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The late posterior negativity in ERP studies of episodic memory: action monitoring and retrieval of attribute conjunctions

Mikael Johansson*, Axel Mecklinger

Department of Psychology, Experimental Neuropsychology Unit, Saarland University,
66123 Saarbrücken, Germany

Abstract

The focus of the present paper is a late posterior negative slow wave (LPN) that has frequently been reported in event-related potential (ERP) studies of memory. An overview of these studies suggests that two broad classes of experimental conditions tend to elicit this component: (a) item recognition tasks associated with enhanced action monitoring demands arising from response conflict and (b) memory tasks that require the binding of items with contextual information specifying the study episode. A combined stimulus- and response-locked analysis of data from two studies mapping onto these classes allowed a temporal and functional decomposition of the LPN. While only the LPN observed in the item recognition task could be attributed to the involvement of a posteriorly distributed response-locked error-related negativity (or error negativity; ERN/Ne) occurring immediately after the response, the source-memory task was associated with a stimulus-locked negative slow wave occurring prior and during response execution that was evident when data were matched for response latencies. We argue that the presence of the former reflects action monitoring due to high levels of response conflict, whereas the latter reflects retrieval processes that may act to reconstruct the prior study episode when task-relevant attribute conjunctions are not readily recovered or need continued evaluation.

Keywords: Event-related potential; Item recognition; Source memory; Late posterior negativity; Action monitoring; Error-related negativity

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1. Introduction

In order to succeed in challenging situations, our on-going behavior needs to be monitored as to evaluate whether we act appropriately for the task at hand and, if required, to be

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* Corresponding author. Tel.: +49-681-302-64365; fax: +49-681-302-6516.
E-mail address: m.johansson@mx.uni-saarland.de (M. Johansson).

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modified as to reduce processing conflicts and minimize performance errors. An extensive amount of research has identified an electrophysiological correlate of such action monitoring processing, which has been termed the error negativity (Ne, e.g. Falkenstein et al., 1990) or error-related negativity (ERN, e.g. Gehring et al., 1993). Typically, erroneous responses are characterized by a negative peak about 50–100 ms following response execution at fronto-central scalp locations (see Holroyd and Coles, 2002, for a recent review). While this line of research has generally examined performance in choice reaction-time tasks in which errors most likely result from fast guessing or impulsive responding (Coles et al., 2001) less is known about the involvement of action monitoring processes during memory retrieval. In the present paper, we will argue that a similar ERN/Ne component is sensitive to such processes taking place in recognition memory tasks as well, in particular, when memory retrieval is accompanied by high levels of response conflict.

The focus of the present paper is a late posteriorly distributed negative-going slow wave (LPN) that has consistently been observed in a number of recent event-related potential (ERP) studies of episodic memory. The LPN is an ERP component that onsets before or at around the time the subjects respond to a retrieval cue in the test phase. In most cases it has an extension of several hundred milliseconds and a bilateral posterior parietal distribution centered at the Pz recording site. Even though it is observed in a substantial number of episodic memory tasks, the LPN is lacking a satisfactory functional explanation. Given the characteristics of the memory tasks used in those studies, there are reasons to examine the view that the LPN at least to some extent reflects action monitoring processing taking place in demanding memory tasks.

To broadly outline the paper, we will begin by reviewing the studies that have reported the LPN in an attempt to extend our understanding about the experimental conditions eliciting this component. Based on predictions suggested by this overview, we will next present re-analyzed data from two studies (Johansson et al., 2002; Nessler and Mecklinger, 2003) that draw on a combination of stimulus- and response-locked ERP analyses. These re-analyses demonstrate that the LPN may be decomposed into at least two functionally distinct components. We will discuss the potential neural generators of these components and their functional role during memory retrieval. It will be argued that one is associated with action monitoring in tasks characterized by high levels of response conflict and the other with processes related to the retrieval of attribute conjunctions.

1.1. ERP memory effects and the late posterior negative slow wave

Recognition memory studies employing ERPs have demonstrated that correctly remembered old items elicit more positive-going ERPs than those elicited by correctly rejected new items (see Friedman and Johnson, 2000; Johnson, 1995; Rugg, 1995; Rugg and Allan, 2000, for reviews). This so called old/new effect onsets approximately 300 ms post-stimulus and may last for several hundred milliseconds. Based on different spatio-temporal distributions, the effect has recently been dissected into a number of subcomponents to which different aspects of memory retrieval have been linked (Allan et al., 1998; Friedman and Johnson, 2000; Mecklinger, 2000). Briefly, interpreted in terms of dual-process models of recognition memory (e.g. Mandler, 1980; Yonelinas, 1999), an early mid-frontal effect (300–500 ms) has been related to familiarity, whereas a somewhat later effect (400–800 ms) maximal over left parietal regions is considered to index recollection. This view is supported by results showing that only the left parietal effect is sensitive to manipulations that promote recollection (Paller and Kutas, 1992; Rugg et al., 1998a; Ullsperger et al., 2000), to measures of the subjective experience of remembering (Düzel et al., 1997; Rugg et al., 1998b; Smith, 1993; Trott et al., 1999), and to whether recognized items are assigned to their correct study source or not (Wilding, 2000; Wilding et al., 1995; Wilding and Rugg, 1996).

Several memory studies in which subjects were required to retrieve episodic information about the study context of recognized items have revealed an additional old/new effect. This effect typically shows a right frontal distribution and a sustained time course, starting around 600 ms and often lasting until the end of the recording epoch. However, as the effect has been found to be greater for correct than for incorrect source judgments (e.g. Wilding and Rugg, 1996), comparable for correct and incorrect source judgments (Senkfor and Van Petten, 1998; Van Petten et al., 2000), and (modestly) greater for incorrect as compared with correct source judgments (Trott et al., 1999), different proposals about the functional significance have been made: post-retrieval processes operating on the products of retrieval (Allan et al., 1998; Mecklinger, 1998), monitoring and verification processes (Rugg et al., 2000), strategic search for source-specifying information (Senkfor and Van Petten, 1998; Trott et al., 1999) or an ensemble of control processes that enable task appropriate behavior (Friedman and Johnson, 2000). Since the effect covers such an extended period of time, it remains unclear whether it reflects a single continued type of processing or, rather, comprises several subcomponents (see Friedman and Johnson, 2000, for a discussion).

We now shift our focus to the fact that the early frontal and later parietal old/new effects frequently are followed by a posteriorly distributed effect that is reversed in polarity. That is, old items tend to elicit a greater LPN relative to correct rejections of new items. This negative-going old/new effect typically onsets before or at around the time a response is given, shows a sustained time course and, similar to the right frontal effect mentioned above, remains readily visible in the waveforms after the memory judgments have been made. Before describing previous interpretations of this effect, we will take a closer look at the experimental conditions that tend to elicit the LPN.

Table 1 provides an overview of the studies in which late negative-going old/new effects have been reported. We include summaries about task and stimulus characteristics, ERP and behavioral findings, and, when applicable, a brief description of the proposed interpretation.

A clear majority of the studies included in Table 1 employed memory tasks that required subjects to retrieve not only item information that is sufficient for accurate recognition, but also contextual information about the study episode that is necessary for accurate source memory (e.g. color, voice, encoding task, etc.). The relation between the LPN and source memory is further strengthened by the results of two studies that directly contrasted item and source memory tasks (Cycowicz et al., 2001; Johansson et al., 2002). Both of these studies indicated that the LPN elicited by recognized items was much larger when source information had to be retrieved relative to when item information alone was sufficient for accurate performance (see also Ranganath and Paller, 2000; Senkfor and Van Petten, 1998). However, as is evident in Table 1, marked LPNs have also been observed in mere item recognition tasks.

