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

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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 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

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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 LPN-like 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

Table 1
Selective overview of the studies that report an LPN and were published since our initial report in 2003. LPON: Left parietal old/new effect.

Study	Task	Stimuli	Findings	Interpretation	Specials
Item and Source Memory tasks					
Addante et al. (2012a)	Item and Source Memory (study task) with confidence ratings	Words	LPN-like negativity for items recognized with low confidence with correct source judgments with widespread topography.	Contextual familiarity	Replication of prior findings with a modified design
Alhaj et al. (2006)	Source memory for speaker's voice	Visual words	LPN enhanced in group with DHEA (steroid hormone)	DHEA leads to a stronger ACC involvement in memory processing	
Bergström et al. (2013)	Source memory for study location and study task	Famous faces	LPN in both source conditions in EEG/MEG data; enhanced metabolic activity in the precuneus	Late retrieval search processes	Combined EEG/MEG and fMRI data; Source localization of the LPN
Chen et al. (2012)	False memory paradigm	Chinese words	LPN to lure false alarms	Retrieval monitoring failure	
Cruse and Wilding (2009)	Source memory for study color	Words	Right lateralized LPN to correct source judgments, not modulated by decision confidence		
Cycowicz and Friedman (2007)	Incidental and intentional item memory	Familiar and unfamiliar symbols	Largest LPN for familiar objects in incidental tasks	Not interpreted due to lacking exp. manipulation	
Dzulkifli and Wilding (2005)	Memory exclusion task	Words studied with one of two tasks	LPN for both tasks	Extended retrieval processing/response conflict	
Dzulkifli et al. (2006)	Memory exclusion task	As in D&W 2005	LPN for both tasks	Same as D&W 2005	
Ecker et al. (2007)	Source memory task for intrinsic and extrinsic object color	Line drawings of everyday objects	Topographically widespread late negativity for old (repeated) objects in extrinsic condition	Control or evaluation processes associated with feature integration	
Evans et al. (2010)	Memory Exclusion task with target (drawing task) and similar (size) and dissimilar (pleasantness) non-targets	Words	Both nontarget types	Item–context binding when few item/context is available	
Friedman et al. (2005)	Memory exclusion/inclusion task	Pictures	Larger in exclusion than Inclusion	Search and evaluation of general source specifying information	
Goffaux et al. (2008)	Task switching with semantic classification tasks	Concrete nouns	Larger posterior LPN-like negativity in single task trials for old adults with low than high WM capacity	Context monitoring and retrieval of task relevant attributes	
Groh-Bordin et al. (2006)	Item recognition memory	Objects and impossible objects repeated with same or different color	Largest LPN for objects in different color	High evaluation demands when retrieval cue is lacking	
Hayama et al. (2008a,b)	Source memory and semantic judgments	Pictures	LPN to old source judgments	Extended retrieval processing/enhanced response conflict	LPN and right frontal effect are dissociable
Herron and Wilding (2005)	Memory exclusion task with high and low retrieval difficulty	Low frequency words	LPN for all conditions except for targets in easy condition	Enhanced action monitoring due to the fact that different classes of old items required different responses	

Table 1 (*Continued*)

Study	Task	Stimuli	Findings	Interpretation	Specials
Hu et al. (2015)	Recognition memory (concealed-information test)	Crime relevant and crime irrelevant words	LPN to crime relevant targets in a group that suppressed guilt knowledge	Enhanced need to monitor (response) conflict between suppression and automatic retrieval	LPN is dissociable from ERP index of recollection
Johnson et al. (2008)	Item recognition memory with R/K judgments	Words studied in different contexts (sentence generation vs image generation)	Larger LPN for sentence context	Post retrieval maintenance/evaluation of contextual information	
Kayser et al. (2007)	Continuous recognition memory tasks	Spoken and written words	Late LPN-like negativity in both modalities	Final evaluation or response decision	Stimulus- and response-locked analyses
Kayser et al. (2009)	As in Kayser et al. (2007) with schizophrenic patients	Ditto	Late LPN-like posterior negativity reduced in visual modality for schizophrenic patients	Impaired performance monitoring	Stimulus- and response-locked analyses
Kayser et al. (2010)	Continuous recognition memory task with schizophrenic patients	Words and faces	Late, LPN-like post-response negativity	Functional significance not addressed	
Koenig and Mecklinger (2008)	Source recognition memory (time vs location)	Pictures	LPN more anterior for source time	Search for/retrieval of attribute conjunctions	Topographic variations of the LPN in the two testing conditions
Kuo and Van Petten (2006)	Source recognition memory	Object-color pairings	LPN larger for weakly encoded pairings	Delayed readiness potential due to 300 ms delay of old responses	Response hand specific analysis allows an estimation of Readiness Potential contribution to LPN
Leynes and Kakadia (2013)	Source memory task with discrimination between performed, watched and interrupted actions	Actions	Largest LPN to interrupted actions when discriminated from performed	Extended retrieval processing because only few diagnostic features	
Leynes and Nagovsky (2016)	Source memory guided by semantic knowledge (gender stereotypes)	Words spoken in male and female voice	LPN larger under self- focused encoding	Higher demands on the retrieval of memory features under self-focus	
Leynes and Phillips (2008)	Source judgments (male vs female voice) followed by R/K judgments.	Auditory words in male or female voice	Larger for R judgments	Systematic and deliberate decision processes	Huge (4–5 μV) effect. Sentence generation requirements at study lead to extended retrieval processing
Leynes (2012)	Memory exclusion task/reality monitoring	Seen vs imagined words Self-generated vs imagined words	LPN in all conditions but attenuated to self-generated words	Evaluation of retrieved information not crucial because of clear evidence of self-generation in memory trace	Word pairs but otherwise very similar to Leynes and Kakadia (2013)
Leynes et al. (2005)	Source memory for heard and generated words (reality monitoring) vs male and female voices (external source monitoring)	Auditorilly (study phase) and visually (test phase) presented words	LPN for female voices (external source monitoring). No LPN differences in reality monitoring	LPM is only generated when highly similar sources (male vs female voices) have to discriminated.	
Leynes et al. (2006)	Source recognition and recall	Performed and motioned actions	Motioned > performed > New	Detailed inspection of memory information	

Table 1 (*Continued*)

Study	Task	Stimuli	Findings	Interpretation	Specials
Leynes et al. (2013)	Source memory guided by semantic knowledge (gender stereotypes)	Words spoken in male and female voice	LPN only when source judgments were not guided by semantic knowledge	Semantic knowledge is assessed to inform episodic memory	Discrepancy with other source memory (speaker voice) tasks: Self focus decreased binding of perceptual features and enhanced monitoring demands.
Mecklinger et al. (2007)	Source Memory for study task or screen location	Pictures/Task vs Screen location as sources	Larger for Source Task than Source Screen Location)	Amount of contextual information potentially available	Spectral analysis of LPN. LPN reflects inter-trial phase locking of theta and delta activity
Nie et al. (2013)	Source recognition memory for color of words and backgrounds	Chinese words	LPN to old items in both color source tasks	Search for and retrieval of color sources	
Nowicka et al. (2009)	Directed forgetting paradigm	Polish words	Posterior negativity to forgotten to-be-forgotten words in the same time window as the LPON	Low response confidence	
Riby et al. (2008)	Memory exclusion task with high and low frequencies of task-unrelated thoughts at study	Words and line drawings	Large LPN (and small LPON) in retrieval situation with large unrelated intrusive thoughts at study	Additional strategic processes for task completion when recollection is impaired	LPN is modulated by mind wandering
Rosburg et al. (2011a)	Memory exclusion task/reality monitoring	New items for different target designations	LPN effect when ERPs to new items are contrasted.	Larger action monitoring demands for the more difficult retrieval condition.	Present in response-locked analysis only
Rosburg et al. (2011b)	Memory exclusion task/reality monitoring	Imagined and perceived items	Larger for imagined than perceived items, irrespective of target status	High need for continued evaluation for imagined item/more contextual details available	LPN to missed items
Rosburg et al. (2013)	Memory exclusion task/reality monitoring	Perceived and generated words	Same effect for perceived and generated words	Study led to the idea that contextual information actually used for reconstruction is critical for the LPN amplitude.	
Rosburg et al. (2015)	Source memory task/reality monitoring	Imagined and perceived items	No converging effects of previous testing on the LPN (900–1800 ms)	Larger amount of contextual details for previously tested items might have offset the effect of better accessibility of such memory traces.	LPN larger for imagined than perceived items
Ross et al. (2015)	Item and source recognition memory task	Words encoded in an imagery or in a pleasantness task	LPN in item and source memory tasks is not modulated by polymorphism of serotonin transporter gene	Extensive evaluation of memory-bound information as reflected in the LPN is not modulated by serotonin polymorphism.	LPN in combination with genetic data
Sprondel et al. (2012)	Memory exclusion task	Words studied in one of two colors (high vs low color similarity)	LPN not modulated by task difficulty	Different aspects of post retrieval processing	
Stenberg et al. (2009)	Item recognition	Rare and common names of famous and non-famous Swedes	Large LPN to famous names	Effortful reconstruction of study information to decide whether retrieved information derives from media or study phase.	

