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Neural processes during encoding support durable memory

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ABSTRACT

The ability to form durable memory is critical for human survival and development, but its underlying cognitive and neural mechanisms have not been well understood. In particular, existing studies have not clearly dissociated the neural processes supporting short- and long-duration memories. The present study addressed this issue with functional MRI and a modified subsequent memory paradigm. Participants were asked to make semantic judgment on a list of 320 words in the scanner. Half of the words were tested after a short delay (i.e., 1 day, T1) and again after a long delay (i.e., 1 week, T12), whereas the other half were tested only once after the long delay (T2). Materials forgotten during T1 were categorized as forgotten trials, and those remembered during T2 were categorized as long-duration trials. In contrast, trials remembered during T1 but not during T12 were categorized as short-duration trials. We found that compared to forgotten trials, short-duration trials showed decreased activation in the posterior cingulate cortex (PCC) and precuneus, which is consistent with many previous observations. Importantly, long-duration trials showed stronger activity in the left inferior frontal gyrus (LIFG) but less deactivation in the PCC relative to short-duration trials. Psychophysiological interactions (PPI) analysis revealed stronger functional connectivity between LIFG and PCC for long-duration trials than for forgotten trials. Our results suggest that strong PCC activity, in combination with strong LIFG activity, supports long-lasting memory.

Introduction

It is a common observation that, even with apparently similar learning processes, some items can be remembered after a long delay whereas others are quickly forgotten. This difference can be attributed to many factors during the various stages of memory formation and retention, including encoding, consolidation, and retrieval. Focusing on the encoding stage, early behavioral studies suggested that the "level-of-processing" has a significant impact on memory durability: more durable memory is achieved by deep encoding (e.g., processing based on semantic components) than by shallow encoding (e.g., processing based on phonemic and orthographic components) (Craik and Lockhart, 1972; Craik and Tulving, 1975). Even more effective than semantic encoding is self-relevant encoding ("Does the word describe you?") (Rogers et al., 1977; Symons and Johnson, 1997). However, the neural mechanisms underlying these mnemonic benefits have not been clearly elucidated.

Using functional imaging and a subsequent memory paradigm (Brewer et al., 1998; Wagner et al., 1998), studies have examined extensively the neural processes that support lasting memories, by comparing neural activities for the items that were either remembered or forgotten subsequently (minutes to days after learning) (Kim, 2011; Paller and Wagner, 2002; Uncapher and Wagner, 2009). These studies have consistently revealed that the subsequently remembered items showed greater activation than the subsequently forgotten items in the inferior frontal gyrus (IFG), fusiform cortex, and hippocampus; and greater deactivation in the default network, including the anterior and posterior middle-line.

Because most of the previous studies used a single memory test after a delay, it was not possible for them to directly examine whether the same processes supported both short- and long-duration memories. To address this issue, several studies have compared the subsequent memory effect across different lengths of delay, typically using two different strategies. The first strategy is to test half of the studied material at a short delay and the other half at a long delay. In the first such study, Uncapher and Rugg (2005) asked participants to study a list of words, and half of the words were tested 30 min after learning and the other half 2 days later. Several regions, including the left hippocampus and left dorsal IFG, showed the common subsequent memory effect under both short and long delays. In contrast, whereas the bilateral IFG supported recollection after a 2-day delay, the fusiform gyrus supported recollection after a 30-minute delay. Similar strategies have been used by Ritchey et al. (2008) and Steinmetz et al. (2012) to study how the memory durability effect is modulated by emotion. For example, in Ritchey et al.'s study, emotional and neutral items were tested at 20-minute and 1-week delays. They found that amygdala activation supported the memory of emotional pictures at both short and long delays,

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whereas the amygdala-MTL (medial temporal lobe) connectivity was increasingly important as the delay became longer.

A second strategy, first used by Carr et al. (2009), is to test all studied materials at both short (e.g., 10 min) and long delays (e.g., 1 week). By integrating memory performance in both tests, items could be categorized as consistently recollected items (recollected at both tests), transiently recollected items (recollected at the first but not the second test), consistently familiar items (judged as familiar at both tests), or consistently forgotten items. Using a paired associative learning task and focusing on the MTL, they found that activity in the perirhinal cortex (PRC) showed greater activity for items that were consistently recollected than that for the transiently recollected and consistently familiar items, whereas the parahippocampal cortex showed a subsequent memory effect during encoding of items that were both consistently or transiently recollected (Carr et al., 2009).

Both strategies provide unique and complementary contributions to our understanding of the neural mechanisms of memory durability, but each has its own limitations. For the second strategy, the retrieval process during the first test could enhance subsequent memory performance because all of the items were tested twice (Roediger and Karpicke, 2006). More importantly, it is entirely possible that items with different memory strengths during the short-delay test could benefit differently from this retrieval practice, an idea originally proposed by Ebbinghaus, and experimentally demonstrated by many studies (Anderson et al., 1994). By testing only half of the material at each test, the first strategy avoids the confound of the retrieval effect but at the expense of not being able to clearly isolate items with true transient memory from those with long-lasting memory. That is, some items that were remembered during the first test, thus categorized as short-duration memory, could have been remembered if they were tested one week later, which would have led them to be categorized as long-duration memory.