The reported studies may broadly be divided in two main classes of tasks based on the following characteristics: (a) memory tasks that are associated with high demands on action

Table 1
Overview of the studies reporting the late posteriorly distributed negative-going slow wave

Study	Task	Stimuli	Finding	Interpretation	False alarm rate	Response times	Frontal positive slow wave	Specials
[1] Curran (1999)	Item recognition & lexical decision	Words and pseudo words	Old items in item rec. & lex. dec. (1000 ms)	Response preparation	I: Low	n.a.	Yes (right)	Polarity reversal between superior parietal and inferior parietal recording sites
[2] Curran (2000)	Exclusion task	Words: singular/plural ambiguity	FA to sim. words (700 ms)	n.a.	I: High High (sim.)	n.a.	Yes (right)	
[3] Cycowicz et al. (2001)	Exclusion task	Object drawings: color 1 vs. color 2	Cor. and incor. source jud. (900 ms)	Sensory-based source search and/or retrieval	I: Low S: High	Equal	No	Nose reference
[4] Donaldson and Rugg (1998)	Item + associative recognition	Word pairs: same vs. rearranged	Rearranged word pairs (900 ms)	n.a.	I: High A: High	Inconclusive	Yes	Right lateralisation
[5] Donaldson and Rugg (1999)	Item + associative recognition & recall	Words: pairs and single words	Recalled word pairs (800 ms)	n.a.	I: Low A: Low	n.a.	Yes	Right lateralisation
[6] Dywan et al. (2002)	Exclusion task	Words: repeated words (fam.)	Old and familiar words (800 ms)	Dissipation of a previously coordinated neural response	I: Low S: High (fam.)	Equal	No	

[7] Gonsalves and Paller (2000b)	Exclusion task	Words: word + picture vs. word only	Word only condition (900 ms)	n.a.	I: Low S: High	Slower	n.a.	
[8] Johansson et al. (2002)	Source memory	Words: perceived vs. imagined pictures	Cor. source jud. (1000 ms)	Response competition	I: Low S: Low	Slower	Yes	
[9] Kazmerski and Friedman (1997)	Cross-form item recognition	Words & line drawings	Cross-form and within-form retrieval (not for word-picture) (1000 ms)	n.a.	I: High	Faster	No	As [3]
[10] Leynes and Bink (2002)	Source memory	Action phrases: performed vs. planned actions	Cor. source jud. (1200 ms)	Response confidence	I: Low S: Low	Equal	Yes (right)	Additional left frontal negative slow wave
[11] Nessler and Mecklinger (2003)	Item recognition	Words: semantically similar	Cor. old resp. and FA to sim. words (800 ms)	Action monitoring	I: Low High (sim.)	Slower	Yes (right)	
[12] Nessler et al. (2001)	Item recognition	Words: semantically similar	FA to sim. words. (800 ms)	Response conflict	I: Low High (sim.)	Slower	Yes (right)	
[13] Rugg et al. (1998)	Item + source memory	Words: male vs. female voice	Cor. source jud. (800 ms)	As in [20]	I: Low S: High	Equal	Yes (right)	
[14] Rugg et al. (1996)	Item recognition + associative recall	Words	Recalled and unrecalled words (800 ms)	As in [20]	I: Low	n.a.	No	Right lateralisation
[15] Senkfor and Van Petten (1998)	Source memory	Words: male vs. female voice	Cor. and incor. source jud. (1000 ms)	n.a.	I: Low S: High	Slower	Yes	

Table 1 (*Continued*)

Study	Task	Stimuli	Finding	Interpretation	False alarm rate	Response times	Frontal positive slow wave	Specials
[16] Trott et al. (1999)	Item + source memory & R/K	Words: list 1 vs. list 2	Cor. and incor. source jud. and for R/K jud. (1000 ms)	n.a.	I: Low S: High	Equal	Yes (right)	As [3]
[17] Wegesin et al. (2002)	Item + source memory	Words: list 1 vs. list 2	Cor. source jud. (800 ms)	As in [3]	I: Low S: Low	Equal	Yes (right)	As [3]
[18] Wilding and Rugg (1996)	Item + source memory	Words: male vs. female voice	FA and incor. source jud. (800 ms)	n.a.	I: High S: High	Equal	Yes (right) for incor. source jud.	
[19] Wilding and Rugg (1997a)	Item + source memory	Words: spoken vs. heard	Cor. source jud. (800 ms)	n.a.	I: Low S: High	Equal	Yes (right)	
[20] Wilding and Rugg (1997b)	Exclusion task	Words: male vs. female voice	FA and cor. resp. to old items (800 ms)	Response-related processes	I: High S: High	Slower	Yes (right) for cor. resp.	
[21] Wilding (1999)	Item + source memory	Words: male vs. female voice	Cor. and incor. source jud. (800 ms)	As in [20]	I: Low S: High	Slower	Yes (right) for cor. resp.	

Stimuli. The stimulus material presented in the test phase. *Finding.* The conditions and item types that elicited greater late posterior negative slow waves (LPN) than correct rejections; the approximate onset of the negative-going old/new effect is given in the parentheses; cor. = correct; CR = correct rejection; jud. = judgment; FA = false alarm; fam. = familiar; incor. = incorrect; K = know; R = remember; sim = similar. *False-alarm rate.* Values higher or lower than 10% are considered as high and low, respectively. A = level of erroneous associative judgments; I = item recognition false alarm rate (to new items); S = source misattribution rate (correctly recognized items assigned to the wrong source). *Interpretation.* n.a. = not available. *Response times.* Slower = slower response times in the conditions that elicited the LPN; Faster = faster response times in the conditions that elicited the LPN. Equal = no differences in response times in the conditions that elicited the LPN and those that did not. *Frontal positive slow wave.* Yes/No refers to whether or not the LPN was accompanied by a positive slow wave at frontal recording sites.

monitoring due to the presence of response conflict, and (b) memory tasks that either require the binding of items with sources or with other contextual information specifying the study context (e.g. an object drawing and the color in which it was studied). Even though it is impossible to make a clear-cut classification of studies according to this distinction (e.g. the presence of high levels of response conflict in a source memory task), it should be noted that both aspects potentially make separate contributions to the observed LPN.

1.2. Item memory tasks

A defining aspect of the item recognition studies reported in Table 1 is that the memory tasks were associated with high action monitoring demands. This view receives support by the observation that the experimental conditions in which the LPN was observed yielded high levels of false alarms (FA) (i.e. larger than 0.10) and prolonged response times (RT) (see Curran, 1999, for an exception). In fact, most of those studies aimed at investigating ERP correlates of false memories and were for this purpose designed to give rise to high FA rates to non-studied items that shared a resemblance to the studied material. For example, Nessler et al. (2001), and Nessler and Mecklinger (2003), demonstrated robust false recognition effects to new items that were semantically associated to the old items. In a similar vein, Curran (2000) used singular/plural-ambiguous test words to provoke false memory responses. As can be seen in Table 1, these studies reported large LPNs that were especially pronounced for FAs to the similar items that were also associated with prolonged RTs relative to correctly rejected new items. In order to refrain from falsely responding ‘old’ to the non-studied (but similar) items, subjects had to carefully monitor their responses. The elevated FA rates and the longer RTs suggest that high levels of response conflict accompanied the mnemonic processing of these items. Interestingly, the magnitude of the LPN elicited by falsely recognized similar items has been found to correlate with subjects’ susceptibility to making errors of this kind (Nessler et al., 2001). That is, subjects showing a low level of false recognition elicited a greater LPN than subjects with a high level of false recognition.