Table 1 (*Continued*)

Study	Task	Stimuli	Findings	Interpretation	Specials
Tsivilis et al. (2015)	Recognition memory study with objects encoded 5 min (recently) or 4 weeks ago (remote)	Pictures of animate and inanimate objects	LPN for recently encoded objects (and no LPON)	More effortful memory search due to reduced retrieval fluency for remote items/ High contextual familiarity in the absence of recollection	LPN is dissociable from ERP measure of recollection (LPON)
Wilding and Sharpe (2004)	Exclusion tasks with and without time constraints at response	Spoken (study) and visual (test) words	LPN only with time constraints	Higher rechecking demands with time constraints	
Wilding et al. (2005)	Memory exclusion task	Words in two different colors	LPN for targets and nontargets	Search for/retrieval of attribute conjunctions (not sensitive to context of conjunctions	Larger with nose tip reference
Wolk et al. (2007)	Recognition memory followed by R/K	Words	In response-locked analyses LPN: R > K > N	Confidence evaluation	LPN present in response-locked analysis
Studies explicitly addressing action monitoring/response conflict issues					
Curran and DeBuse (2007)	Item recognition memory with conservative and liberal payoff condition	Words	Large LPN (stim locked) and ERN (resp. locked) for conservative hit condition	Post-response ERPs reflect conflict sensitive post retrieval control mechanisms	Stimulus- and response-locked analyses
de Chastelaine et al. (2007)	Memory exclusion task	Line drawings of common objects	Parietal Negativity for nontargets in response- locked averages	Inhibition of prepotent target response to nontargets	Response-locked analysis
Geng et al. (2007)	False memory paradigm	Chinese words	Large LPN to false alarms to lures	Enhanced response conflict	
Herron (2007)	Source recognition memory with discrimination between study tasks	Words	Three dissociable LPNs Being sensitive to retrieval fluency, action monitoring and post-retrieval processing	LPN is heterogeneous and multiply determined	Topographic variations of the LPN/Stimulus- and response-locked analysis
Studies reporting late negativities in aging studies					
Duarte et al. (2006)	Item memory with R/K judgments	Photographs of meaningful objects	LPN-like late negativity to R—responses in low performing old adults	Functionally different from the LPN due to anterior scalp distribution	
Dulas and Duarte (2013)	Source memory for object color	Images of nameable objects	LPN-like topographically widespread negativity in old adults	Controlled search for source specifying perceptual features	
James et al. (2016)	Source memory	Objects studied in the presence of a color or a scene	Late negativity to context attended and unattended at study; larger in old adults	Episodic reconstruction	Early onset (~500 ms before old/new decision)
Kamp and Zimmer (2015)	Associative memory	Colored photographs of common objects	Sustained late negativity to old and recombined pairs for old adults	Functional significance unclear but different from the LPN	
Li et al. (2004)	Source memory for study task	Pictures of familiar objects	Late negativity to correct source judgments with brought and left lateralized topography in old adults	Higher reliance of old adults on more literal (sensory) information	
Newsome et al. (2012)	Source recognition memory task	Emotional pictures	LPN-like component for emotional pictures in both age groups	Extended retrieval processing for sources of arousing pictures	LPN-like ERP component. But topography differs from the LPN
Scheuplein et al. (2014)	Item memory task with response speed manipulation	Line drawings of objects	Posterior negativity in pre- and post-response time period for low performing old adults	Recruitment of alternative retrieval strategies to cope with high task demands.	

Table 1 (*Continued*)

Study	Task	Stimuli	Findings	Interpretation	Specials
Wiese et al. (2012)	Recognition memory	Faces of old and young adults	Late (left lateralized negativity) in old adults	Increased effort to retrieve study phase details	
Wolk et al. (2013)	Source memory for the font color of words	Words	Centrally distributed negativity in old adults but not In a-MCI patients	Recapitulation of study details at test	
Studies without explicit memory manipulation					
Brattico et al. (2010)	Musical judgment task/Correctness and liking judgments	Tonal chord sequences	Late negativity (preceding judgments) for incorrectness judgments	Response conflict or memory integration	
Frings and Groh-Bordin (2007)	Negative priming	Letters	LPN to repeated targets	Extended retrieval processes to recapitulate the characteristics of the previous target display	
Goffaux et al. (2008)	Task switching with semantic classification tasks	Concrete nouns	Larger posterior LPN-like negativity in single task trials for old adults with low than high WM capacity	Continuous context monitoring and retrieval of task relevant attributes in low performing old adults	
Groh-Bordin and Frings (2009)	Negative priming	Letters (probe display without distractors)	LPN to repeated targets	As in Frings and Groh-Bordin (2007)	
Liu et al. (2011a)	Plausibility judgments for audio-visual pairings	Natural scenes & semantically congruent/incongruent natural sounds	LPN-like negativity to incongruent pairings	Binding of auditory information with visual context information	
Liu et al. (2011b)	Audio-visual congruency judgments	Natural scenes & and semantically congruent/incongruent natural sound or speech	LPN-like negativity to incongruent speech but not incongruent sound pairings	Speech to sound conversion & integration with visual information.	
Liu et al. (2011c)	Congruency judgments for audio-visual pairings	Moving visual particles & frequency modulated tones	LPN-like negativity for incongruent pairings	Search and retrieval of context-specifying information (long-term learned associations)	
Schankin et al. (2011)	Artificial grammar learning	Letter strings	Negativity in trial after regularity violation detection	Re-evaluation of detected violation	
Xu and Plaks (2015)	Reading of stereotype-confirming and -violating sentences.	Sentences with "math geek"-consistent and inconsistent behavior	Larger late posterior negativity for inconsistency in participants who believe that human qualities are fixed (entity theorists)	As effect determinates after 600 ms: N400 response to stereotype violating behavior.	
Episodic recall memory task					
Bai et al. (2015)	Cued-recall task with testing and restudy condition	Swahili-German word pairs	LPN enhanced in testing conditions with history of unsuccessful retrieval attempts.	Highly specific search in episodic memory	LPN in cued recall task
Hellerstedt and Johansson (2016)	Semantic generation task	Words	LPN to unsuccessful and impossible semantic retrieval	Highly specific search in semantic memory	LPN present in cued recall task
Study reporting a late posterior negativity without citing the J & M (2003) study					
Massand and Bowler (2015)	Item memory and memory exclusion tests in adults with Autism Spectrum Disorder (ASD)	Line drawings	LPN to targets and nontargets in ASD and control group	Late posterior negativity associated with the recollection of contextual information. LPN temporally more extended in ASD group	LPN in adult patients with ASD

response-locked ERPs took the form of a posteriorly distributed negativity that peaked around 70 ms after the response. This negativity was most pronounced for false recognition of lure items that were semantically related to studied items. In its time course, it resembled the error-related negativity (ERN), an ERP component that has been associated with error detection and conflict monitoring in choice reaction time tasks (Falkenstein et al., 2000). In the stimulus-locked data, this phasic negativity was temporally jittered across trials and resulted in an extended negative slow wave in the ERP. In contrast, for the ERP data of a source memory task (Johansson et al., 2002), a clear LPN was observed in the stimulus-locked ERPs that was virtually absent in a response-locked analysis of the data. Thus, the response-locked analysis of these data did not reveal any hints that enhanced action monitoring contributed to the LPN. In fact, the LPN remained when controlling for response times. These observations gave rise to the view that at least two classes of processes contribute to the LPN: Mnemonic processes visible in stimulus-locked ERP waveforms and non-mnemonic action monitoring processes initiated by enhanced response conflict, visible in stimulus- and response-locked waveforms of episodic memory tasks.

At that time only a few studies had explored the mnemonic functional significance of the LPN. Therefore, we could only tentatively propose that it reflects processes that help to reconstruct the prior study episode when difficult source discriminations are required and retrieved contextual information needs continued evaluation. An important specification, however, results from the observation that the LPN can be elicited by correct and incorrect source (context) judgments, suggesting that it is not necessarily tied to successful source (context) retrieval. By this it differs from the parietal old/new effect that is related to successful contextual retrieval and covaries with the amount of retrieved information (Wilding, 2000; Vilberg et al., 2006).