In all these studies, the short-duration memory was probed within 1 h of the initial study session, whereas the long-duration memory was tested after 24 h to 1 week. Although this design can help to maximize the differences between short and long memory durations, these results can be affected by the differences in consolidation processes. After encoding, memories are consolidated at the cellular level for up to several hours (Dudai, 2004). After that, consolidation continues, with sleep playing an important role in this process (Cartwright, 2004; Gais et al., 2007). It is unclear, therefore, whether the results of previous studies have been confounded by a lack of sleep-facilitated consolidation for the short-duration condition. Research is needed to examine how the encoding process differentially supports short- and long-duration memories when both have had consolidation during sleep (e.g., 1-day vs. 1-week delay).

The present study aimed at examining the neural processes that support long-lasting episodic memory. Participants were asked to make semantic judgment about a list of 320 words in the scanner. Half of the words were tested after a short delay (i.e., 1 day, T1) and again after a long delay (i.e., 1 week, T12); whereas the other half were tested only once after a long delay (T2). This design allowed us to compare memories of different durations with all items having had similar encoding and initial consolidation during sleep. More importantly, it allowed us to clearly isolate short- and long-duration trials while avoiding the contamination of the retrieval practice effect.

Material and methods

Participants

Twenty-four college students (11 males, mean age = 21.5 ± 1.22 years, ranging from 19 to 24 years) were recruited for this study. All participants had normal or corrected-to-normal vision, and were self-reported to be right-handed and to have no previous history of neurological or psychiatric diseases. Informed written consent was obtained before the experiment. This study was approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University.

Material

In total, 320 medium to low frequency, two-character Chinese nouns were used as the learning material in an incidental encoding task. Half of the words were tested twice (after both short [1 day] and long [1 week] delays), and the other half were tested only once after the long delay (Fig. 1A). They were counterbalanced across subjects. All words were presented visually in white color on black background. Forty additional words were also included for another purpose (an examination of mental representations of words as affected by linguistic factors). These words were presented in the same way as the words used in the current study, so they should not have affected the results of the current study. Furthermore, these additional words were not tested, and were excluded from this analysis. Another 480 words were used as foils in the two memory tests, so that the ratio of targets to foils was 1:1 at both tests, and none of the foils was used twice. To minimize the primacy and recency effects, three words were added at the beginning and the end of each encoding run, respectively, which were excluded in both behavioral and MRI analyses.

fMRI procedures

Participants lay supine on the scanner bed, and viewed visual stimuli back-projected onto a screen through a mirror attached onto the head coil. Foam pads were used to minimize head motion. Stimulus presentation and timing were achieved using MATLAB (MathWorks) and Psychtoolbox (www.psychtoolbox.org) on an IBM-compatible PC. During the scan, participants were explicitly instructed to judge whether each word represented a concrete or abstract concept, by pressing their index fingers. The hand used to indicate an abstract or concrete response was counterbalanced across participants. Participants' responses were collected online using an MRI-compatible button box. Event-related design was used in this study. For each trial, the stimulus was presented up to 2 s until a valid response was received, which was then followed by a cross fixation at the center of the screen until the designated onset time of the next stimulus. Random jitters from 0.5 to 6.5 s (mean: 2 s) were added between words and the sequence was optimized for design efficiency (Dale, 1999) using an in-house program. In total, participants finished two 13-minute runs of the “abstract-concrete” semantic judgment task, each including 186 trials.

MRI acquisition

Imaging data were acquired on a 3.0 T Siemens MRI scanner in the MRI Center at Beijing Normal University. A single-shot T2-weighted gradient-echo, EPI sequence was used for functional imaging acquisition with the following parameters: TR/TE/θ = 2000 ms/25 ms/90°, FOV = 192 × 192 mm, matrix = 64 × 64, and slice thickness = 3 mm. Forty-one contiguous axial slices parallel to the AC–PC line were obtained to cover the whole cerebrum and partial cerebellum. Anatomical MRI was acquired using a T1-weighted, three-dimensional, gradient-echo pulse-sequence (MPRAGE). The parameters for this sequence were: TR/TE/θ = 2530 ms/3.09 ms/10°, FOV = 256 × 256 mm, matrix = 256 × 256, and slice thickness = 1 mm. In total, 208 sagittal slices were acquired to provide high-resolution structural images of the whole brain.

Post-scan memory tests

Two recognition memory tests were administered 1 day and 1 week after the scan respectively (Fig. 1A). Half of the words were tested after a short delay (T1) and again after a long delay (T12), whereas the other