To summarize, while the LPN is seldomly observed in mere item recognition studies, it is clearly evident in such tasks when the experimental settings give rise to high levels of FAs with prolonged RTs, suggesting a relation between the LPN and action monitoring processes associated with response conflict.

1.3. Source memory tasks

As noted above, the second group of studies in which the LPN has typically been reported employed memory tasks with an explicit requirement to retrieve the source or other contextual information about the study episode. Different experimental procedures have been employed to probe subjects’ memory for various details about the study event. In some of the studies included in Table 1, subjects have been instructed to discriminate between new items and more than one class of old items (Johansson et al., 2002; Leynes and Bink, 2002; Senkfor and Van Petten, 1998; Wilding, 1999). Other tasks required subjects to make an initial old–new discrimination and a subsequent source/context judgment for each item given an ‘old’ response (Donaldson and Rugg, 1998, 1999; Rugg et al., 1998a; Trott et al., 1999; Wegesin et al., 2002; Wilding and Rugg, 1996, 1997a). Another type of studies have employed exclusion tasks (cf. Jacoby, 1991) in which subjects have been instructed to press one key for old target items (i.e. source 1) and a second key for both old non-targets (i.e. source 2) and new items (Curran, 2000; Cycowicz et al., 2001; Dywan et al., 2002; Wilding and Rugg, 1997b). In yet another set of studies, subjects encoded word pairs and were in the following test asked to recall the study associate when probed by a recognized word (Donaldson and Rugg, 1999; Rugg et al., 1996). Moreover, a few studies included in Table 1 have used the 'remember/know' procedure (Tulving, 1985) to tap the subjective experience of remembering (Trott et al., 1999). In general, all of these procedures aimed at delineating the ERP correlates of recognition memory with and without recollection and it is important for present purposes that LPNs have been elicited in both of these conditions (see Table 1).

Given the finding that the LPNs observed in item recognition tasks primarily are elicited under conditions promoting extensive action monitoring, as revealed by high FA rates and long RTs, we should consider the relevance of such processes in the reported source memory investigations as well. As can be seen in the table, even though the FA rates to new items may be low, subjects frequently misattributed recognized items to the wrong study source/context (e.g. Cycowicz et al., 2001; Dywan et al., 2002). It is thus conceivable that the additional requirement to retrieve contextual information and to map the outcomes of such processing to an overt response enhances the action monitoring demands. However, speaking against this as a conclusive explanation for the LPN is the fact that similar LPNs have been observed in three-way source memory tasks as in tasks in which the source judgment is postponed until after an initial old–new judgment. Furthermore, prominent LPNs have been reported in source memory studies in which subjects' performance was near perfect. For example, the FA rates and the source misattribution rates observed in the studies by Johansson et al. (2002), Leynes and Bink (2002), and Wegesin et al. (2002) were at very low levels (≤ 0.05) and it is, therefore, not readily apparent why these tasks would induce action monitoring processes to a particularly great extent.

1.4. Additional characteristics

The studies included in Table 1 have frequently reported late frontal slow waves giving rise to the late frontal old/new effect. We are here mainly concerned with whether the conditions eliciting LPNs have been associated with similar frontal positivities as well. As can be seen in the table, this is the case for the majority of the included studies. However, a clear understanding of the relationship between the frontal effect and the LPN is somewhat complicated by the fact that they exhibit reversed polarities and have similar timing characteristics. Thus, the reported modulation of one of the effects may, due to component overlap, affect the presence of the other.

We also note that the use of a nose reference (Cycowicz et al., 2001; Kazmerski and Friedman, 1997; Trott et al., 1999; Wegesin et al., 2002) tends to increase the amplitude of the LPN as compared to the more frequently reported use of a linked-mastoid reference. It can be assumed that a mastoid reference, located close to the recording sites over the posterior parietal cortex at which maximal LPNs are observed, more likely picks up the same electric field activity as the active electrodes than a more distant (e.g. nose) reference (Nunez, 1981). This pattern suggests that the LPN is mediated by local generators in the posterior parietal cortex. In further support of this hypothesis, a study using an average reference to minimize the effects of reference site activity reported a polarity reversal of the LPN between superior parietal and inferior parietal recording sites (Curran, 1999).

Despite the variation in memory task procedures and stimulus material that is represented in Table 1, the observed LPNs have exhibited similar scalp distributions across experiments. Therefore, the present data do not allow a separation between the two classes of memory tasks suggested above on the basis of topography. However, it should be noted that it is possible that subtle topographical differences do exist, but that they are obfuscated by an overlapping involvement of a common set of processes, having a more prominent impact on the waveform. We will discuss this issue further in Section 3.

1.5. Previously proposed functional interpretations of the LPN

Despite the fact that the LPN has been reported in at least as many studies as included in Table 1, relatively few attempts have been made to directly elucidate its functional role. One of the first extended discussions of the LPN was given by Wilding and Rugg (1997b). Subjects in their study encoded words presented in either a male or a female voice and were subsequently given an exclusion task in which voice retrieval was crucial. LPNs were observed for correct responses to old items and for FAs. Wilding and Rugg performed a correlation analysis to examine the relationship between RT and the amplitude of the negative-going slow wave. Using mean across-subject RTs and amplitudes associated with five conditions (correct rejections, target hits, non-target hits, target misses, and false alarms), the analysis revealed a significant negative correlation. That is, greater LPNs were related to longer reaction times across conditions. Based on this finding and on the fact the negativity did not separate between correct and incorrect memory judgments, Wilding and Rugg concluded that the LPN appears to reflect response-related rather than mnemonic processes. However, as is evident in Table 1, the relation between the magnitude of the LPN and RT is not conclusive. In fact, a number of studies have reported similar RTs in the conditions that give rise to the late negativity and those that do not (Cycowicz et al., 2001; Dywan et al., 2002; Leynes and Bink, 2002; Rugg et al., 1998b; Trott et al., 1999; Wegesin et al., 2002; Wilding and Rugg, 1996, 1997a).

Another finding that challenges the view of a close relationship between the LPN and RTs is the fact that the late negativity has been found in tasks in which no key-press responses were required. For example, Donaldson and Rugg (1999) observed a pronounced LPN even though subjects were instructed to (verbally) recall the study associate not earlier than 3 s after the onset of the test word. While there clearly appears to be a relation between RTs and the negative wave, the overall pattern of findings does not speak in favor of this as an exhaustive account.

A different account was offered by Cycowicz et al. (2001) who proposed that the LPN reflects processes related to sensory-specific source search and/or retrieval. During study, subjects were presented with line drawings displayed in either red or green color and were in the following test phase given an inclusion and an exclusion task, the latter making the retrieval of color information necessary for accurate performance. As noted above, LPNs elicited by old items were substantially greater in the exclusion as compared with the inclusion task. This negative-going old/new effect was, moreover, found to be of comparable magnitude for items associated with correct and incorrect source assignments. Based on the visual nature (i.e. color) of the relevant contextual information and the fact that the LPN was maximal at occipital recording sites, Cycowicz et al. argued that the LPN reflects activation of sensory-specific areas supporting a reinstatement of the drawing in the color in which it was previously studied.

While the aforementioned accounts represent the most elaborated explanations of the LPN, it should be noted that other suggestions (more or less similar to the ones above) also have been made. Dywan et al. (2002) proposed that the LPN reflects the 'dissipation of a previously coordinated neural response'. Ranganath and Paller (2000) suggested that it reflects processes related to response confidence or to continued evaluation of contextual information. A few other studies have related the LPN to processes associated with enhanced action monitoring demands (Johansson et al., 2002; Nessler and Mecklinger, 2003; Nessler et al., 2001).

