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# Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

# Reconstructing the past: The late posterior negativity (LPN) in episodic memory studies

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# ARTICLE INFO

Article history: Received 23 March 2016 Received in revised form 17 June 2016 Accepted 17 June 2016 Available online 27 June 2016

Keywords: Late posterior negativity Event-related potentials Episodic memory Source memory Action monitoring: error-related negativity Recognition memory Memory retrieval

## ABSTRACT

The late posterior negativity (LPN) is an ERP effect frequently reported in episodic memory tasks. In 2003, we proposed that both non-mnemonic action monitoring processes and reconstructive mnemonic processes contribute to the LPN. Here, we review more recent studies and provide additional evidence that the LPN reflects dissociable (though not mutually exclusive) mnemonic and non-mnemonic processes. The idea that the LPN is related to the modality-specific reactivation of brain regions activated during encoding is critically evaluated. We suggest that the LPN is modulated by the amount of information actually used to reconstruct prior episodes and in parts mediated by source specifying factors, like the amount and overlap of memory bound attributes. We propose that the LPN reflects domain general mechanisms recruited not just during episodic but also during semantic memory tasks, in particular in situations that require highly specific reconstructive processing or continued evaluation of retrieval outcomes. Finally, we relate these ideas to recent accounts of the role of the parietal cortex in allocating attention for the inspection of memory contents.

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# 1. Introduction

An impressive though vulnerable function of our episodic memory is its capability to distinguish between different sources of

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http://dx.doi.org/10.1016/j.neubiorev.2016.06.024 0149-7634/© 2016 Elsevier Ltd. All rights reserved. information. Source memory is the general process of ascribing a remembered detail to a specific context and failures of source memories can have discomforting consequences or worse. Imagine that you are on your way to a well-deserved holiday and everything is prepared for leaving the house and heading to the airport. However, you suddenly realize that your car keys are not where you usually put them. You remember that you placed them in a safe and also particular place to ensure that you would find them later on, but







you cannot remember which place it was. Your burgeoning holiday feelings are gone from one moment to the next and you are getting worried about being too late for the flight departure. Luckily, digging through your luggage reveals that you put the keys in your notebook bag, which you had considered at that very moment as a perfect place for them. In order to find the keys without digging through your luggage it would be necessary that you could remember, upon the presence or self-generation of a retrieval cue (e.g. the notebook), the context when you had them the last time in your hands.

The voluntary retrieval of such context (or source) specifying information from episodic memory can be supported by a number of strategic processes that are engaged before, during, or after retrieval takes place (Burgess and Shallice, 1996; Simons and Spiers, 2003). Such strategic processes are initiated in pursuit of successful remembering and comprise the specification of retrieval cues (by biasing the retrieval towards particular memory contents), the allocation of attentional resources, and the monitoring, as well as the evaluation of retrieval outcomes for diagnostic characteristics.

Episodic memory processes, including the mentioned strategic control processes, have been extensively studied by event-related potentials (ERPs) (for reviews Rugg and Wilding, 2000; Mecklinger, 2010). ERPs represent averaged, time-locked responses of the electroencephalogram (EEG) to an event. ERPs have an excellent temporal resolution in the range of milliseconds. By this, they complement neuroimaging techniques that have a high spatial resolution for localizing functionally relevant brain areas, but a poor temporal resolution, such as functional magnetic resonance imaging (fMRI) and position emission tomography (PET). ERP studies on episodic memory have consistently reported systematic differences between correctly recognized old items and correctly rejected new items (old/new effects). An early old/new effect at frontal and central recording sites, the mid-frontal old/new effect or FN400 effect, has been identified as the ERP correlate of familiarity (Mecklinger, 2006; Rugg and Curran, 2007) or, as alternative interpretation, of conceptual priming (Paller et al., 2007). In tests that necessitate the retrieval of contextual (source) information, a later old/new effect is observed that onsets at about 400-500 ms after retrieval cue presentation and tends to be largest at parietal recording sites. As this effect is usually larger for old responses with correct retrieval of contextual information than for old responses with no or incorrect contextual retrieval, it is regarded as the ERP correlate of recollection (Wilding, 2000; for review see: Rugg and Curran, 2007).