2.2. Does the LPN reflect modality specific processes?

One proposal for the mnemonic function of the LPN was that it reflects modality specific processes (Friedman et al., 2005), a view that has been derived from the cortical reinstatement hypothesis of remembering (Tulving and Thomson, 1973). According to this hypothesis, retrieval of contextual information includes the reactivation of brain areas involved in the initial processing of the stimulus (Wheeler et al., 2000). The posterior distribution of the LPN and the visual nature of the typically used retrieval cues and their source features (i.e. color, location) are, at the first glance, consistent with the view that modality-specific (visual) areas are searched and reactivated to reinstate an item in its study context.

Friedman et al. (2005) explored the LPN (labeled 'late negative episodic memory effect' in their study) in an inclusion and exclusion memory task using colored pictures as stimulus materials. Counter to the modality-specificity view, the LPN in the exclusion task did not differ between conditions in which the colors were identical at study and test and conditions in which the colors varied between study and test. Moreover, parieto-occipital LPNs were observed even when non-pictorial stimuli (words) with non-visual source attributes (e.g. encoding task, gender of voice) were retained in memory (Wilding, 1999), providing further evidence against a modality-specific view of the LPN.

A previous study of our own reported topographical variations of the LPN as a function of the task-relevant source attributes (Mecklinger et al., 2007). In this source memory study, LPNs with a parietal maximum were elicited when participants had to indicate at which screen location a picture was presented. The LPN was more anteriorly distributed in a second retrieval condition in which they indicated how they interacted with the picture in the study phase (indoor/outdoor task vs approach/withdraw task) (Fig. 1). This difference suggests that the LPN topography is not solely determined by modality, but that the LPN topography is also modulated by task-related, domain-specific factors.

However, the aforementioned studies (Friedman et al., 2005; Mecklinger et al., 2007) did not entail a direct test of the modality-specificity view of the LPN, because the topographic information was not used for determining the underlying neural generators. By this, any conclusion regarding modality specificity on the basis of these studies had to remain tentative. However, more recently, the issue of the neural generators of the LPN was directly addressed in an excellent multimodal imaging study (Bergström et al., 2013).

Bergström and colleagues recorded EEG/MEG and fMRI from the same subjects in separate sessions and explored whether modality-specific information would be reactivated and re-instantiated during episodic recognition. Participants saw pictures of famous faces at different screen positions and were first required to perform one of two study tasks (judgment of the pleasantness or 'Britishness' of the depicted face). Thereafter, they had to indicate whether the picture was presented near or far from the middle of the screen. In the test phase, faces were presented as cues and the participants had to indicate either their location at study or the task performed at study. Across test conditions, a pronounced LPN was observed in the EEG/MEG recordings. For both test conditions, source localization of the EEG/MEG effects revealed a source in the medial posterior parietal cortex (PPC) between 600 to 1600 ms. The time course of its activation resembled the LPN in the EEG/MEG recordings. Further evidence for this localization was provided by a spatial overlap between the estimated source and the metabolic peak activity, as measured in the fMRI session. Of particular interest for the current review, there was no evidence for modality specific activations in the visual cortex at test: visual areas were not differentially activated when participants had to retrieve the study task as compared to the location of the studied faces. Domain specific activation were, however, found in the left dorsolateral PFC, where activations were larger in the task condition. The study of Bergström et al. (2013) represents the first study that sought to localize the neural generator of the LPN and is, up to now, unique in its kind. The observation that the retrieval of both visual (study location) and non-visual (study task) source attributes was associated with overlapping activity in the medial PPC (and not in visual cortices) represents strong evidence against the modality specificity view of the LPN.

From this it follows that the topographical differences in the LPN reported in the Mecklinger et al. (2007) study cannot be attributed to different visual cortex areas involved in the reconstruction of source attributes of a previous study episode. We rather assume that the observed more anterior LPN distribution in the task condition (Fig. 1) reflects the higher need for cognitive control processes in this conceptually-based retrieval condition (see Bergström et al., 2013; for a similar view).

2.3. What is the contribution of action monitoring and motor preparation to the LPN?

Another issue that was addressed in a couple of ERP studies concerned the contribution of response-related processes to the LPN. Our initial review revealed that the LPN was obtained in item recognition tasks that were characterized by high false alarm rates and prolonged response times. The form of a response-locked phasic negativity resembled the error-related negativity (ERN) (Johansson and Mecklinger, 2003), suggesting that the LPN reflects high response conflict associated with such error-prone recognition tasks. This evidence was provided by contrasting response-locked and stimulus-locked ERP data in a false memory study (Nessler and Mecklinger, 2003).

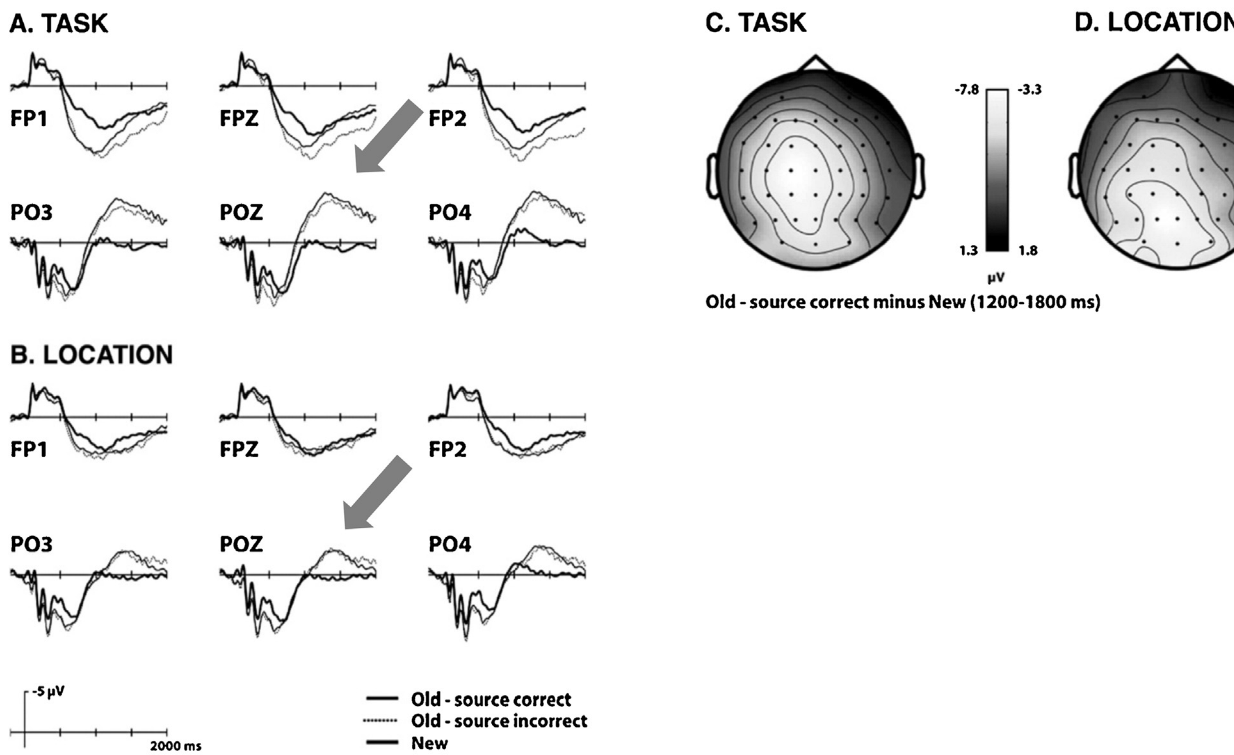

Fig. 1. ERP waveforms elicited by correct and incorrect source judgments and correct rejections at anterior and posterior recording sites in the two retrieval conditions in the Mecklinger et al. (2007) study (A and B). The LPN is depicted by the gray arrows. Topographic maps of the LPN in the old correct minus new difference wave in the 1200–1800 ms time interval in both conditions (C and D).

Employing a similar false memory paradigm, Geng et al. (2007) reported a late stimulus-locked LPN that was largest for false alarm responses, intermediate for true recognition and smallest for new responses. These results resemble the LPN findings in the Nessler and Mecklinger (2003) study. Unfortunately, no response-locked analysis was conducted by Geng and co-workers and, therefore, no further inferences on action monitoring can be derived from this study. Wolk et al. (2007) employed a two-step recognition procedure in which old/new decisions were followed by R/K judgments. The ERPs time-locked to the old/new decisions revealed an LPN that was largest for R responses, intermediate for K responses and smallest for correct rejections of new items. This LPN showed a clear parieto-occipital maximum and reached its largest amplitude at around 500 ms after the old/new decision, i.e. at the time the R/K prompt appeared. The authors interpreted it as a reflection of memory search attempts and the amount of perceptual features retrieved. Even though a response-locked analysis was conducted, the two step response procedure and the lack of response conflict manipulations do not allow inferences on action monitoring on the basis of this study.