Based on the notion that the studies included in Table 1 may, from a functional point of view, be broadly divided in two types: (a) item memory tasks with high action monitoring demands and (b) source memory tasks, we next attempt to further elucidate the functional characteristics of the LPN by a more detailed consideration of two studies that map onto this division.

2. Contrasting stimulus- and response-locked ERPs

In this section we will present data from two studies in which prominent LPNs were observed. The two studies differ, however, in two essential aspects. First, the employed memory tasks were associated with different levels of action monitoring demands. Second, they varied in their explicit requirements to retrieve contextual information pertaining to the study episode. Our approach is to conduct a combined analysis of stimulus- and response-locked ERPs in order to disentangle the subcomponents contributing to the LPN. By this, the presented data show an overall pattern of effects that speaks against a unitary account of the LPN.

2.1. Item retrieval with high action monitoring demands

Nessler and Mecklinger (2003) investigated the electrophysiological correlates of true and false recognition. During study, subjects ($N = 15$) listened to lists of words (e.g. blackbird, starling, parrot, titmouse) that were exemplars of semantic categories (e.g. bird). In the subsequent test phase, subjects were visually presented with previously studied words, non-studied within-category words—so called lures (e.g. finch), and new unrelated words, and were instructed to make old–new discriminations.

In accord with previous false-memory research using similar experimental paradigms (e.g. Roediger and McDermott, 1995), subjects tended to falsely recognize the lures more often than they made false alarms to new unrelated words (see Table 2). Although true memory performance was at a high level, the presence of the lures enhanced response conflicts and, by this, strengthened the need for action monitoring processes. As is evident when examining the ERPs in Fig. 1A, the early positive-going old/new effects for true and false recognition were both followed by posteriorly distributed negative-going old/new

Table 2
Memory performance and response-time (RT) measures

Study and condition	*P*	Index	RT
Nessler and Mecklinger (2003)			
Old	0.87	0.85	743
Lure	0.18	0.16	959
New	0.98		749
Johansson et al. (2002)			
Perceived	0.95	0.93	1458
Imagined	0.95	0.92	1500
Old	0.95	0.93	1479
New	0.98		1221

P-values represent accurate performance for all conditions except for Lure for which the probability of responding 'old' is displayed. Index represents a discrimination measure calculated as *p*(hits)–*p*(false alarms). RTs are given in ms.

effects, especially marked for erroneous responses to the lures. The difference in magnitude was mirrored by RTs, that is, RTs were significantly longer for false as compared to true recognition. In order to examine the extent to which the LPN is related to action monitoring processes during memory retrieval, Nessler and Mecklinger subsequently performed a response-locked analysis that revealed two important results. First, true and false recognition elicited a larger negative component relative to correct rejections at midline anterior recordings sites. This response-locked negative component peaked at around 70 ms following response execution and resembles the ERN/Ne observed in choice reaction-time tasks. Second, the ERN/Ne at midline posterior recordings was slightly delayed as compared to the anterior portion and significantly larger for false recognition than for true recognition. Furthermore, topographical analyses conducted on rescaled data (McCarthy and Wood, 1985) indicated that different neural generators contribute to the ERNs associated with true and false recognition.

Since erroneous responses in choice reaction-time tasks usually elicit the anteriorly (i.e. fronto-centrally) distributed ERN/Ne, but do not lead to ERP modulations at posterior recording sites, Nessler and Mecklinger tentatively proposed that the anterior portion of the ERN/Ne is related to error detection and that the posterior part reflects action monitoring triggered by high levels of response conflict.

Presumably, response conflict arose as subjects were required to respond 'new' to words that were semantically related to the studied words and therefore might have been experienced as familiar (Mecklinger, 2000). Additionally, lures might have been associated with a higher level of response uncertainty if these items were falsely recognized with lower confidence than actually studied words were correctly recognized.

For present purposes, however, the main finding is that the LPNs characterizing true and false recognition in the stimulus-locked averages functionally and temporally closely match the pattern of effects observed in the posterior portion of the ERN/Ne component. This result suggests that posterior response-related ERN/Nes, sensitive to action monitoring processes, shaped the LPN and, further, that the cross-trial variability in RTs gave rise to the sustained time course evident in the stimulus-locked ERPs.

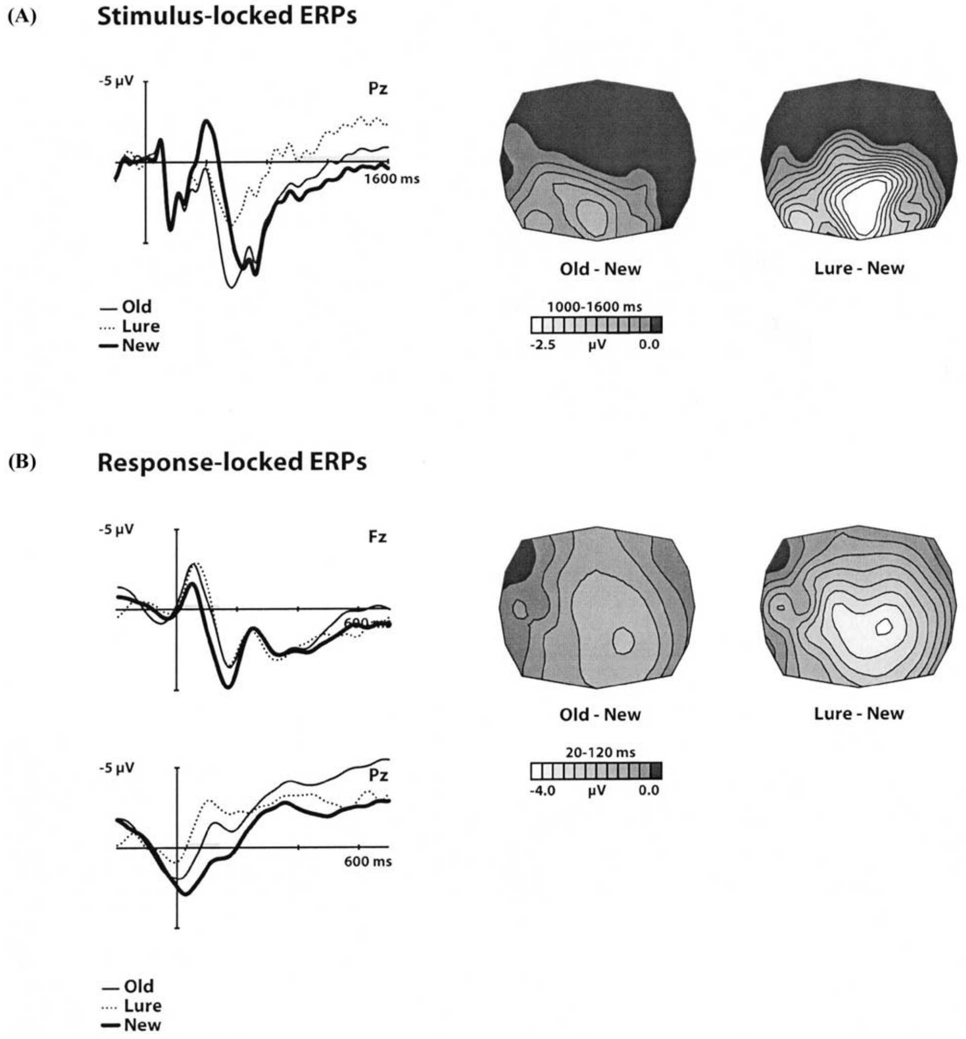

Fig. 1. Stimulus-locked (A) and response-locked (B) grand averages representing correct performance to old and new items and falsely recognized lures at Pz and Fz (response locked). Topographic maps of (A) the negative-going old/new effects and (B) the ERN/Ne component associated with true and false recognition. The gray horizontal bars depict the time intervals of the discussed effects.

