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Working with Schemas, Predicting with Schemas

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Review of van der Linden et al.

Introduction

The question of how prior knowledge influences the formation of new memories has intrigued behavioral researchers for decades (Bransford and Johnson, 1972; Craik and Tulving, 1975), and has more recently received attention in the neuroscience community (for review, see van Kesteren et al., 2012; Gilboa and Marlatte, 2017). Neurobiological theories suggest that schemas support new learning by accelerating consolidation processes with schema-consistent information achieving rapid assimilation into cortical structures and independence from the hippocampus (Tse et al., 2007; McClelland, 2013; Gilboa and Marlatte, 2017). In support of this rapid consolidation theory, several studies find differential engagement of cortical structures versus the hippocampus during encoding and retrieval of items that are consistent or inconsistent with prior knowledge (van Kesteren et al., 2010, 2013; Bein et al., 2014; Brod et al., 2015; Reggev et al., 2016). However, to date, no study has examined the influence of prior knowledge on neural processes that specifically support the endurance of memories after a period of consolidation.

In a recent paper, van der Linden et al. (2017) addressed this gap by examining the learning of schematically consistent and inconsistent information in a 2 d fMRI study. Participants viewed numerous images of objects grouped into sets of four. Each quartet belonged to one of three conditions. In the schema condition, the four items related to a single theme (e.g., the "knight" schema). In the incongruent condition, the first three items related to a theme, but the fourth was associated with a different theme. Finally, objects in the no-schema condition were unrelated. Participants studied half of the quartets on the first day (remote items) and studied the remaining quartets (recent items) immediately before a memory test on the second day. During the memory test, participants viewed the fourth item of each quartet, intermixed with similar lures and novel items. Recognition of remote items was better for the schema condition compared with incongruent and no-schema conditions.

Of interest is the finding that activation of the left angular gyrus (AG) increased as schemas unfolded over encoding, as measured by greater responses to the fourth item relative to the first item. This buildup was found in the remote schema condition when including only successfully remembered items in the analysis. In the recent schema condition, however, AG buildup was observed when collapsing across later remembered and forgotten items, but not for remembered items alone. The finding that the buildup of AG encoding activity was linked to memory performance only after a 24 h delay (i.e., that it was specific to remote schema items that were subsequently remembered) led the authors to suggest that the buildup of schema representations in AG was particularly important for retaining long-term schema-consistent memories. This raises important questions about the specific computations that AG performs in encoding durable, schema-consistent memories. Is the AG a "binding zone" for combining and storing schema components, as the authors propose? If so, does AG simply reinstate prior schemas, or does it combine new elements to form a coherent representation? Does the sequential nature of the task provide insight about the interplay between AG and hippocampus in schema-supported predictions? Consideration of the role of AG in working memory (WM) and the potential AG-hippocampus interplay in forming predictions might help answer these questions.

AG and working memory

An interesting aspect of the study by van der Linden et al. (2017) is that objects were presented sequentially. Schemas therefore unfolded over time and required the maintenance of prior relevant representations in WM to form a single unified event (Zacks et al., 2007). The AG is frequently implicated in WM studies (e.g., Vatansever et al., 2017) and is thought to sustain activated representations to support cognition (Guerin and

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Miller, 2011; Cabeza et al., 2012). The AG buildup might therefore be related to increasing WM demands in the schema condition: participants may have spontaneously combined items to form a unified representation, adding and holding more items in memory, as long as items were related to the same schema/event. In contrast, in the no-schema condition, participants did not hold items in WM across the sequence; hence, AG activity was low. In the incongruent condition, the change in content in the fourth item may have spontaneously triggered the processing of the last item as a new event, leading to removal of previous items from WM, hence decreasing AG activity (Zacks et al., 2007). van der Linden et al. (2017) did not require participants to actively integrate across items in a sequence. Interestingly, a study that did encourage participants to integrate schema-inconsistent information into a single schema found higher AG activity for inconsistent than for consistent information (Mende-Siedlecki and Todorov, 2016).

Indeed, the AG has been previously linked to the integration of information into unified representations (Binder and Desai, 2011; Ramanan et al., 2017). For instance, the left AG has been implicated in integration of information during retrieval (Guerin and Miller, 2011), and it is critical for the integration of semantically related words (Price et al., 2016). This laterality of activity in the AG corresponds with the schema buildup observed in the left AG in the study by van der Linden et al. (2017): the right AG was associated with a decrease in activity for incongruent items, in contrast to a buildup in activity for schemas. Thus, the left AG involvement in the current study may reflect the WM processes involved in the combination of individual objects into a unified template: the schema. Together these findings suggest that, rather than reflecting the activation of schema representations per se, the buildup of AG activity found by van der Linden et al. (2017) may reflect increasing WM load and integrative processes.