A few studies explored the contribution of action monitoring to the LPN directly, by systematically manipulating response conflict or response selection demands and by comparing stimulus and response locked ERP data (Herron 2007; de Chastelaine et al., 2007; Curran and DeBuse, 2007). Herron (2007) sought to dissociate several LPN subcomponents within the same study by analyzing stimulus- and response-locked ERP data in four consecutive blocks of a source memory task in which the conducted encoding operations had to be retrieved. She reported that a response-locked negativity, present between 50 and 300 ms after the response was given, varied with response fluency. The LPN was largest at the beginning of the experiment, when task fluency was low, and in the third test block when response fluency was compromised due to the switching of response key assignments. These findings for the response-locked LPN support an action monitoring account of the LPN. Notably, in the Herron (2007) study, the response-locked LPN was dissociable from two other LPN subcomponents that were present between 600 and 1900 ms in the stimulus-locked analyses and presumably reflect mnemonic aspects of the task like the search for episodic features and the maintenance of retrieved information. By this, the report by Herron (2007) is one of the few studies describing functionally dissociable (mnemonic and non-mnemonic) LPNs within the same experiment. As such, this finding supports our original claim that the LPN reflects two functionally dissociable classes of processes that are not mutually exclusive.

Curran and DeBuse (2007) explored the effects of response conflict on recognition memory ERPs using a payoff manipulation by which either a conservative (respond "old" only when certain) or a liberal response (respond "new" only when certain) criterion was induced. In two studies with immediate and delayed response requirements, the LPN in the stimulus-locked ERPs was enhanced for old responses in blocks with a conservative response criterion (high payoff for new responses) relative to blocks with a liberal criterion. An additional response-locked analysis conducted for the immediate response condition revealed a selectively enhanced negativity in a 40–80 ms post response window (termed 'ERN-LPN' by Curran and colleagues) with a mid-central maximum for the conservative response criterion condition only. Interestingly, a much weaker LPN and no ERN-LPN were obtained for the liberal response condition, i.e. in blocks with a high payoff for old responses. On the one hand, the presence of a response-locked LPN can be taken as support for the action monitoring account of the LPN. Notably, however, this response-locked component was only observed for old responses for which the response conflict could be resolved by assessing memory-stored information, but not for new items in the liberal condition. Consequently, the Curran and DeBuse (2007) findings indicate that action monitoring processes modulate the LPN when memory-stored information is supportive for the decisions at hand and is inspected to resolve response conflict (as for the conservative old responses). By this the latter findings also support the mnemonic account of the LPN.

de Chastelaine et al. (2007) explored stimulus- and response-locked ERPs in a memory exclusion task in different age groups. In the test phase, objects studied in one color had to be classified as old (targets) and objects studied in another color (nontargets) had to be rejected together with new pictures. There were reliable parietal old/new effects in all age groups to correctly identified targets and nontargets, indicating that source information was retrieved for both kinds of old items. In young adults, the parietal old/new effect was followed by a posterior LPN that onset at around 600 ms post-stimulus. The response-locked ERP analysis revealed an additional posterior negativity preceding the response to nontargets. As response times were longer for nontargets than for targets and new items, the authors concluded that nontargets engendered high response conflict due to the requirement to reject a studied object as new. The authors presumed that the posterior negativity reflected top down control processes operating at the response level, such as response selection or inhibition, to overcome this response conflict. Even though, the functional characteristics ascribed to the posterior negativity bear similarities to the action monitoring account of the LPN, this component was present prior to the subjects' response. By this, the response-locked negativity reported by de Chastelaine and colleagues differs remarkably from the aforementioned response-locked negativities of Johansson and Mecklinger (2003), Herron (2007), and Curran and DeBuse (2007), which were all confined to the post response interval. See Rosburg et al. (2011a) for another report of an LPN, which is limited to a post response time period in a response-locked analysis.

A unique feature of the memory exclusion task is the requirement to reject previously study items (nontargets) as new. This enhances response conflict and ensuing response monitoring demands when responses to these nontargets are given. Thus, it is conceivable that the LPN in the response-locked analyses is generally larger for nontargets than for targets. Inspection of the few studies that explored the LPN to nontargets in response-locked analyses in Table 1 (Rosburg et al., 2011a; de Chastelaine et al., 2007), however, suggests that this is not a consistent pattern. Further studies with systematic comparisons of target and nontarget LPN will be required to shed more light on this issue.

Motor processes have also been discussed to contribute more directly to the LPN: In a source memory study, Kuo and Van Petten (2006) recorded ERPs while subjects retrieved object—color conjunctions. In an effort to explore how retrieval processing is modulated by encoding procedures, the authors used encoding tasks that focused either on object identity or on object-color relationship, leading to weakly or strongly encoded associations, respectively (see Leynes and Nagovsky, 2016 for a similar approach). A late negativity starting at around 1000 ms was larger after object identity encoding, i.e. when object and colors were only weakly bound in memory. This finding is consistent with the view that the LPN reflects additional retrieval processing to reconstruct the prior study episode when attribute conjunctions are not readily recovered. In this condition, reaction times were about 300 ms longer for correct old responses than for correct new responses, likely caused by the more difficult retrieval of source information. The authors argue that differential response preparation for old and new responses, rather than mnemonic processing, could have contributed to the late negativity in the stimulus-locked ERP. Their view is derived from an additional ERP analysis that controlled for response hand and revealed a late negativity to old items that was larger contralateral to the response hand over motor and premotor regions and, by this, resembled the Readiness Potential (Kornhuber and Deecke, 1965; Shibasaki and Hallett, 2006). The authors conclude that the LPN reflects a temporally extended Readiness Potential, rather than memory related mechanisms.

We agree that differential response preparation may have contributed to the late negativity at fronto-central and central recordings in the Kuo and van Petten study, but we do not think that motor response preparation can account for the whole variance of the late negative slow waves in episodic memory tasks. In fact, the late negativity in the Kuo and van Petten study was broadly distributed and also present at frontal and temporal recording sites overlying motor cortex regions, contrary to most other studies that reported a clear posterior maximum of the LPN.

Further evidence against the Readiness Potential view of the LPN comes from studies showing that LPNs are reliably present when the eliciting conditions are matched for response times so that differential response preparation can be excluded (Leynes and Bink, 2002; Johnson et al., 2008; see also Johansson and Mecklinger 2003 for a direct test of the impact of response latencies on the LPN). Moreover, as outlined above, LPN differences were also observed with procedures, in which subjects were required to delay their response to test cues until a response cue was presented (Curran and DeBuse, 2007). In such a design, the impact of motor preparation on the ERPs elicited by the test cues can be considered as negligible.

To summarize, it has to be acknowledged that only few studies explicitly addressed the action monitoring account of the LPN. One reason may be that action monitoring is a topic that is not frequently tackled in episodic memory studies, and ERP studies on item and source memory primarily use only stimulus-locked ERPs to unravel electrophysiological correlates of the underlying memory processes. However, inferences on the contribution of action monitoring to the stimulus-locked LPN can only be made when the stimulus-locked analyses are complemented by response-locked analyses that show either the absence or presence of ERN-like negativities. If the negativities in the response-locked analyses are larger for false alarms than for hits (as for example in Nessler and Mecklinger, 2003) this can be taken as additional evidence that these negativities reflect an ERN.

One has to presume a major influence of action monitoring on the stimulus-locked LPN when the amplitude of the negativity is greater for the response-locked than for the stimulus-locked ERP data. However, when interpreting such stimulus- and response-locked ERP data, one has to keep in mind that response-locked activity might not just modulate the stimulus-locked ERPs, but that response-locked data in memory experiments are also possibly influenced by the presence of (stimulus-locked) old/new effects. Two studies that reported stimulus-locked analyses complemented by response-locked analyses (Curran and DeBuse, 2007; Herron, 2007; see Table 1) show that memory tasks with experimental manipulations that tap into action monitoring processes give raise to reliable late negativities in the response-locked analysis. Taken together, the balance of mnemonic and non-mnemonic factors contributing to the LPN becomes visible when analyzing both stimulus-locked and response-locked ERPs. Previous analyses of response-locked ERP data have clearly shown that in conditions with high response conflict action monitoring contributes to the LPN but adds little variance to the stimulus-locked (memory-related) LPN when response conflicts are widely absent.