2.2. *Source retrieval with low action monitoring demands*

The focus of the study reported by Johansson et al. (2002) was to examine item and source memory for previously perceived and imagined pictures (cf. reality monitoring, Johnson and Raye, 1981). During study, participants ($N = 32$) were presented with word labels denoting common objects (e.g. bike). One half of these words were followed by a line drawing that illustrated the given object, and the other half was followed by an empty frame that cued subjects to mentally visualize an image that represented the object. Following the study session, subjects were assigned to either an item- or a source-memory task. While subjects in the item memory task were instructed to make mere old–new judgments to new and previously studied words, subjects in the source memory task were told to discriminate between words that corresponded to previously perceived pictures, imagined pictures, and non-studied word labels. Because one of the aims was to compare the ERP correlates of successful source memory for perceived and imagined items, the experimental parameters were set as to maximize the chances of judgments based on recollection for both sources. We will restrict our presentation below to data from the source memory task.[1]

As can be seen in Table 2, subjects' overall recognition performance was very high as was their source accuracy (90%)[2] and they generally reported having 'reexperienced' the studied pictures or imagined images at the time of retrieval. Turning to the ERP data depicted in Fig. 2A, both types of accurately remembered old items elicited pronounced LPNs relative to correct rejections from approximately 1000 ms post-stimulus onset until the end of the epoch. In agreement with previous findings, these negative-going old/new effects were coupled with prolonged RTs relative to correct rejections of new items. Furthermore, the effects were characterized by a posterior distribution and were maximal at left parietal sites (P3) at which the effect was found to be slightly greater in magnitude for perceived as compared to imagined items.

Given the high performance level and the fact that subjects virtually made no false alarms (2%; source errors: 5%), suggesting a generally low level of response conflict, we decided to reanalyze the data in a response-related fashion in order to examine whether a posterior response-locked negativity accounts for the LPN in the present source memory task as well. Despite the good performance, it should be noted that it still might be the case that old items, for which subjects had to indicate the correct source, were associated with relatively greater response conflict than correct rejections. As can be seen in Fig. 2B, all three item types were associated with a negative deflection that peaked at the time of response execution over anterior regions and approximately 100 ms later at posterior sites, suggesting that a response-locked negativity was also present in this analysis.[3] However, most important for present purposes is the fact that the perceived $\leq$ imagined $<$ correct rejection-pattern

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[1] As discussed in Section 1.1, the LPN was substantially reduced in the item memory task as compared with the source memory task (cf. Cycowicz et al., 2001; Ranganath and Paller, 2000, inclusion vs. exclusion tasks) and, furthermore, only found reliable for perceived items relative to correct rejections.

[2] Source accuracy was calculated as: [P(correct source-attribution)–P(wrong source-attribution)]/[P(correct source-attribution) + P(wrong source-attribution)].

[3] To achieve an acceptable signal-to-noise ratio, one subject had to be excluded due to excessive eye-movement artifacts at the time of the responses. The remaining 15 subjects were included in the response-locked grand averages that are depicted in Figure 2B (mean trials/condition: perceived = 60, imagined = 61, new = 133). Mean amplitudes in the 0–150 ms time window were subjected to two-way repeated-measures analyses of variance (ANOVAs) using the factors of Item type (perceived vs. imagined vs. new) and Site (left vs. midline vs. right) for frontal, central, and parietal recording sites, separately. The only significant effect involving the factor of Item type was a main effect at frontal leads [$F(2,28) = 6.80$, $P<0.01$]. Since the peak of the frontal negativity occurred at the time of response execution, an additional analysis was conducted on data in the 0–25 ms time window. The main effect of Item type was significant [$F(2,28) = 4.46$, $P<0.05$], but subsequent pairwise comparisons failed to show any reliable difference among item types.

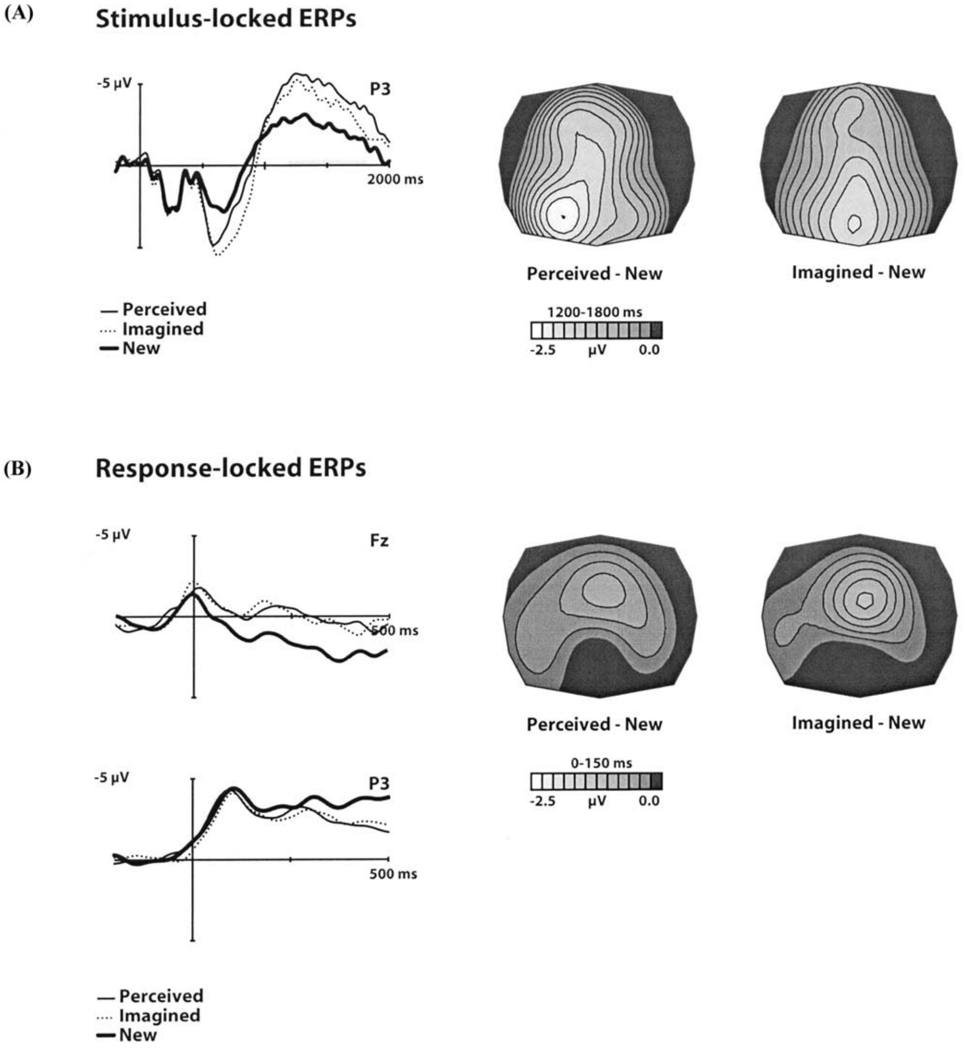

Fig. 2. Stimulus-locked (A) and response-locked (B) grand averages representing correct performance to perceived, imagined, and new items at P3 and Fz (response locked). Topographic maps of (A) the negative-going old/new effects and (B) the ERN/Ne component associated with perceived and imagined items. The gray horizontal bar depicts the time interval of the discussed effect.

