from rodents and amnesia patients shows that hippocampal damage affects the formation of new declarative memories while leaving remote memories (at least partially) intact [2]. An influential computational model [Complementary Learning Systems (CLS)] [2] suggests that the hippocampus and neocortex act synergistically to allow new learning while preserving old information.

Specifically, the neocortex learns slowly and specializes in storing the statistical structure of experiences. The hippocampus learns quickly and specializes in rapidly encoding and binding together new cortical associations. Repeated interactions between the two systems allow new information to slowly shape neocortical representations. If the hippocampus is damaged before enough hippocampal–neocortical interactions can occur, long-term memory will be impaired. These ideas constitute systems-level consolidation, or the process by which newly acquired information is transformed into a stable, long-term memory representation [3].

The gradual transformation that a memory undergoes during systems-level consolidation is promoted by the memory’s repeated offline reactivation (‘replay’) in hippocampal–neocortical circuits. Reactivations during non-rapid eye movement (NREM) sleep arguably play a unique role in embedding information in the neocortex, facilitated by low cholinergic activity and coordinated oscillatory interactions between the hippocampus and neocortex [4]. Replay occurring during both post-learning wakeful rest and sleep has been shown to enhance memory retention [3,4]. Critically, we propose that the neural reactivation of recently acquired memories, as triggered online by incomplete reminders (pattern completion), promotes long-term retention in a way similar to offline replay.

We argue that retrieval and sleep can qualitatively transform memories in at least two distinct ways: by integrating new memories into preexisting neocortical knowledge structures and by adaptively differentiating memories (i.e., reducing their neural overlap) so as to minimize competition between overlapping memories. From a computational perspective, both the integration and differentiation effects can be explained by the tendency of retrieval to be imprecise; that is, to coactivate memories that are semantically or episodically linked to the target memory [5]. Repeated imprecise reactivations in hippocampal–neocortical

circuits afford an opportunity to integrate an initially hippocampus-dependent memory into the coactivated neocortical knowledge structures, similar to replay events during NREM sleep (Figure 1). According to [5], the nature of learning driven by coactivation depends on how strongly memories are activated: strong coactivation of memories leads to integration of those memories, whereas moderate activation of competing memories triggers their adaptive weakening [6] and pushes retrieved and competing memories apart in representational space [7], leaving the retrieved memory in a distinct, accessible state for future recall (Figure 1). Importantly, restudy (i.e., simple re-exposure to a complete, previously stored memory) does not share these computational characteristics [6,7]. Restudy may re-impose the memory’s original pattern onto the hippocampus and neocortex, causing some strengthening of the original trace. However, because restudy triggers less coactivation of related memories it does not adaptively shape the hippocampal–neocortical memory landscape in the same way as active retrieval.

So far we have outlined the similarities between retrieval and offline consolidation on a theoretical, computational level. We next examine behavioral and neural parallels between memory retrieval effects (indexed by differences in retrieved versus restudied information) and consolidation effects (indexed by sleep versus wake intervals) that empirically support our rapid consolidation view.

Similarities between Retrieval and Consolidation

If retrieval rapidly embeds a memory in the neocortex, future retrievals of this memory can utilize neocortical in addition to hippocampal representations to access the memory. Retrieval-mediated memory boosts should thus be most evident whenever hippocampal traces are weak and recall is relatively more dependent on the neocortex. Consistent with this notion, testing effects are strongest at long delays of several days to weeks

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