If AG activity reflects WM demands, one would expect an AG buildup in both recent and remote encoding sessions, regardless of later memory performance. Indeed, when collapsing across remembered and forgotten trials, a gradual increase in activity within the quartets was observed in the schema condition during the recent session. Activity for subsequently forgotten remote schema items was not reported, precluding the drawing of an equivalent inference for remote items. Nevertheless, the suggestion by van der Linden et al. (2017) that AG buildup is essential only for remote memory begs the question: How might a WM interpretation of AG buildup account for remote, but not recent, item memory? Possibly, holding items together in WM during encoding for both recent and remote schema-consistent items facilitates the creation of a detailed, elaborate memory that includes the associations between items (Craik and Tulving, 1975; Bein et al., 2015). These detailed traces may be more likely to be retained over time than traces that do not include rich associations, and thus specifically support remote memory. For recently learned information, where the memory strength for individual items is still strong, successful recognition of individual items, as was tested by van der Linden et al. (2017), may not require such precise associative traces; thus, performance is unrelated to WM encoding signals in the AG. This account offers a prediction for future studies: AG buildup would correlate with successful memory of the associations between items (i.e., associative memory) for both recent and remote conditions. In contrast, AG buildup would support memory of individual items only in the remote condition (van der Linden et al., 2017).

AG-hippocampus interplay in the formulation of predictions

The sequential presentation of items in the van der Linden et al. (2017) study taps a key aspect of schemas: they allow us to make predictions about the environment (Ghosh and Gilboa, 2014). Sequential presentation of the stimuli allowed the generation of schema-based predictions that were either met or violated. Theoretical models and empirical investigations point to the hippocampus as a neural substrate for memory-based predictions (Marr, 1971; Schapiro et al., 2012). Interestingly, in the schema condition, when predictions were met, hippocampal responses to the fourth item of a sequence were lower than in the incongruent condition (violated predictions), or the no-schema condition (no predictions; this finding was observed specifically for subsequently remembered remote items). Thus, the observed increase in AG activation was accompanied by disengagement of the hippocampus, and these two neural signals were correlated across participants. Notably, past work has found a seemingly opposite effect: greater hippocampal engagement when prior knowledge influenced memory of novel associations (Liu et al., 2017). Crucially, Liu et al. (2017) did not use sequential presentations. One possibility is that involvement of the AG-hippocampus circuit is specifically required for the temporally extended formulation of predictions, and it tracks the match or violation of these predictions. In this framework, building up these predictions involves the AG (as mentioned above) and potentially the hippocampus as well. Yet, when events match our predictions, the hippocampus disengages. This suggestion dovetails with recent observations of increases in hippocampal activity in response to prediction violations (e.g., Kumaran and Maguire, 2006).

How might matches and violations of predictions differentially influence memory? Interestingly, van der Linden et al. (2017) report more gist-level memory in the schema condition, as marked by more false alarms, which correlated with AG-hippocampus functional connectivity. This suggests that, when predictions are met, the broader schematic knowledge that formulated these accurate predictions is enhanced. This process may be accompanied by reduced encoding of the specific details and corresponding hippocampal disengagement. Importantly, when predictions are not involved (due to simultaneous presentation), behavioral studies consistently find that prior knowledge enhances memory for contextual details (DeWitt et al., 2012; e.g., Bein et al., 2015), a function widely attributed to the hippocampus (Davachi, 2006). An intriguing and testable hypothesis is that, when the presentation of events encourages predictions and their confirmation, schematic processing is enhanced, potentially mediated by increased AG and decreased hippocampal processing. In contrast, if predictions are not involved, increased hippocampal processing may facilitate more detailed encoding.

In conclusion, while previous accounts promote a view of prior knowledge as reducing hippocampal encoding in favor of cortical learning (Sharon et al., 2011; van Kesteren et al., 2012; McClelland, 2013), a more nuanced view might be more accurate: Different hippocampal and cortical mechanisms may come into play, depending on the intersection of prior knowledge, goals, prediction-formation, and other factors. The study by van der Linden et al. (2017) advances our knowledge of some of these factors, and we hope more will follow, to develop a detailed account of the means by which prior knowledge may influence memory.

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