observed in the stimulus-locked averages over posterior regions is not evident in this component. Given the proposed relationship between posterior response-locked negativities and action monitoring, this finding suggests that processes related to response conflict were engaged to similar extents irrespective of item type. That is, we found no support for the idea that relative differences in action monitoring associated with old items (requiring a source decision) and new items give rise to the negative-going old/new effects observed

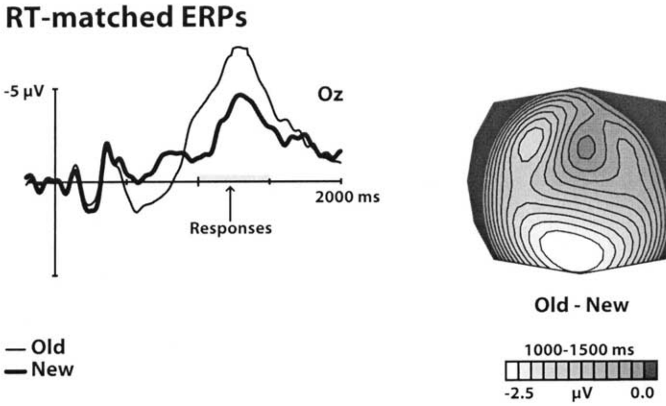

Fig. 3. Grand averages of RT-matched trials of correct performance to old (collapsed across perceived and imagined) and new items at Oz. Topographic map depicts the negative-going old/new effect. The gray horizontal bar depicts the time interval of the discussed effect.

in the stimulus-locked ERPs. Thus, the LPN observed in the present source memory task may not as readily be explained by referral to response-related activity as in the Nessler and Mecklinger (2003) false-memory paradigm presented above.

However, this conclusion is based on a null result, which, needless to say, could be caused by a number of factors. We therefore chose to perform a second analysis to examine whether the LPN in the stimulus-locked ERPs remained reliable when the trials included in the analysis were matched with respect to response latencies. Fig. 3 depicts the stimulus-locked grand averages for RT-matched old and new items. As is evident in the figure, the LPN is still readily visible for old responses when differences in response times are leveled out. In light of the outcome of the response-locked analysis, it is interesting to note that the LPNs for old and new items are both peaking at about 1300 ms after the onset of the test words. This corresponds well with the fact that the posterior response-locked negativity peaked approximately 100 ms following response (i.e. 1215 and 1220 ms). The difference between old and new items is instead characterized by a sustained additive effect causing the ERPs elicited by old items to be more negative than those elicited by new items.[4] As can be seen in the topographic map displayed in Fig. 3, the effect shows a pronounced parieto-occipital distribution (maximal at Oz).

In summary, the additional analyses of the data reported by Johansson et al. (2002) gave no support for the view that the posteriorly distributed negative-going old/new effects were

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[4] Signal-to-noise considerations required: (a) the exclusion of two subject due to an insufficient number of artifact-free trials (< 16) in the critical RT interval and (b) the averaging of trials collapsed across the two sources (i.e. perceived and imagined; mean trials/condition: old $= 33$, new $= 23$). The included trials were restricted to correct responses obtained in the 1100–1350 ms time window and response latencies were matched for the two item types with mean values of 1215 and 1220 ms for old and new items, respectively [$t(13) < 1$]. Two-way repeated-measures ANOVAs using the factors of Item type (old vs. new) and Site (left vs. midline vs. right) were conducted on the mean amplitudes in the 1000–1500 ms time windows at the posterior recording sites. These analyses confirmed that the negative-going old/new effect was significant at occipital recording sites [$F(1,13) = 5.38$, $P < 0.05$] and marginally so at parietal sites [$F(1,13)=3.61$, $P = 0.08$].

caused by enhanced action monitoring processes induced at around the time of response execution. Rather, in as much as posterior response-locked negativities reflect response conflict, such processes were engaged to similar degrees irrespective of the type of the test probe. Furthermore, it was demonstrated that the negative-going old/new effect remained reliable in a comparison of trials that were equivalent with respect to response latencies, which again suggests that the LPN is not entirely mediated by response-locked factors. Rather, it may reflect additional mnemonic processing that merits further evaluation.

3. Discussion

We set out to elucidate the functional significance of a posteriorly distributed negative-going slow wave that has frequently been observed in ERP studies of episodic memory. The overview of the relevant studies suggested that two main classes of experimental conditions tend to elicit the LPN. Based on this notion, we presented stimulus- and response-locked data from two studies that mapped onto these classes: (a) item memory coupled with high action monitoring demands due to the presence of response conflict and (b) source memory characterized by a very high level of successful retrieval of contextual information and low action monitoring demands. The key finding was that the LPN can be decomposed into at least two temporally and functionally distinct subcomponents. While the LPN observed in the high-conflict item recognition paradigm can be attributed to the involvement of a posteriorly distributed ERN/Ne component, no such response-related activity appears to account for the negative-going wave evident during the successful source memory retrieval. The overall pattern of results, thus, argues against a unitary account of the LPN and draws attention to two sets of processes that contribute to this pronounced effect: action monitoring and the retrieval of attribute conjunctions.

3.1. Action monitoring during memory retrieval

As is apparent from the studies summarized in Table 1, one class of memory tasks in which LPNs have frequently been reported is characterized by item recognition tasks that are designed to establish conflict in the test phase by including non-studied material that share a resemblance with the studied material. The elevated FA rates and prolonged response times found in these tasks suggest that the test probes activated conflicting response tendencies, and that selecting the relevant responses presupposes enhanced action monitoring processes. The view that the LPN observed in memory tasks of this kind indeed reflects higher action monitoring demands was supported by the response-locked ERP analyses outlined in Section 2.1. These analyses revealed that correct ‘old’ responses and erroneous ‘old’ responses to lure words, but not correct rejections of new words, elicited a negative-going component at fronto-central sites, highly reminiscent of the ERN/Ne found for errors in choice reaction time tasks (e.g. Coles et al., 2001; Falkenstein et al., 1995). In addition, erroneous responses to lures gave rise to a second response-locked negative deflection that was slightly delayed and more pronounced at parietal recording sites. In the following, we will argue that the anterior and posterior portion of the ERN/Ne may serve two different but related action monitoring functions: error detection and conflict monitoring.

Much research has been devoted to elucidate the nature of the processing system that underlies the ERN/Ne. It has been shown that the ERN/Ne is sensitive to the importance of the error for the subject (Gehring et al., 1993), that it can be elicited by errors committed with the feet, hands, or eyes (for an overview, see Holroyd and Coles, 2002), and can even be elicited in the absence of response generation processes, that is, by the presentation of negative feedback that indicates that a response was inappropriate (Miltner et al., 1997). These findings, together with the observation that the component is elicited in a wide variety of tasks and by stimuli presented in different modalities suggest that the error processing system underlying the ERN/Ne is highly flexible. It seems to be adjustable to various sources and consequences of errors. This is supported by a recent study in which ERN/Ne-like activity was found in association with financial loss in a ‘gambling’ task (Gehring and Willoughby, 2002), or by findings that link the ERN/Ne to affect-related aspects associated with error commission (Luu et al., 2000; Tucker et al., 1999). This error monitoring or detection system may be part of a more general executive control system involving the lateral prefrontal cortex (PFC) and the anterior cingulate cortex (ACC) that monitors for conflicts and guides compensatory behavior (Gehring and Knight, 2000). The present finding of a fronto-centrally distributed ERN/Ne elicited by erroneous responses in an item recognition task further emphasizes this system’s high flexibility and adaptability to different task demands.

