Journal Club

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Making Memories That Last

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Review of Sneve et al.

Although we have countless experiences daily, relatively few are retained in memory. Great efforts have been devoted to understanding the neural processes and mechanisms that contribute to making memories that last. Much of this research has focused on delineating encoding-related patterns of neural responses that predict subsequent memory. Yet, even though humans can remember experiences after substantially long delays, most studies measure memory after relatively short retention intervals (within minutes or hours of encoding).

Pushing the envelope on this topic, Sneve and colleagues (2015) used fMRI to identify encoding-related brain activity patterns that predicted what information would be remembered after 1.5 h (short delay) and after 6 weeks (long delay). Not surprisingly, subsequently remembered items were those that were associated with increased brain activation during encoding. This pattern was observed regardless of the retention interval examined. However, memories that were retained over the long delay were uniquely associated with stronger encoding-related coupling between the hippocampus and cortical regions, suggesting that distinct encoding processes lead to more durable memories. The authors propose that this observed pattern of hippocampal–cortical functional connectivity may reflect a tagging mechanism that potentiates subsequent consolidation of certain experiences into enduring memories. In other words, as we encode some types of information, we are already preparing it for the long haul.

An emerging literature indeed suggests that memory-related neural processes also extend beyond the formation of the initial memory trace. For example, recent work has shown that encoding-related brain activity "spills over" into post-encoding resting states, and the magnitude of this persistent brain activation is related to subsequent memory performance across individuals (Tambini and Davachi, 2013), in accordance with the notion that the replay of encoded experiences during rest (or sleep) facilitates memory consolidation (see also van Kesteren et al., 2010). Intriguingly, Tompary and colleagues (2015) recently demonstrated that patterns of post-encoding functional connectivity between the hippocampus and the ventral tegmental area predicts episodic memory performance after a delay (24 h), but is unrelated to immediate memory performance. Moreover, the authors showed that although both encoding and post-encoding connectivity patterns predicted subsequent delayed memory independently, these patterns of connectivity were not related to each other. Together, these findings suggest that both common and distinct encoding and consolidation mechanisms predict the formation of long-lasting memories. Furthermore, the notion of systems consolidation, i.e., that some memories are reorganized as information moves from the hippocampus to the cortex (Dudai, 2004), suggests that differences in brain activity for memories retained over long intervals, relative to shorter intervals, may also manifest when memories are being retrieved (Takashima et al., 2009). Hence, it may be fruitful to examine encoding-, consolidation-, and retrieval-related brain activation patterns within the same study to determine not only how the patterns observed at each memory stage relate to long-lasting memories, but also how these patterns specifically evolve across these stages.

More broadly, if the authors' hypothesis is correct, i.e., that increased functional connectivity between hippocampal and cortical regions for long-lasting memories reflects a tagging mechanism, it remains important to determine the precise neural locus of this tagging effect. As connectivity analyses do not specify the direction (causality) of information flow, this approach cannot be used to determine whether the tagging signal originates in the hippocampus or elsewhere in the brain. Moreover, it is not yet known what types of memories undergo this kind of tagging process (i.e., are episodic and nonepisodic memories associated with common or distinct tagging mechanisms?). Such inquiries can shed important light on the nature of systems consolidation, which is poorly understood and greatly debated in humans.

Apart from pinpointing the neural mechanisms that support the formation of more durable memories, it is also important to understand the cognitive factors that may account for this enhanced durability. In addressing this, one would need to determine whether there were specific types of items

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that participants were more likely to retain over the long delay in Sneve et al.'s (2015) study. Although the authors used stimuli that were comprised of everyday objects, it is possible that some items were more likely to elicit cognitive processes that are known to enhance memory. To illustrate, a to-be-encoded item such as "cake" is more likely to elicit positive emotional valence and appetitive reward value relative to an item such as "hammer." To the extent that these cognitive processes can affect how items are encoded (for review, see Madan, 2013), they may account for differences in patterns of learning and associated functional connectivity (Ritchey et al., 2008) and predict the stability of memory traces over a long delay. Indeed, many studies have found that emotional memories are retained over longer delays relative to neutral memories, whereby emotional information is forgotten more slowly (for in-depth discussions, see Talmi, 2013; Yonelinas and Ritchey, 2015). A similar case could be made for reward-related processes; for example, Wittmann et al. (2005) did not observe a reward-related memory effect in an immediate memory test, but found significant differences after a 3 week delay. Thus, it is possible that item-specific properties may have played an important role in the formation of long-lasting memories and associated brain activity in Sneve et al. (2015). Still, which items were remembered may have also been specific to an individual, as noted by the authors, suggesting that interindividual differences in how people processed the stimuli (e.g., prior experiences or transient mind wandering during the experimental session) are likely also be critical in the formation of long-lasting memories. An item analysis could provide insight into the cognitive mechanisms that underlie more durable memories.

In addition to item-specific features influencing memory, procedural details of Sneve et al.'s (2015) study may have played a role in the greater hippocampal–cortical connectivity found to be involved in the formation of long-lasting memories. Specifically, during encoding, the presented items were accompanied by one of two questions: "Can you eat it?" or "Can you lift it?" The authors speculate that the involvement of right hippocampal connectivity in long-lasting memory retention may be related to constructive simulations, i.e., the imagination of the items in relation to the encoding instruction (e.g., eating a hammer). We additionally suggest that these simulations likely involved automatic motor simulations of body–object interactions (Witt et al., 2010; for an in-depth discussion, see Madan and Singhal, 2012) and thus may have elicited greater connectivity with cortical regions in the ventral pathway (Sneve et al., 2015, their Fig. 5) related to automatic processing of body–object interactions (Kellenbach et al., 2003). Importantly, such body–object simulations may have varied across stimuli. For example, given the nature of their stimuli, there may have been a compatibility effect between a given object and its associated encoding instruction; food objects, such as apples, can readily be thought of as objects that may be eaten, while such is not true of nonfood objects such as a hammer. Here we would predict that objects which were more compatible with the provided instruction (e.g., eating an apple) would elicit a more shallow level-of-processing relative to judgments that were more difficult or unnatural, which would have instead resulted in more deliberate and effortful (deeper) processing. Critically, these differences in levels of processing may have influenced the longevity of a given memory, as this is a well known predictor of subsequent memory performance (Craik and Lockhart, 1972). This type of motor-simulation processing could be avoided, for instance, if the stimuli were abstract nouns (e.g., "virtue," "ratio") and the encoding judgments were more perceptual, e.g., word length (odd or even number of letters), capitalization (all uppercase or lowercase letters), or font color. Thus, item- and instruction-related effects likely play a critical role in the formation of memories that last. This topic would be a fruitful avenue for future research.

Despite outstanding questions regarding the precise neural and cognitive mechanisms that can account for the findings of Sneve et al. (2015), the approach used by the authors represents an important step toward bridging the gap between two dominant approaches used in human memory research: one that examines episodic memory in the context of laboratory stimuli at shorter intervals (often minutes to hours), and another that examines real-life (autobiographical) memories after longer intervals (often months to years). While studies of the latter have greatly shed light on the neural and cognitive mechanisms underlying memory for distant events, they inherently lack the ability to examine the encoding of such experiences. Sneve et al.'s (2015) approach, particularly if applied to even longer retention intervals, offers a promising window of opportunity for determining not only the factors influencing the fidelity of long-lasting memories but also the manner by which their neural instantiation changes over time.

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