2.4. Late negativities in aging studies on episodic memory

ERP recognition memory studies conducted with older adults have revealed the presence of late negative components that tend to overlap with the parietal old/new effect that is of opposite polarity. As a consequence, the magnitude of the latter effect is reduced (Duarte et al., 2006; Scheuplein et al., 2014) and/or its topography differs remarkably from the effects in young adults (Li et al., 2004; Kamp and Zimmer, 2015; for a review see Friedman, 2013). In most cases, these late negativities were only found for older adults and were topographically more widespread and less posteriorly focused than the typical LPN observed in source memory tasks or in tasks with high action monitoring demands.

In an illustrative example, Wiese et al. (2012) explored the own-age bias in recognition memory for faces in young and older adults. While the young adults showed a typical parietal old/new effect for young but not for old faces (consistent with an own-age bias), old participants showed a reversed (old < new) old/new effect for old faces, but only when they reported high daily contact with other elderly. This negative old/new effect had its onset 500 ms before the subjects responded and the authors interpreted it as a reflection of the increased effort of old adults to retrieve details from the prior study phase. Notably, this effect showed a clear frontal and left lateralized scalp topography. Even though the functional description offered by Wiese and colleagues resembles our functional account of the LPN, we hesitate to consider the reported negativity in old adults as an LPN, as it lacks a posteriorly accentuated scalp distribution. Li et al. (2004) employed a source memory task to explore age differences in contextual retrieval. In young adults, a left parietal old/new effect was observed for correct source judgments, whereas this effect was absent in older adults due to a broadly distributed, left lateralized late negativity to old items. Following the modality-specificity view of the LPN, Li et al. (2004) argued that older adults relied to a greater extent on visual details when retrieving details from the prior study episode. Similar to the findings of Wiese et al. (2012), we are reluctant to interpret the observed late negativity for the old adults in the Li et al. (2004) study as an LPN, due to its lacking posterior scalp distribution.

In another recent aging ERP study, Dulas and Duarte (2013) explored how attentional processes at encoding affect source memory performance. The results show that an attentional focus on source features can attenuate the demands on post-retrieval monitoring (as reflected by a reduced late right frontal old/new effect) to a similar extent in young and old adults. However, old adults show an attenuated parietal old/new effect, as compared to young adults, and only old adults exhibited a widespread late negativity that was interpreted as a reflection of controlled search for perceptual source-specifying features to compensate for impoverished retrieval processing. Similar broadly distributed late negativities elicited by old items have also been described in the aging studies of Kamp and Zimmer (2015) and Wolk et al. (2013) for old adults and for young and old adults in the studies by James et al. (2016) and Newsome et al. (2012).

In summary, in all ERP memory studies that report late negative old/new effects in older adults, the negativities show heterogeneous scalp distributions that differ remarkably from the typically posteriorly distributed LPN. These negativities have been taken as accounts for the attenuated parietal old/new effect in some of the aforementioned studies (Li et al., 2004; Scheuplein et al., 2014). Even though these late negativities have been associated with attempts to reconstruct memory-stored information, processes usually ascribed to the LPN, the non-posterior scalp distributions suggest that it is unlikely the same ERP component as the LPN. The same objection holds for the late negativities reported for young adults in the studies by Addante et al. (2012a), Leynes and Zish (2012), Leynes et al. (2013) and, for amnesia patients, by Addante et al. (2012b). All of these studies report negativities that are larger for studied than unstudied information but due to a lacking posterior scalp distribution these components are unlikely the same ERP component as the LPN.

In addition, the fact that these negativities in the majority of the aging studies reviewed above were virtually absent in the tested young adults, even when attempts were made to match age groups for source memory performance (Dulas and Duarte, 2013), is difficult to reconcile with the idea that these negativities reflect processes set in train to reconstruct a prior study episode. However, even though it seems clear that the negativities in old age ERP data are not one-to-one related to the functions usually ascribed to the LPN, their functional significance needs yet to be determined in future studies in order to better understand how compensatory and reconstructive processes at retrieval interact in elderly people.

2.5. LPN-like modulations in tasks without explicit memory requirements

The majority of studies as described in this review so far report negativities in explicit memory tasks that require that memory contents are actively searched and retrieved upon presentation of a retrieval cue. Notably, however, LPN-like modulations have sometimes also been observed in tasks without explicit memory requirements. As the tasks that will be reviewed in this section differ remarkably from the episodic memory tasks discussed in the remainder of the paper the conclusions that can be drawn from these studies are necessarily limited.

Two recent studies explored ERP correlates of negative priming, i.e. impaired processing of a target event when it served as a to-be-ignored distractor event in a preceding trial. As expected, a negative priming effect was obtained when the probe trial (letter) was surrounded by distractor letters (Frings and Groh-Bordin, 2007), but not when the probe contained no distractor (Groh-Bordin and Frings, 2009). In both studies, trials in which the target stimulus was repeated from the previous trial were characterized by a larger P300 followed by a posteriorly distributed LPN-like deflection (see Stahl and Gibbons, 2007 for similar results). Groh-Bordin and Frings (2009) argue that the P300 reflects context updating and an allocation of attention to the unexpectedly repeated target (Geng and Vossel, 2013; Donchin 1981), which in turn initiates the retrieval of characteristics of the preceding stimulus display. Thus, one might speculate that, even without explicit retrieval instructions, features of the immediately preceding trials are recovered and used to reconstruct the previous context, which leads to the elicitation of an LPN.

Three studies exploring evaluative processing of music rules (Brattico et al., 2010), artificial grammars (Schankin et al., 2011), and multi-sensory events (Liu et al., 2011a,b,c) complement the list of studies that report late LPN-resembling negative potentials in designs without explicit memory requirements. Brattico et al. (2010) recorded ERP while participants made tonal correctness and liking judgments for tonal cord sequences (musical cadences). Pronounced differences between the ERPs in both judgment conditions were obtained at posterior recordings at about 200 ms after the end of the cord sequence and about 200 ms before the response. A pronounced negativity was obtained for sequences judged as incorrect (but not for those judged as disliked) that was interpreted to reflect either action monitoring or memory integration mechanisms. Schankin et al. (2011) observed a late negative ERP potential in trials that followed regularity violations of a previously learned artificial grammar. Visual inspection of their Fig. 3 suggests that this component is an LPN-like deflection that follows correct classifications of letters strings, possibly reflecting a re-evaluation of the preceding grammatical decision. Liu et al. (2011c) report a N400 followed by an LPN-like negativity for incongruent pairings between moving particles and tone frequencies (i.e. slow moving particles paired with high frequency tones), which, however, had a less posteriorly focused topography than the LPN typically observed in memory tasks. Similar LPN-like negativities were reported by Liu and colleagues for other visual-auditory incongruencis, as for example videos of visual scenes paired with incongruent natural sounds or speech. These negativities were, however, either rather short-lasting (Liu et al., 2011b) or had a quite early onset at around 250 ms (Liu et al., 2011a).

In summary, the evaluation of these studies is complicated by the fact that the task characteristics and stimulus materials were very heterogeneous across studies. However, a common feature of the tasks used in the aforementioned studies is the requirement to make decisions which are guided by previously acquired general knowledge, like the trial sequence in a letter classification task, music or grammar rules, or the congruency between perceived actions and sounds. In situations in which such knowledge is not readily recovered, decisions might be accompanied by a continued evaluation with the purpose of rechecking the appropriateness of the chosen response. In those situations, LPN-like negativities can be observed even though the presumed retrieval processing is not explicitly required by the task at hand.

2.6. The LPN is modulated by the specificity with which memory is searched

An interesting though not well understood feature of the LPN is its remarkable variability in magnitude. We assume that the LPN in part reflects the specificity with which memory is searched and memory contents are reconstructed and evaluated. To illustrate this point, in a study by Leynes and Phillips (2008) source judgments (male vs female voice at study) were immediately followed by R/K judgments. A prominent LPN was found for accurate source judgments. As estimated from their Fig. 1, this effect was more than 5 μV in magnitude. Also, it began earlier and was also larger for R than K responses. Similarly prominent LPNs were observed in a source memory study that contrasted source memory for performed and motioned actions (Leynes et al., 2006). In this study, the to-be-motioned actions, for which source accuracy was lower and reaction times were longer, elicited larger LPNs than performed actions. Groh-Bordin et al. (2006) explored recognition memory for objects and nonsense objects that were repeated in the same or different color at test. A pronounced LPN was observed for objects (∼4 μV as estimated from their Fig. 6) that was also larger for color incongruent than color congruent trials. For non-objects, the LPN was virtually absent. Bai et al. (2015) recently explored ERP correlates of the testing effect. Participants learnt Swahili-German word pairs and thereafter in several circles either practiced the retrieval of the German words in a cued recall test or simply restudied the word pair. Notably, an LPN was observed during retrieval practice relative to restudy. This effect was largest for cues for which participants could not recall correctly the associate, both during retrieval practice and at the later final test. As revealed by a re-analysis of the cued-recall data by one of the authors (A.M.) these failures were omission errors in the majority of trials. During retrieval practice, the history of previous unsuccessful retrieval attempts may have imposed high demands on the reconstruction of the prior learning episode. See also Hellerstedt and Johansson (2016) for another example of an LPN elicited by unsuccessful retrieval attempts in an episodic cued recall task.