However, why was a similar ERN/Ne elicited by correct responses to old words?[5] This question was recently addressed directly by Coles et al. (2001). They argue that an ERN/Ne to correct responses may result from a modified or compromised representation of the correct response. A modified representation of the correct response can emerge in tasks in which subjects are required to give speeded responses. Under such conditions, the representation of the correct response will also include temporal information, leading to a mismatch for a correct but slow response, which gives rise to an ERN/Ne. Since the response times in the Nessler and Mecklinger (2003) study were rather long and no speed instruction was given to the subjects, it seems implausible that this accounts for the present ERN/Ne to correct responses. The long response times also argue against the view that the present response-locked components reflect residual stimulus-related activity, not removed by response-locked averaging (Coles et al., 2001).

Compromised representations of the correct response can according to Coles et al. (2001) emerge by misperception of a stimulus or by wrong applications of the stimulus-response mapping rule, that is, when subjects misclassify correct trials as incorrect. In support of this view, Scheffers and Coles (2000) found a large ERN/Ne for correct responses that subjects with high confidence judged as being incorrect. It is conceivable that compromised or inaccurate representations of the appropriate response also account for the present ERN/Ne on correct trials. Due to the semantic association between lure words and studied words,

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[5] Several recent studies have reported ERN/Ne-like activity for correct responses in choice reaction-time tasks (Bates et al., 2002; Falkenstein et al., 2000; Ford, 1999; Gehring and Knight, 2000; Kopp and Rist, 1999; Mathalon et al., 2002; Swick and Turken, 2002; Vidal et al., 2000). Because of the apparent ambiguity in using the term ERN/Ne (a component that per definition is elicited by errors) on correct trials, some researchers have referred to these negative deflections as correct response negativities (CRN; Ford, 1999). However, since our main focus is the response-locked negativities affecting the LPN (i.e. erroneous responses to the lure words), we will use the expression ‘ERN/Ne on correct trials’ for reasons of consistency.

some of the correct 'old' responses may have been classified as incorrect, resulting in a mismatch between the actual and the intended response, giving rise to an ERN/Ne.

An alternative view on the presence of an ERN/Ne on correct trials has been proposed by Vidal et al. (2000); see also Falkenstein et al., 2000). They argued that the ERN/Ne may not reflect the outcome of the process that compares the representations of the actual and the intended response (i.e. error detection), but rather the comparison process itself. Since both correct and incorrect responses undergo such a comparison, they may both elicit ERN/Nes. Vidal et al. further suggested that error detection instead is indexed by the later positive component (the error positivity or Pe, Falkenstein et al., 1991). However, the data reported here do not provide further support for this hypothesis as we found no evidence for an enhancement of the Pe following the erroneous responses in the item recognition task (see Fig. 1B). Another potential explanation for ERN/Nes on correct trials is offered by the view that frontal negativities reflect motivational and/or affect-related aspects of the response (Gehring and Knight, 2000; Gehring and Willoughby, 2002; Luu et al., 2000; Tucker et al., 1999). Although such processes may be more easily detected for errors, response evaluation takes place for all responses, leaving open the possibility for frontal negativities also on correct trials. However, it is not clear how this view accounts for the data in the present task in which both correct and incorrect 'old' responses generated larger ERN/Ne-like activity than correct 'new' responses.

While the ERN/Ne observed at fronto-central recording sites was not differentiated on the basis of correct and incorrect responses, incorrect responses were associated with a more pronounced negative deflection at parietal sites. Given the elevated FA rates and prolonged response times for the incorrect responses, the posterior ERN/Ne can be taken to reflect enhanced conflict monitoring demands. Consistent with this view, a recent event-related functional magnetic resonance imaging (fMRI) study using the same stimulus materials revealed two activation foci for erroneous responses to lure words relative to correct rejections of new words: the caudal ACC and the fronto-medial wall (i.e. BA 9/10/32) (von Zerssen et al., 2001). A source analysis with a single dipole seated in the caudal ACC accounted for 86% of the variance in a 400 ms time interval of the ERP difference waves (erroneous responses to lures minus correct rejections of new words) in which the LPN was maximal. This pattern of results implies that neuronal activation in the caudal ACC contributes to the LPN and—given the high correspondence between the stimulus- and response-locked ERPs at posterior recording sites—also to the posterior ERN/Ne. A second line of evidence for the view that the posterior ERN/Ne in the present study reflects caudal ACC activation due to conflict monitoring rather than error processing comes from additional recent brain imaging studies. Two such studies reported greater activation in the caudal ACC for trials associated with enhanced response conflict but not with errors (Braver et al., 2001; Kiehl et al., 2000). Interestingly, both studies consistently found more rostral ACC activation for error trials, confirming the view that the anterior ERN/Ne is related to error processing. In support of the notion that the rostral and caudal portions of the ACC are differentially involved in error and conflict processing, respectively, Swick and Turken (2002) reported that a patient with a focal lesion of rostral ACC showed an attenuated ERN after incorrect responses and an even enhanced (stimulus-locked) negativity to correct conflict trials, suggesting that error processing can be selectively impaired after rostral ACC lesions. The overall pattern of findings suggests that the ACC houses a variety of processing functions in the service of goal directed behavior (Bush et al., 2000). Presumably, the anterior ERN/Ne observed in the present data set reflects enhanced rostral ACC activation related to error processing, whereas the posterior ERN/Ne most likely reflects enhanced caudal ACC activation due to enhanced conflict monitoring demands.

Taken together, the analyses show that a retrieval situation with high resemblance between studied and non-studied test words may be characterized by enhanced error and conflict processing, compromised representations of the correct responses, and/or inadequate applications of stimulus-response mapping rules. Such additional and non-mnemonic processing features enhance action monitoring demands as reflected by elevated caudal and rostral ACC activation and, measured at the scalp, by a LPN and an ERN/Ne in the stimulus and response-locked ERP averages, respectively. In contrast to choice reaction-time tasks, the present item recognition task revealed an additional posterior ERN/Ne, a component that deserves further experimental evaluation.

3.2. Retrieval of attribute conjunctions

As was evident in the overview of the eliciting experimental conditions, the LPN has primarily been observed in tasks that included the requirement to retrieve conjunctions of attributes from memory (i.e. a recognized item and source/context-specifying information). The low rates of source misattributions observed in a subset of the reviewed studies suggest that action monitoring associated with elevated response conflict is not the only eliciting factor. Consistent with this interpretation, the re-analysis of the data reported by Johansson et al. (2002) failed to show an association between the negative-going old/new effect and a posterior response-locked negativity. Moreover, old responses elicited a greater LPN relative to new responses even when the included trials for both item types were matched for response latencies (cf. Fig. 3). This finding suggests that the negative-going old/new effect found in the present data cannot readily be attributed to action monitoring processes related to response conflict. The data rather indicate that an additional type of processing contributes to the generation of the LPN. As can be seen to the left in Fig. 3, correctly judged old items elicited more negative-going ERPs than correct rejections approximately 300 ms before responses were executed, a finding that supports the idea that the LPN reflects processes that potentially influence the outcome of the memory decision.

Given the nature of the tasks, it seems reasonable to argue that this second type of processing reflected in the LPN is somehow tied to the specific task characteristics, namely, the retrieval of attribute conjunctions from memory. For example, the relevant conjunctions in the typical memory tasks may comprise a recognized item and attributes such as representations of color, size, location, encoding operations, etc.

Consistent with the findings reported by Cycowicz et al. (2001), the RT-matched effect showed a pronounced parieto-occipital distribution, which may be taken as support for the view that sensory-specific regions (e.g. visual) are searched and reactivated at the time of retrieval to reinstate a representation of the item with its corresponding study attributes. However, before drawing any firm conclusions, we should consider the proposed functional interpretations of the positive-going old/new effects preceding the LPN. Most critically, as noted in Section 1.1, the left parietal effect has been taken as an index of recollection. In contrast to familiarity, recollection is characterized by the successful retrieval of an item accompanied by contextual information specifying the prior encoding episode. It has been proposed that the left parietal effect is correlated with the amount or quality of such retrieved contextual information (e.g. Rugg et al., 1995; Wilding, 2000). Thus, the reinstatement of an old item with its previous study attributes should be manifested in the left parietal old/new effect. If this is the case, what is the additional function of the processes reflected in the LPN?

