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Review

Peri-encoding predictors of memory encoding and consolidation

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ABSTRACT

We review reports of brain activations that occur immediately prior to the onset or following the offset of to-be-remembered information and can predict subsequent mnemonic success. Memory-predictive pre-encoding processes, occurring from fractions of a second to minutes prior to event onset, are mainly associated with activations in the medial temporal lobe (MTL), amygdala and midbrain, and with enhanced theta oscillations. These activations may be considered as the neural correlates of one or more cognitive operations, including contextual processing, attention, and the engagement of distinct computational modes associated with prior encoding or retrieval. Post-encoding activations that correlate with subsequent memory performance are mainly observed in the MTL, sensory cortices and frontal regions. These activations may reflect binding of elements of the encoded information and initiation of memory consolidation. In all, the findings reviewed here illustrate the importance of brain states in the immediate peri-encoding time windows in determining encoding success. Understanding these brain states and their specific effects on memory may lead to optimization of the encoding of desired memories and mitigation of undesired ones.

Contents

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1. Introduction

The ability to form new memories and to consolidate them into a long-term form is considered to depend on a variety of brain processes and mechanisms. In delineating these mechanisms, the focus of much research has centered on memory-predictive brain activations during encoding (Kim, 2011). However, a complementary line of research also explores brain activations that predict memory outcome and occur *prior* to encoding (pre-encoding activity) and *following* encoding (post-encoding activity). The rationale underlying this attention to peri-stimulus time windows is that for real brains in the real world, experiences and memoranda do not exist in isolation, but rather proceed on a temporal continuum: time present is at least partially a consequence of time past and is expected to provide cues concerning time future.

It is only natural, therefore, to expect that at any given point in time, brain activity resulting from experiences or expectations will affect the memory of the information encountered. It is important, however, to define at the outset the time window of interest. Events far in the past (i.e. development and remote memory) and processes occurring long after learning (i.e. long-term consolidation) also affect the outcome of experience. In the present discussion, we limit ourselves to only those brain and cognitive processes that occur immediately before or after encoding, and can predict memory success or failure; we define them as “peri-encoding predictors of memory”. We will focus on human studies, unless otherwise indicated. Examples and conclusions from animal models would be provided to support data from human studies, given that human studies have limited access to cellular analysis that could markedly benefit mechanistic interpretations.

A typical protocol used to elicit human brain activations that predict whether an event will be remembered or forgotten is the ‘subsequent memory’ paradigm (Brewer et al., 1998; Kim, 2011; Paller et al., 1987; Wagner et al., 1998). In this paradigm, brain activity is recorded, using methods such as electroencephalography (EEG) or functional magnetic resonance imaging (fMRI), while participants encode new information (i.e., study phase). In the subsequent test phase, which – depending on the specific protocol – takes place minutes to months later, memory performance relating to the information presented in the study session is assessed, and this performance is correlated with the brain activity measured in the study session. In this way, differences in brain activity during the study session that predict subsequent memory performance (Dm) are detected and used to identify the engagement of candidate brain regions in encoding.

Using the subsequent memory procedure, researchers have delineated memory-related brain activations that occur during encoding. Commonly, combining subsequent memory protocols with human functional imaging identifies memory predictive activity in areas including (but not restricted to) the medial temporal lobe (MTL), including the hippocampus (e.g., Davachi et al., 2003; Eichenbaum et al., 2007; Kensinger and Schacter, 2006; Ranganath et al., 2004). These findings are in line with studies of amnesic patients and lesion studies in non-human primates pinpointing the role of the MTL in memory formation (Alvarez and Squire, 1994; Scoville and Milner, 2000).

The subsequent memory protocol is used also in combination with electrophysiological measures, such as scalp EEG, magnetoencephalography (MEG), and intracranial recordings (iEEG). Human studies using this protocol revealed that encoding-related activity mostly include theta (oscillatory patterns of approximately 4–8 Hz), but also gamma (30–100 Hz) rhythm (Axmacher et al., 2006; Kahana et al., 2001; Osipova et al., 2006). These activations are typically observed in hippocampal as well as other cortical and subcortical regions, following the onset of the to-be-remembered information. Compared to EEG and MEG, intracranial recordings (iEEG) are considered to be less influenced by interferences related to saccadic movements and are more sensitive to high frequency bands, e.g. gamma (Lachaux et al., 2012; Yuval-Greenberg and Deouell, 2009).

As noted above, since in real life memory formation occurs on the fly, it is pertinent to define the conditions that subserve successful memory formation not only during the encoding session, but also immediately prior to and following encoding. Here we will review selected data on memory-predictive brain activity immediately preceding (Table 1) or following (Table 2) encoding, referring to timescales ranging from fractions of a second to minutes. We will then discuss cognitive operations that may be associated with this peri-encoding activity. While there is extensive literature on immediate pre-encoding conditions determining memory outcome in humans, the literature on memory-predictive immediate post-encoding conditions is still sparse. Most literature on post-encoding memory deals with consolidation processes that occur hours or days following the encoding phase, and a substantial part of it concerns consolidation during sleep (Walker and Stickgold, 2006). We will not discuss here the rich literature on consolidation at large, which is covered elsewhere (Dudai, 2012). Thus, our discussion of post-encoding memory-predictive processes is relatively terse.

2. Pre-encoding brain activity

Ample data indicate that brain activity occurring between hundreds of milliseconds to minutes prior to stimulus onset can predict memory outcomes for that stimulus. We first review empirical findings showing memory-predictive prestimulus brain activity occurring milliseconds or seconds (Section 2.1) and minutes (Section 2.2) prior to event onset. We then proceed to discuss possible cognitive mechanisms (attention, contextual processes, and preceding encoding or retrieval) that may underlie these findings (Section 2.3).

2.1. Brain activity within seconds prior to encoding

Evidence for memory-predictive pre-encoding brain activity has been mainly amassed from studies that presented a cue several seconds prior to stimulus presentation and measured brain activity during the cue-stimulus interval. Park and Rugg (2010) presented a cue that signaled whether an upcoming word stimulus would be written or spoken. They found that hippocampal activation in the cue-stimulus interval (1.5–4.5 s) predicted later recollection success of the words (see also Addante et al., 2014; Turk-Browne et al., 2006). Of note, Yoo et al. (2012) found that decreased prestimulus parahippocampal activity (−2 to 0 s prior to stimulus onset) predicted successful encoding of scenes in a subsequent memory protocol. These authors first identified parahippocampal activity that resulted in poor or successful encoding. Then, using a real-time fMRI procedure, activation in parahippocampal cortex was monitored, and to-be-encoded information was displayed when participants entered what was posited to be “good” (low parahippocampal activity) or “bad” (high activity) brain states for learning. Memory performance was better for scenes presented in “good” as opposed to “bad” brain states. The authors suggested that lower parahippocampal activation prior to encoding may enhance memory formation by keeping available resources for encoding. However, they pointed out inconsistencies between their results and other studies which showed that increased, and not decreased, MTL activation predicted successful encoding (Park and Rugg, 2010; Turk-Browne et al., 2006).

In a study by Adcock et al. (2006) participants were informed that correctly remembering a picture of a scene would award them with the amount of money presented in a preceding cue. In a