A common characteristic of the latter studies is that they entail the retrieval and examination of highly specific details of a prior study episode. To illustrate this point, in the encoding phase of the Leynes and Phillips (2008) study, subjects were required to type a sentence that included the previously heard study word and to incorporate a fictitious male or female person in their sentence. This sentence production requirement was a unique feature of the Leynes and Phillips (2008) source memory task and may have led to enriched, multi-featured memory traces of these study episodes. Hence, the requirement to give an R or K response after the source judgment may – for R responses – have engaged the search for specific features of these prior episodes, including details of the sentence generation process. In our view, it is mainly this peculiarity, i.e. sentence generation at study followed by the R/K procedure at test, that accounts for the large LPN in this study.

In a similar vein, motioning an action (i.e. perform the motions that complete an action without touching the object) as done in the Leynes et al. (2006) study is much more unusual than performing an action and may leave more vivid and multi-faceted memory episodes which in turn allow to recapitulate highly specific details of each episode. Also, memory for real objects (as in Groh-Bordin et al., 2006) may entail much more specific details than memory for non-objects. The cued recall testing format in the Bai et al. (2015) study necessitates highly specific search in memory as the German word initially paired with the Swahili word has to be recovered among lexically similar competing words and these demands on the reconstruction of the associate may have been elevated when prior retrieval attempts were unsuccessful.

The aforementioned view that the LPN is modulated by the specificity with which memory bound information is searched for or retrieved has recently also been forwarded by Leynes and colleagues (Leynes and Kakadia, 2013). In one illustrative study, they compared the discrimination between performed and watched actions with the discrimination between performed and interrupted actions. While a pronounced LPN was observed in the latter case, it was remarkably attenuated in the former case. It was argued that for the discrimination between performed and interrupted actions the multiple characteristics of performed actions have to be retrieved and due to the high feature overlap between both conditions very specific and discriminating information from the study phase needs to be continuously evaluated. In other words, the high feature overlap between two sources reduces the differentiation of the two memory sources and leaves only very few diagnostic features for the source decision. This will foster a detailed and continued inspection of the memory traces as reflected by the LPN. Conversely, this specificity in the search for attribute conjunctions is not required for the discrimination between performed and watched actions, which have much less features in common and can be discriminated on a simple 1st vs. 3rd person perspective (Leynes and Kakadia, 2013).

On a more general level, Leynes and colleagues were the first who interpreted their LPN findings in the Source Monitoring Framework (SMF) (Johnson et al., 1993) according to which source memory decisions involve the activation of qualitative memory characteristics and their evaluation (Leynes and Phillips, 2008). According to the SMF, memories from different sources tend to be associated with different relative amounts or types of memory characteristics, and the distribution of these characteristics may be used to infer the source of a memory. Memory traces can be evaluated using systematic or heuristic decision processes. Heuristic decisions are fast, require few retrieval processing, can be based on one qualitative difference between the various sources (i.e. on a single diagnostic feature). Such decisions usually do not require extended retrieval processing. Conversely, systematic decisions are deliberate and are set in train when two sources share many characteristics. In this case a detailed inspection of memory traces is required, and this is suggested to be reflected in the LPN (Leynes and Kakadia, 2013). In this vein, a range of factors, such as memory strength or the features of the memory traces and their discriminability, determines the source attribution in memory tasks and post-retrieval processing, as reflected in the LPN.

2.7. The LPN in semantic memory tasks

In this review, we have so far mainly considered the functional significance of the LPN based on available ERP studies of episodic memory. It is interesting to note, however, that an LPN has recently also been observed in tasks that require a highly specific search in semantic memory. In one such study (Hellerstedt and Johansson,

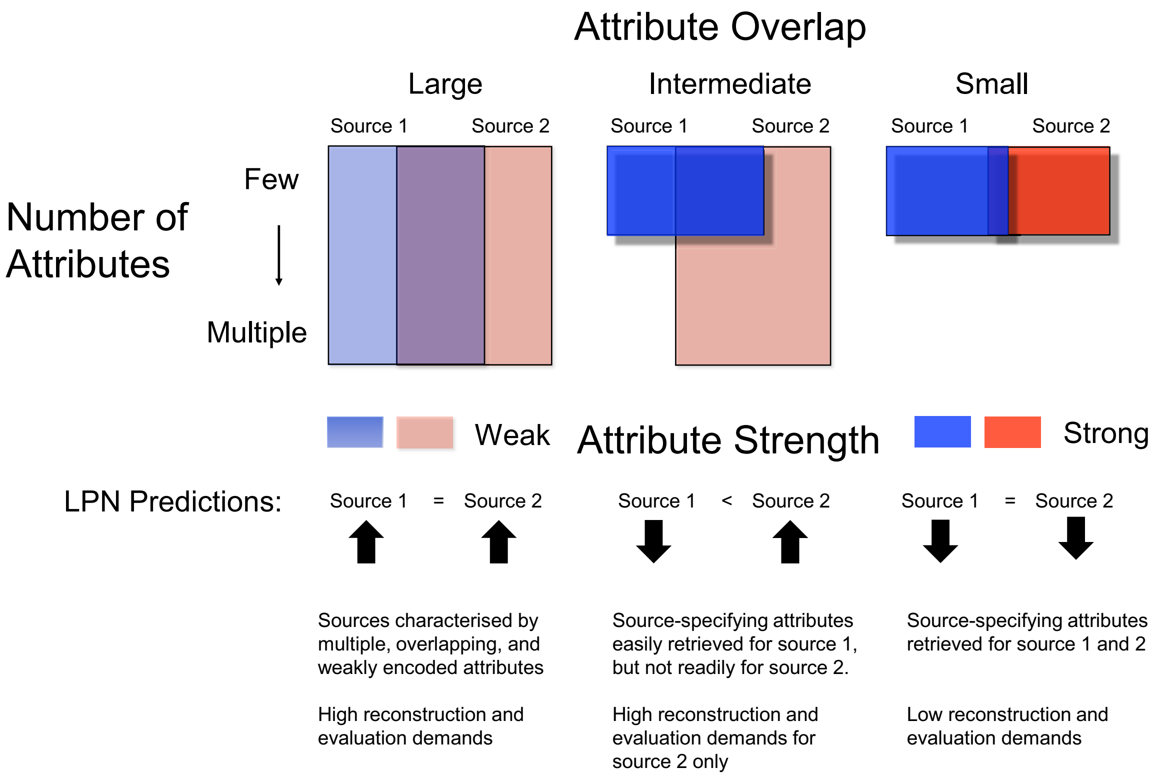

Fig. 2. Variations in the multitude, overlap and strength of memory bound attributes and their putative effects on LPN generation. In our view the LPN is modulated by the amount of information actually used to reconstruct prior episodes. This reconstructive and evaluative processing is mediated by the amount, similarity and strength of memory bound attributes. The lower part of the figure depicts three retrieval situations with either high or low reconstruction and evaluation demands (left and right side, respectively) or differential demands on the reconstruction and evaluation of retrieval outcomes. Large (small) LPNs are illustrated by upwards- (downwards-) oriented arrows.

2016; see also Hellerstedt and Johansson, 2014) a category label (e.g. FRUIT) followed by a two-letter word stem (e.g. Ma___) was presented and participants were instructed to complete the word stem in order to generate a category member (e.g. Mango). Compared with a non-memory, perceptual baseline condition in which the category members were presented intact, the semantic cued-recall condition gave rise to a prominent LPN that lasted until the end of the recording epoch, at which time the participants were asked for a verbal response (i.e. outcome of semantic memory retrieval versus reading). Analogously to the episodic memory tasks reviewed above, the LPN observed during semantic cued recall showed a posterior scalp distribution and a sustained temporal profile. Notably, the LPN was attenuated for successful as compared with unsuccessful semantic retrieval. Moreover, the memory task in Hellerstedt and Johansson (2016) included an impossible semantic retrieval condition, in which the participants were presented with a word stem that did not match any exemplar in the category (e.g. FRUIT-Tu___). The participants were unaware of this and tried hard throughout the available time period to generate a category member. For unsuccessful semantic retrieval trials of this kind a large sustained LPN was observed. These results are interesting not only because they reflect the outcome of a direct test of the functional characteristics of the LPN. They also suggest that the LPN reflects reconstructive mnemonic processes characterizing both episodic and semantic memory.