ERP studies on source memory also report two old/new effects with a later onset than the parietal old/new effect, which are related to post-retrieval processing, i.e. an ensemble of processes that act upon the products of retrieval. The late right frontal old/new effect is assumed to reflect processes initiated by the successful retrieval of source information (Cruse and Wilding, 2009). There is a range of functional accounts for this old/new effect (see e.g. Friedman and Johnson, 2000 for a selective review; Cruse and Wilding, 2009; Hayama et al., 2008a,b). For the purpose of the current review, we will not further address this debate.

A second late ERP old/new effect usually observed in source memory tasks is the late posterior negativity (LPN). The LPN takes the form of more negative-going ERPs at posterior recording sites for old as compared to new items. The LPN already onsets before the rememberer indicates his source decision by button press, but reaches its maximum clearly thereafter. In 2003, two of the authors (MJ & AM) published a review article in which they provided evidence for the view that the LPN in episodic memory studies reflects two different classes of processes: (1) action monitoring due to high levels of response conflict, and (2) retrieval processes that act to reconstruct a prior study episode when task-relevant source features (attributes) are not readily recovered by the test probe or need continued evaluation (Johansson and Mecklinger, 2003). The main purpose of the current review is to critically evaluate the prevailing assumptions about the functional significance of the LPN, to discuss studies that examined the LPN since the time of the initial review, and to propose an updated and elaborated functional account of the LPN.

The current review is primarily based on studies published between 2004 and June 2016 that reported an LPN or LPN-like effect and referred to our previous review. In this time period 75 studies cited the Johansson and Mecklinger (2003) paper. Eight of these studies were not considered for this review because they were either reviews or theoretical articles (Kent and Lamberts, 2008; Levy, 2012; Zimmer and Ecker, 2010), empirical reports that did not employ the ERP methodology (Nieuwenhuis et al., 2008; Waldhauser et al., 2016), or ERP studies that did not report an LPNlike negativity for other reasons (Czernochowski et al., 2005; Hill and Windmann, 2014; Pergola et al., 2013). As a cross-check, we ran a literature search on Pubmed using the search terms "late posterior negativity" AND ("memory" OR "retrieval" OR "recognition"). This research revealed only a single LPN study that did not refer to Johansson and Mecklinger (2003). A comprehensive overview of the included studies, their methodology and main findings is given Table 1. In addition we selectively added other literature that used ERPs for studying memory functions.

The review is structured in eight sections: The first section summarizes the highlights of our previous review and research study (Johansson and Mecklinger, 2003); section two discusses the evidence for the modality-specificity view of the LPN; the third section reviews previous studies suggesting that non-mnemonic functions such as action monitoring and motor processes contribute to the genesis of the LPN; in the fourth section, we review the modulation of late negativities in aging studies of episodic memory; in section five, we evaluate whether an LPN can also be elicited in task situations without explicit memory requirements, the sixth section includes a proposal on the functional significance of the LPN, the seventh section reviews evidence for LPNs in semantic memory tasks, and in the eighth section we provide an updated functional account that seeks to integrate more recent findings into our mnemonic functional account of the LPN, as a component reflecting the continued reconstruction of study episodes and evaluation of retrieval outcomes.

# 2. Evaluation of the late posterior negativity

### 2.1. The Johansson and Mecklinger (2003) paper

Thirteen years ago, we encountered a considerable number of episodic memory studies that reported a prominent negative going old/new effect at posterior recording sites. This effect has its onset shortly before a response is given and remains visible in the ERP waveforms well after the response is made. At that time, the functional significance of the LPN was unclear because a broad range of rather heterogeneous experimental manipulations gave rise to this effect. The until then 21 studies that had reported an LPN could be broadly divided into two classes: (a) recognition memory tasks for single items that imposed high demands on action monitoring due to response conflicts, and (b) memory tasks that required the retrieval of contextual information specifying the encoding episode (e.g. source memory). Even though the LPN in both types of tasks appeared to be highly similar in its temporal and topographical characteristics, our combined stimulus and response locked analysis of two representative ERP studies revealed an important dissociation.

In an item recognition task with high action monitoring demands (Nessler and Mecklinger, 2003), the LPN in the Download English Version:

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