Journal Club

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When Anticipation Aids Long-Term Memory: What Cognitive and Neural Processes Are Involved?

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Review of Bollinger et al.

In our daily life, we continuously anticipate and prepare for upcoming events. One question in cognitive neuroscience has been whether anticipation produces behavioral benefits and, if so, what the neural correlates of effective anticipation are. So far, several studies have shown that neural activity that occurs before an event can influence how that event is processed. Anticipatory activity modulates performance on several cognitive functions, including perception, attention, and memory.

In a recent report published in *The Journal of Neuroscience*, Bollinger et al. (2010) demonstrated that both working memory (WM) and long-term memory (LTM) benefit from anticipation of a stimulus from a given category. Participants were instructed to memorize faces or scenes in a delayed matching-to-sample task. Crucially, target pictures were preceded by one of two types of cue: predictive cues ("remember face" or "remember scene") that indicated the category of the upcoming picture, and neutral cues ("remember face or scene") that did not indicate the category. Target pictures followed the cue after a fixed interval of 6 s. The experiment also involved blocks of passive viewing of faces and scenes. A postexperiment recognition task allowed investigation of LTM performance.

Results showed that WM and LTM performances were better in the predictive condition than in the neutral one. The comparison between predictive and neutral conditions extends the literature about anticipation-related effects on LTM. So far, studies have investigated how different types of cue impact LTM formation [e.g., visual vs auditory cues (Otten et al., 2010), low vs high reward (Gruber and Otten, 2010), emotional vs neutral (Mackiewicz et al., 2006)], but those studies did not compare informative and neutral cues (or absent and present cues). As a consequence, the relationship between anticipation and LTM could be assessed at the neural level (for example, contrasting anticipatory brain activity for items that were later remembered with items that were later forgotten), but the effects of anticipation on LTM performance could not be directly assessed. Comparing cues with different degrees of predictability enables one to investigate the effectiveness of anticipation on behavior; this approach should be useful for future research.

Interestingly, Bollinger et al. (2010) showed that predictive cues enhanced memory for faces but not for scenes. This result mirrored fMRI data reported by the authors. Predictive cues of faces elicited an increase of activity in the fusiform face area (FFA). An analogous increase was not observed for scenes in the equivalent stimulus-selective region, the parahippocampal place area. In addition to the univariate analysis, the authors used the

β-series correlation method to examine functional connectivity. This analysis approach uses trial-by-trial variability to measure correlations in activity between different brain regions. Bollinger et al. (2010) showed that FFA activity following face-predicting cues was functionally connected with a network of frontoparietal regions that are thought to bias sensory processing of expected stimuli. Connectivity measures between these regions and the FFA were then correlated with WM and LTM performance. The authors reported that WM performance was positively correlated with increased functional connectivity between the FFA, the right inferior frontal gyrus, and the left precuneus, whereas LTM performance was correlated with increased functional connectivity between the FFA and the left middle frontal gyrus. Bollinger et al. (2010) suggested that top-down signals bias processing in visual-selective regions when foreknowledge about the stimulus is available. The authors have convincingly shown that this mechanism may benefit WM and LTM performance. However, it is not clear what specific mechanisms enhance memory performance.

Notably, the brain regions showing significant activations in Bollinger et al. (2010) do not correspond to areas identified in previous studies on anticipatory neural activity. For instance, fMRI studies investigating the effects of anticipation on LTM formation showed enhanced hippocampal activity following cue onset for items that were later recognized (Adcock

et al., 2006; Mackiewicz et al., 2006; Park and Rugg, 2010). In the study by Bollinger et al. (2010), the analyses focused on the FFA and its connectivity to frontoparietal areas, and correlations with memory performance were strictly based on these regions of interest. The authors only reported that the hippocampus was functionally connected with the left middle frontal gyrus, whose connectivity with FFA increased as a function of subsequent memory. Therefore, the link between the hippocampus and LTM performance was indirect. The hippocampus is a key brain structure for memory encoding, and an investigation of the correlations between hippocampal activity and LTM in the study of Bollinger et al. (2010) would have allowed a comparison with previous studies. This, in turn, may have provided supplementary insights into the mechanisms involved in their neurobehavioral correlations.

Unfortunately, a limitation of the experimental design used by Bollinger et al. (2010) complicates the interpretation of their findings. In the predictive condition, faces and scenes were presented in separate blocks, whereas in the neutral condition, faces and scenes were intermixed within the same block. This design introduces a potential confound that may have contributed to the behavioral and neuroimaging results. In the predictive condition, participants were aware that the same category would be presented throughout the block, and this may have promoted cognitive processes that are maintained across trials. In the neutral blocks, the set of processes engaged in the cue–target interval had to be reset on a trial-by-trial basis. As a consequence, the memory benefit found for the predictive condition might have resulted from the specific distribution of conditions across blocks, rather than from a genuine effect of predictability of the cue. This is a significant concern, because it has been shown that when different categories are intermixed within the same experimental block, category-specific correlates of memory are attenuated (Galli and Otten, 2010). This might also explain why the predictive cues enhanced LTM performance for faces, but not for scenes. Because the predictive condition engages cognitive and neural processes that are maintained across trials, it may be easier to adopt specific category sets

(Summerfield et al., 2006) in the predictive than in the neutral blocks. Any such process is likely to be more engaged for faces than for scenes because, as suggested by Bollinger et al. (2010), faces are a more homogeneous category compared with scenes, and it is therefore easier to form and maintain a face template.

The distribution of conditions across blocks also challenges the interpretation of the neuroimaging findings. The analyses mainly involved the contrast between the predictive and the neutral condition. Because in this contrast, the predictability of the cue was confounded with the distribution of conditions across blocks, alternative interpretations cannot be ruled out. For instance, if differences across categories were emphasized in the predictive condition, it could be argued that the significant correlations with memory performance found in this condition are heavily dependent upon category-specific processes. Low-level processes may thus play a more significant functional role in Bollinger et al. (2010) compared with previous work on anticipation and memory encoding.

As a consequence of the experimental design, the predictive and the neutral conditions may also differ with respect to the temporal characteristics of neural activity. The neutral blocks likely involve transient changes in neural activity related to individual trials. The predictive condition may instead involve neural activity that is maintained throughout the block. This distinction is relevant because partially dissociable brain regions exhibit the two types of activity during memory formation (Donaldson, 2004). Unfortunately, the experimental design and the fixed interval between the cue and the target in Bollinger et al. (2010) do not allow an examination of the exact time of occurrence of anticipatory activity. Methods with excellent temporal resolution (like electroencephalography and magnetoencephalography) have shown that anticipatory activity related to encoding increases in proximity of the stimulus (Guderian et al., 2009; Gruber and Otten, 2010). Similar temporal characteristics have been observed in fMRI studies (Mackiewicz et al., 2006; Park and Rugg, 2010). In future studies, it may prove useful to examine whether the temporal

characteristic of anticipatory neural activity are related to behavioral outcomes.

To summarize, Bollinger et al. (2010) extended previous literature on the effects of anticipation on memory performance. The analysis of functional connectivity allowed them to examine the brain dynamics underlying memory benefits related to anticipation. We propose that in their study, the cognitive and neural processes at play during the cue–stimulus interval might be different compared with previous work. This difference might be due, to a large extent, to the experimental design and the potential confounds that it introduces. Further study is needed to evaluate under what circumstances anticipation aids memory.

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