Interestingly, the effects in the latter condition resemble the findings in the episodic cued recall test in Bai et al. (2015) in which the largest LPNs were obtained when retrieval attempts were completely unsuccessful. The large LPNs in the impossible semantic and episodic retrieval conditions suggest that the LPN reflects processes associated with continued retrieval attempts, whereas during successful retrieval these attempts are stopped, once a legal semantic exemplar has been generated. More generally spoken the LPN may show no correlation with retrieval success when correct and incorrect source memory judgments undergo similar reconstruction or evaluation processes, whereas in other retrieval situations (such as cued recall tasks) the LPN should correlate with retrieval success and be attenuated for successful retrieval trials.

In fact, the cued recall task employed in the aforementioned semantic memory study and in the Bai et al. (2015) study might actually involve very similar mnemonic processes as the item and source recognition memory studies reviewed above. We have argued that the LPN reflects (a) processes that form, retain, and evaluate representations of recognized items bound to contextual attributes in order to solve source memory tasks, and (b) action monitoring that detects conflict and errors. It is conceivable that overlapping mechanisms are involved in cued recall tasks in which participants are instructed to generate words from semantic or episodic memory and to evaluate the extent to which the generated representations fit with the presented retrieval cue. The large LPN observed during unsuccessful retrieval trials (impossible condition and retrieval failure trials) in the Hellerstedt and Johansson (2016) and the Bai et al. (2015) studies may reflect the continuous generation of candidates accompanied by the ensuing detection of conflict between the erroneously constructed exemplars and the cue. While further research is needed to disentangle the relative contribution of the proposed generation and evaluation processes and their putative neuronal substrates, it is interesting to note that data from these recent cued recall studies are consistent with our functional account of the LPN (see Section 2.8), and that it may reflect domain general mechanisms recruited during both episodic and semantic memory retrieval.

2.8. The functional significance of the LPN reconsidered

In our view, the LPN is modulated by the amount of contextual attributes actually used to reconstruct a prior study episode (Rosburg et al., 2013). This amount is in parts determined by characteristics of the to-be-reconstructed study episodes, in particular the overlap/similarity of their attributes, the number and detailedness of attributes, and the strength of the memory traces. These three dimensions and their putative influence on LPN generation are illustrated in Fig. 2.

If the discriminability between sources is weak because memory traces are fragile, the attributes of two study episodes are highly overlapping, and both sources are characterized by enriched multi-featured representations, the need for a continuous evaluation of memory bound information is high and this is reflected in a large LPN (see Fig. 2, left column). The quality and amount of attributes bound in memory also constitute boundary conditions for the amount of contextual information actually used for a memory decision. On the other hand, if source information is readily retrievable and contains only few attributes, as for example when pictures shown in the upper or lower part of the screen (Mecklinger et al., 2007) or words studied in one of two colors have to be discriminated (Sprondel et al., 2012), the amount of retrievable and source specifying information is necessarily limited and only small LPNs are presumably elicited (Fig. 2, right column). Also, perceptually rich items may lead to easy-to-access and highly distinguishable memory traces so that memories of this kind can be discriminated from each other on the basis of only few contextual features. Thus, small LPNs should be elicited in conditions in which memorized items can be attributed to the study context on the basis of such distinctive source information, as it was the case for example in the location condition in Mecklinger et al. (2007) (see also Fig. 1).

Conversely, if study episodes contain multiple memory bound attributes (like the generation of a sentence with its grammatical and semantic features or performing a complex decision with an item) the number of attributes that can actually be used to reconstruct a study episode is high but the strength of the trace may be low due to the multitude of attributes. This situation is illustrated by source 2 in the middle column of Fig. 2. The LPN to source 2 should be large when this study context has to be discriminated from another study episode characterized by fewer and readily retrievable source attributes. Consistent with this account, the LPN was larger for words for which mental images had to be created, as compared to words for which pictures were shown in the study phase (Rosburg et al., 2011b). In the former case, the memory traces entail a multitude of attributes including not only visual information about the generated images but also information about the cognitive operations leading to image generation (Johnson et al., 1993). Conversely, memories for seen pictures (as used in this study) entailed fewer but more readily retrievable attributes (visual details of these pictures), so that the amount of contextual information available and required for the reconstruction process of perceived pictures was necessarily lower as compared to the image generation condition in which also the cognitive operations during image construction could be retrieved. Hence, memory performance was higher and the LPN smaller in the picture condition.

The amount of information actually used to reconstruct a prior study episode is not only mediated by the amount of attributes available but also by decision confidence. Addante et al. (2012a) examined ERP correlates of source memory for items that were recognized with high or low confidence. A parietal old/new effect (the ERP correlate of recollection) was obtained for correct source judgments, but only for items recognized with high confidence. Correct source judgments for items that were less confidently recognized elicited a late but broadly distributed negativity, resembling the LPN. It could be argued that the low confident item memory in this study constitutes a paradigmatic case for a high need for continued evaluation of source-specifying memory information and LPN generation. However, it could also be argued that the low confidence for the item judgments is a direct consequence of the failure to retrieve source specifying information. Irrespective of this interpretational ambiguity, the rather broad scalp distribution and the early onset of the negativity do, however, not necessarily support an LPN interpretation of this effect (see also Section 2.4 for similar lines of reasoning).

Our aforementioned view can account for a variety of apparently heterogeneous variations of the LPN across source memory studies. For example, the finding that missed targets can elicit an LPN (Rosburg et al., 2011b) or the fact that the LPN does not covary with task difficulty (e.g. Sprondel et al., 2012; Rosburg et al., 2015) can be reconciled with our functional account of the LPN, given that the information used to reconstruct a prior study episode can be mediated by a variety of factors beyond task difficulty or decision confidence. An apparent inconsistency in the pattern of ERP results that examined the discrimination between two internal sources using words (i.e. imagined vs. generated words) and actions (performed and interrupted actions) can also be reconciled with our account. In the study that used word pairs (Leynes, 2012), imagined, but not generated words elicited an LPN, whereas in the study using performed and interrupted actions (Leynes and Kakadia, 2013) prominent LPNs were obtained for both kinds of actions, with larger LPNs for interrupted than performed actions. Memories for interrupted and performed actions contain many overlapping attributes and interrupted actions are easily confused with performed actions (Leynes and Kakadia, 2013; Fig. 2C). Consequently, rather comprehensive reconstruction of the complex study episode is the most appropriate way to handle this ambiguity, in particular when retrieving interrupted actions. In contrast, generated words in the Leynes (2012) study contained rather distinct source information; the generated words had to be typed on a keyboard whereas in the imagine condition subjects were required to imagine saying the word. Therefore, discriminability between the sources was high (as reflected in the high rate of correct source judgments particularly for generated words) and the multitude of attributes for words imagined as spoken aloud may have driven the large LPN in the imagined words condition.

Our functional account of the LPN places a strong emphasis on the reconstruction and evaluation of information from the prior study phase. Notably, however, there are also situations in which associations between items and sources or other associations from the study phase can be retrieved on the basis of familiarity without effortful reconstructive processing, as for example when unitization strategies were used at encoding (Bader et al., 2010; Parks and Yonelinas, 2015). In these situations in which familiarity is diagnostic for the source decision we do not expect to observe an LPN. Also, our account emphasizes the retrieval of task-relevant context information, i.e. features of the study episode that are diagnostic for the source discrimination, and less so recollection of episodic information that is irrelevant for such discrimination, a form of remembering that has been referred to as noncriterial recollection (Yonelinas and Jacoby, 1996).

The weight on reconstructive and evaluative processes of task-relevant and diagnostic information allows us to explain and predict under what circumstances the LPN should be present together with or in the absence of the left parietal old/new effect (LPON).

The presence or absence of a LPON alone is no sufficient predictor whether an LPN is observed. As the putative ERP correlate of recollection, the LPON should covary with memory retrieval and track the accuracy of source memory. Conversely, the LPN is modulated by the amount of information actually used to reconstruct prior episodes. By this it is not necessarily tied to successful memory retrieval but is also observed during misses or otherwise erroneous memory decisions. This constitutes a first functional distinction between the LPN and the LPON.

At times the rememberer will be able to recollect some attributes from the previous encounter with the recognized item (e.g. color), but fail to retrieve other currently task-relevant attributes (e.g. location). Such a situation would give rise to high reconstruction and evaluation demands, and we would expect to observe an LPN following the LPON. During other retrieval attempts, source-specifying attributes relevant for the discrimination required by the memory test may not be readily retrieved, and in these situations we would expect large LPNs following small or absent LPONs.

