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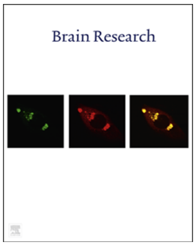

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Research Report

Neural processing of recollection, familiarity and priming at encoding: Evidence from a forced-choice recognition paradigm

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ABSTRACT

The distinction between neural mechanisms of explicit and implicit expressions of memory has been well studied at the retrieval stage, but less at encoding. In addition, dissociations obtained in many studies are complicated by methodological difficulties in obtaining process-pure measures of different types of memory. In this experiment, we applied a subsequent memory paradigm and a two-stage forced-choice recognition test to classify study ERP data into four categories: subsequent remembered (later retrieved accompanied by detailed information), subsequent known (later retrieved accompanied by a feeling of familiarity), subsequent primed (later retrieved without conscious awareness) and subsequent forgotten (not retrieved). Differences in subsequent memory effects (DM effects) were measured by comparing ERP waveform associated with later memory based on recollection, familiarity or priming with ERP waveform for later forgotten items. The recollection DM effect involved a robust sustained (onset at 300 ms) prefrontal positive-going DM effect which was right-lateralized, and a later (onset at 800 ms) occipital negative-going DM effect. Familiarity involved an earlier (300–400 ms) prefrontal positive-going DM effect and a later (500–600 ms) parietal positive-going DM effect. Priming involved a negative-going DM effect which onset at 600 ms, mainly distributed over anterior brain sites. These results revealed a sequence of components that represented cognitive processes underlying the encoding of verbal information into episodic memory, and separately supported later remembering, knowing and priming.

1. Introduction

On any given day, we encounter and experience many events. Only some of these experiences are transformed into memories and can be subsequently remembered. One outcome of encoding can be *explicit memory*, which is an expression of memory involving the conscious awareness of prior events, and accompanies voluntary retrieval of studied information. Explicit memory has usually been examined by using intentional tests of recall and recognition memory.

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In such tests of explicit remembering, experiences that cannot be retrieved intentionally are labeled as subsequently forgotten. However, in some indirect or *implicit* tests that present previously studied information in a seemingly unrelated task (e.g., perceptual identification), a recent encounter with an item can be shown to influence responding even in the absence of explicit memory. This phenomenon is called *implicit memory*, or priming, and refers to a long-term change in behavioral response to an item as a result of prior exposure to it, usually taking the form of facilitated processing.

Much evidence from event-related potentials (ERPs) and functional magnetic resonance imaging (fMRI) is consistent with the idea that explicit memory and implicit memory have different neural bases at retrieval. For example, ERPs have revealed different spatiotemporal components associated with implicit and explicit retrieval (Rugg et al., 1998; Paller et al., 2003; Henson et al., 2003; Meng and Guo, 2006; review also see Dew and Cabeza, 2011). fMRI studies have reported reduced neural responses for primed relative to novel stimuli, primarily in the occipitotemporal cortices during implicit retrieval, and enhanced neural responses in medial temporal lobe, prefrontal cortex and posterior medial parietal cortex for explicit retrieval (Henson, 2003; Schott et al., 2005). These results imply that implicit access to memory is supported by neural processing that is qualitatively distinct from that supporting conscious memory access. While many studies have observed dissociations between neural correlates of implicit and explicit memory at retrieval, very few studies have explored similar dissociations at encoding.

The ability to remember a past event is not only influenced by processes at retrieval, but also depends on processes engaged at the time of event encoding. A powerful method of examining the neural basis of successful encoding is to measure neural activity during the study phase of an experiment and then sort these measurements according to subsequent memory test performance. Sanquist et al. (1980) first observed that the ERPs elicited by study items that were subsequently remembered elicited larger positive amplitudes over midline parietal scalp sites than those that were subsequently forgotten. Paller et al. (1987) labeled this parietal-maximal neural signature as the "difference in subsequent memory effect" (DM effect). This DM effect has been replicated in many studies using intentional tests, and has been taken as an indicator of encoding process yielding later explicit memory (Friedman and Trott, 2000; Schott et al., 2002; Guo et al., 2005). Although its timing and topography vary depending upon the precise experimental conditions, typical DM effects tend to have either a frontal scalp distribution or a posterior scalp distribution, which has been attributed to neural processing in the prefrontal cortex (PFC) and medial temporal lobes (MTL) respectively (Donaldson and Rugg, 1999; Buckner et al., 2000; Duarte et al., 2004). Evidence from neuroimaging studies using fMRI and PET has consistently shown that PFC and MTL activation is associated with the encoding of new information into explicit memory (Simons and Spiers, 2003; for a review, Cabeza and Moscovitch, 2013). PFC is assumed to be involved in processing and organization of incoming information (elaborative processing), interacting with the MTL to effect memory storage (Moscovitch, 1992).

However, DM effects reflecting encoding process yielding later implicit memory have not been consistently observed by using implicit tests, and where such effects have been observed, they have tended to resemble explicit memory DM effects (Friedman et al., 1996; Paller et al., 1987; Paller, 1990, for a review, see Schott et al., 2002). One difficulty in interpreting the extant data is the methodological issue that neural substrates of implicit and explicit memory are predominantly identified using very different specialized memory tests. This is problematic, given strong evidence that explicit and implicit memory tests are not necessarily process-pure (Voss and Paller, 2008). In other words, on any given memory test given to a healthy individual, performance may be guided by both explicit memory processes and implicit memory processes. A new methodological approach that can concurrently capture the operation of distinct memory processes for specific episodes in a single memory test is thus essential.

Schott et al., (2002) first employed a novel paradigm to measure explicit memory and priming-without-explicit memory in one test, and contrasted the neural signals of these two processes at the encoding stage via a DM analysis. They used deep (semantic) versus shallow (non-semantic) encoding conditions, followed by a two-stage procedure in which three-letter word stems were presented in the first stage, and participants attempted to complete each stem with a word from the preceding study list. If they could not, they completed the stem with the first word that came to mind. After each stem was completed, subjects indicated whether or not they recognized the word from the encoding phase. Some of the test stems could be completed with study list words, and these stems were divided into three critical trial types: stems completed with studied words and indicated to be from the study list were termed "remembered" trials; stems completed with studied words but indicated not to be from the study list were termed "primed" trials; and stems completed with unstudied words and indicated not to be from the study list were termed "forgotten" trials, that is, the corresponding studied words had been forgotten, thus this trial type forming a suitable baseline. The three types of test trials were used to classify ERPs recorded during the study phase. The DM effect for explicit memory was evaluated by contrasting study ERPs corresponding to remembered and forgotten test trials. This DM effect was similar to that observed in previous studies in which ERPs corresponding to subsequently remembered trials elicited larger positive amplitudes than those corresponding to subsequently forgotten trials. The effect was observed over right frontal sites in the 900–1200 ms time window regardless of level of processing, and central scalp sites from 600 to 800 ms during shallow study processing only. On the other hand, the DM effect for priming-without-explicit memory was evaluated by contrasting study ERPs corresponding to primed and forgotten test items. This DM was distinct from the DM effect associated with explicit memory, that is, ERPs corresponding to subsequently primed trials elicited larger negative amplitudes than those corresponding to subsequently forgotten, and this DM was observed over centroparietal scalp locations from 200 to 450 ms. These results showed for the first time that implicit and explicit memory have distinct neural correlates at encoding.