Several recent studies showing a dissociation between the LPN and the ERP correlate of recollection support the latter view. For example, Riby et al. (2008) explored ERP old/new effects in participants who experienced either high or low intrusive thoughts during encoding. Participants with infrequent intrusive thoughts displayed a large LPON and a negligible LPN (labeled central negativity effect in their study), whereas the reverse pattern (large LPN and negligible LPON) was obtained for participants reporting frequent intrusive thoughts. Tsivilis et al. (2015) compared recognition memory for objects encoded four weeks or five minutes before testing. For objects encoded four weeks ago there was no LPON and by this no evidence for recollection. However, these remotely encoded objects elicited a pronounced LPN. This suggests that the remote presentation in the latter study as well as the presence of task-unrelated thoughts at encoding in the former study have reduced retrievability of contextual information of the prior study phase and enhanced the demands on reconstructive processes. See also the recognition memory study for concealed knowledge (Hu et al., 2015) and the source monitoring study by Leynes (2012) for others dissociations between the LPN and ERP measures of recollection.

As outlined above, our account of the LPN highlights the retrieval of task-relevant information that is diagnostic for the discrimination at test. An important issue to be clarified in future studies is the extent to which also noncriterial recollection, i.e. remembering aspects of the study event not required for the discrimination at test modulates the LPN.

Capitalizing on the well-established view of the role of the medial temporal lobe in episodic memory, we consider the LPON to reflect hippocampus-mediated pattern completion resulting in the reinstatement of the recognized item bound to its study attributes (Yassa and Stark, 2011). Such recollection is driven in a bottom-up fashion by the retrieval cue, whereas the reconstruction and evaluation processes needed when task-relevant attributes are not readily reinstated or interfere with task-irrelevant attributes are top-down controlled. We consider the latter processes, reconstruction and evaluation, to be reflected in the LPN.

Notably, the current framework for the LPN (as well as the one outlined in 2003) bears similarities with models that ascribe the posterior parietal cortex an important role in the recruitment of attentional networks during remembering (Cabeza et al., 2008; Hutchinson et al., 2009; Mecklinger 2010; Wagner et al., 2005). This is consistent with the view that the posterior parietal cortex not only represents sensory information but also its modulation by attention (Silver et al., 2005). In our 2003 paper we proposed that "the LPN reflects processes that form and retain an integrated representation of the recognized item bound to any retrieved attributes and internally generated contextual attributes (accurate or not) that are relevant for the task at hand" (page 110).

At that time, we could only make indirect inferences (on the basis of scalp topography) on the neuronal generators of the LPN and the putative attentional processes it reflects. One recent account posits that ventral and dorsal regions of the posterior parietal cortex can be recruited for the bottom up and top-down control of memory retrieval in a similar way as these regions are used in the allocation of attention to external events (Cabeza et al., 2008). Notably, the top-down-attention-to-memory-retrieval view is much the same function we have ascribed to the LPN in our 2003 paper and the large LPN elicited by previously studied (old) items may reflect the top-down allocation of attention for the inspection of memory traces. Some of these attention-to-memory models have been criticized for being too coarse grained (Hutchinson et al., 2014), and a simple functional account of the ventral posterior parietal cortex as a brain region mediating the bottom-up attention to episodic memory has been disproved by a variety of studies (Hutchinson et al., 2014; O'Connor et al., 2010; Uncapher et al., 2010; see also Levy 2012 for a recent review of mnemonic functions of the posterior parietal lobes).

However, some observations support the view that attention-related posterior parietal regions that are engaged in the control of memory retrieval also may contribute to the LPN. The strongest support for this view is provided by a recent analysis of attention and memory retrieval functions of the posterior parietal cortex (Hutchinson et al., 2014). Using attention mapping and episodic retrieval paradigms in an fMRI study, the authors found four functionally dissociable regions that demonstrated relationships with retrieval subprocesses. One region in the superior parietal lobule (SPL) that has been identified as component of the top-down attention network as described by Corbetta and Shulman (2002) was positively correlated with reaction times and was taken to reflect the top-down allocation of attention to memory signals to support memory-based decisions. Notably this SPL region is almost identical with the posterior parietal region in the precuneus in the Bergström et al. (2013) study, which on the basis of overlap in the MEG and fMRI modality has been identified as the putative neural generator of the LPN. Of note, an fMRI study which contrasted item memory with source memory for imagined and perceived pictures, using a paradigm similar to the one used in the Johansson et al. (2002) study, revealed enhanced activation for source memory relative to item memory and larger activation when imagined as compared with perceived items were retrieved in a highly similar posterior parietal (posterior precuneus, BA7) region (Lundstrom et al., 2003).

Even though the exact functional properties of the SPL during episodic retrieval remain to be specified, the overlap between the domain general recollection region in Bergström et al. (2013) and the attention- and memory-related regions in the Hutchinson et al. (2014) and the Lundstrom et al. (2003) studies is striking and suggests that the LPN may at least in part be generated by brain regions that subserve top-down visual-spatial attention. The temporal characteristic of the LPN further reveals that it reflects functions engaged at a late stage during remembering, i.e. when memory features are not readily recovered and need continued evaluation.

3. Summary and open issues

Since our initial report of the LPN, 75 studies have cited our paper and directly or indirectly tackled the issue of which processes are reflected in the LPN. A few of these studies conducted a combined analysis of stimulus and response-locked ERPs and provided evidence that the LPN reflects, aside from mnemonic functions, action monitoring due to response conflict, highly reminiscent of the error-related negativity (ERN) found in choice reaction time tasks (Falkenstein et al., 2000; Coles et al., 2001).

The current review provides additional evidence for our original claim that the LPN reflects two functionally dissociable classes of processes. Studies that used combined stimulus- and response-locked analyses report functionally dissociable mnemonic and non-mnemonic LPNs in the same experimental set up and also revealed that action monitoring contributes to the response-locked LPN in situations with high response conflict, whereas it leaves the stimulus-locked LPN largely unaffected. In a similar vein, the pronounced LPNs during unsuccessful retrieval attempts in cued recall tasks may reflect the interplay between continued memory search for the cued word and the detection of conflict between the cue and the erroneously retrieved word, suggesting that mnemonic and non-mnemonic (conflict detection) contributions to the LPN are not mutually exclusive.

The majority of LPN studies addressed its functional role during episodic memory retrieval. As outlined in the present review, most of these latter studies are consistent with the view that the LPN reflects processes that are engaged at a late stage of memory retrieval, when memory attributes cannot easily be recovered and require additional evaluation. The posterior distribution of the LPN and the visual nature of most source features (i.e. color, location) and retrieval cues at the first glance are consistent with the view that the LPN reflects the modality-specific (visual) search of reactivated memory contents. This view, however, was not confirmed by the studies reviewed here. Particularly noteworthy, the only combined hemodynamic and electrophysiological imaging study conducted to determine the neuronal generators of the LPN found no evidence for modality specific activations of the LPN, i.e. visual areas were not differentially activated when either the location of study items or the task performed at study had to be retrieved (Bergström et al., 2013).

We propose that the LPN is multiply determined and reflects the amount of information actually used to reconstruct a prior study episode, which is mediated by several factors such as the number of memory bound attributes, the overlap between source specifying attributes of to-be-differentiated sources, and the specificity with which memory is searched by the rememberer. The study by Bergström and colleagues has provided evidence that medial posterior parietal regions (in the vicinity of the precuneus) are involved in LPN generation, and two other brain imaging studies (Hutchinson et al., 2014; Lundstrom et al., 2003) have shown that these posterior partial regions are involved in the reconstruction of memory-stored information.

Of note, ERP studies with brain lesioned patients can also help in localizing the neural generators of the LPN. One still unique example is the study by Addante et al. (2012b), who reported the presence of an LPN-like negativity in three amnestic patients with extended hippocampal lesions. The finding tentatively suggests that LPN generation might not depend on the integrity of hippocampal structures. However, this due to the sample size yet preliminary finding needs to be substantiated by a study with a larger patient population.

Notably, our recent studies using cue-recall paradigms have revealed noteworthy similarities between the LPN in episodic and semantic memory tasks and have provided preliminary evidence that the LPN can be decomposed in generation and evaluation processes. Cued recall studies with episodic information employing a similar logic of contrasting impossible and possible retrieval as in the Hellerstedt and Johansson (2016) study are required to directly test this view.

Further open issues concern the role of top-down attention for the processes reflected in the LPN and their timing characteristics as well as the relationship between the LPN and other late onsetting ERP components in memory tasks, as in particular the right frontal old/new effect. Much needs to be done to better understand the multiple determinants of the LPN, the complex cognitive processes it reflects, and its neural underpinnings. We hope that this review stimulates new research that provides new insights in the cognitive processes associated with the LPN.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neubiorev.2016.06.024.

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