A potential clue may be that the negative-going wave has been observed for both accurate and inaccurate source/context judgments and sometimes even found to be more prominent for inaccurate judgments (e.g. Wilding, 1999). This pattern of results, thus, suggests that the LPN reflects processes not necessarily tied to successful source retrieval.

In keeping with the basic ideas of the reinstatement notion, an alternative proposal is that the LPN reflects the retrieval of conjunctions of attributes including those that are internally generated via sensory-specific search and ‘imagery’ at the time of retrieval. According to such a view, the left parietal effect reflects successful retrieval of contextual information triggered by the test probe, whereas 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. Consistent with the view that the prefrontal cortex regulates neuronal activity in the extrastriate cortex, prefrontal ‘top-down’ processing may select such attributes and guide posterior regions in the service of reconstructing the prior event (cf. Barceló et al., 2000; Miller and Cohen, 2001; Shimamura, 2000). For example, if you remember having studied the word ‘apple’, but fail to automatically retrieve a corresponding picture or records of having imagined one (cf. Johansson et al., 2002), you may try to generate a visualization of an apple and then decide whether or not you have done so previously in the study phase. Similarly, a recognized word for which the gender of study voice is called for may be internally ‘reexperienced’ in a study voice before a source attribution is made. The ease or the salience with which such a representation appears may affect the outcome and the confidence of the memory decision (cf. Jacoby et al., 1989). The broad temporal extension of the negative-going old/new effect suggests that continued evaluation of the integrated representation might take place even after a judgment has been made, possibly with the purpose of rechecking the validity of the chosen response alternative.

The posterior distribution of the LPN fits well with the established relationship between visual imagery and posterior cortical regions (Farah et al., 1988). For example, the precuneus located in the medial posterior parietal cortex has been implicated in memory-related imagery and retrieval of visual images (e.g. Fletcher et al., 1995; Grasby et al., 1993). Several electrophysiological studies of mental rotation of visual information provide support for the idea that parietal negative slow waves may reflect the involvement of mental imagery (e.g. Desrocher et al., 1995; Peronnet and Farah, 1989; Wijers et al., 1989; see Heil, 2002, for a review). Related findings come from studies in which subjects are instructed to retain different types of information in working memory for a subsequent memory judgment (e.g. Mecklinger and Pfeifer, 1996; Ruchkin et al., 1999).

Furthermore, results reported by Corbetta et al. (1995) and Wojciulik and Kanwisher (1999) underscore the important role of the anterior and posterior intraparietal sulcus in tasks that require attention towards a conjunction of features as opposed to a search for single features. Additional support for the view that posterior parietal areas support the processing of attribute conjunction comes from patients with bilateral parieto-occipital lesions, a condition known as Balint's syndrome. For example, following two strokes resulting in nearly symmetrical parieto-occipital lesions (centered in BA 7 and 39), patient RM was still able to recognize single objects, words, or faces, but failed to attend to and perceive more than one object at a time (Friedman-Hill et al., 1995). RM also committed an extensive number of binding errors, that is, when presented with letters in different colors he reported illusory conjunctions between the color and the shape of the letters despite normal viewing conditions. Similar feature-binding deficits after bilateral lesions of posterior brain areas have been reported by Humphreys and Riddoch (1992), confirming the importance of these brain areas for feature-binding processes.

With respect to the notion that the LPN reflects search/retrieval of context-specifying information, it is worth considering the studies on long-term memory retrieval reported by Rösler, Heil, and colleagues (e.g. Rösler et al., 1995). In these studies, pronounced slow negative potentials were elicited by retrieval cues. Importantly, these negative-going slow waves exhibited topographies that differed as a function of the type of information being queried, for example, the spatial and color condition evoked slow waves across parietal and occipito-temporal areas, respectively. Even though the experimental characteristics of these investigations depart in several ways from the ERP memory studies reported throughout this paper, the results support the view that the retrieval of attribute conjunctions may give rise to content-specific negative slow wave activity.

However, a strong conclusion about the aforementioned link between negative slow wave potentials and the search/retrieval of attribute conjunctions induced by recognized items is clouded by some recent findings. Gonsalves and Paller (2000b) presented words in a study phase for which subjects were instructed to visualize the corresponding objects. For half of the words a color photograph of the object corresponding to the word was also shown. In the following test phase, spoken words were presented and subjects were instructed to respond 'old' to words for which a picture was presented at study and 'new' to non-studied words and words presented without a picture at study. For present purposes, the most important findings were that accurate picture memories elicited more positive ERPs (approximately 600–900 ms post-stimulus onset) at occipital sites as compared to the other conditions (see also Gonsalves and Paller, 2000a; Paller and Kutas, 1992), and, moreover, that a similar positivity distinguished between conditions presumed to tap different extents of imagery during study. Similar to our account that the LPN is associated with the retrieval of attribute conjunctions, the authors assume that their occipitally focused ERP effect reflects the reactivation of stored visual engrams.

A possible resolution of this ambiguity may be that Gonsalves and Paller (2000b) used spoken words as retrieval cues, whereas all the abovementioned studies employed visual cues. Given this, it is conceivable that the retrieval of attribute conjunctions by auditory retrieval cues (i.e. spoken words) is mediated by different posterior parietal regions than when visual retrieval cues (i.e. words or pictures) initiate this process. Although speculative, this may give rise to the different polarity and slightly different topographical distribution of the slow wave activity in the Gonsalves and Paller studies and the aforementioned studies.

Interestingly, starting around 900 ms post stimulus correctly rejected old words (presented without pictures at study) evoked an occipitally focused negative slow wave compared to correctly rejected new words, which is highly reminiscent of the LPN described in the present paper. Since a failure to recover pictorial information would support a rejection of these old items, the pattern fits the idea that the effect reflects search for such contextual information. Alternatively, as the difference in the LPN was paralleled in the RTs (1305 vs. 1193 ms), it is conceivable that the LPN indexes an increasing level of response conflict associated with rejecting words seen and imaged in the previous study phase (see Section 3.1).

In summary, the second set of processes reflected in the LPN appears to be related to the retrieval of attribute conjunctions (e.g. word + study voice). However, as is evident from the discussion above, too few studies have focused on addressing the functional significance of this effect to make any conclusion definitive. Based on the available data, it can tentatively be argued that the LPN may reflect processes that act to reconstruct the prior study episode when task-relevant attribute conjunctions are not readily recovered by the test probe or need continued evaluation. To form and retain such an integrated representation these processes would include sensory-specific search and the binding of such information to the recognized item.

3.3. *Conclusions and open issues*

In this paper we provide a selective review of ERP studies of episodic memory reporting a posteriorly distributed negative slow wave, onsetting before or at around the time of the response and lasting up to several hundred milliseconds. A closer examination of the experimental conditions by which the LPN is elicited revealed that at least two classes of processes are contributing: action monitoring due to enhanced response conflict and the retrieval of attribute conjunctions characterizing the former study episode. This view was confirmed by a post-hoc analysis of two ERP data sets that can be taken as representative for these two types of processing. A large LPN is present in both data sets. Item recognition memory with enhanced action monitoring demands gives rise to an ERN/Ne effect in the response-locked averages, whereas no such response-locked effect is evident in the source memory task requiring retrieval of attribute conjunctions. We provide evidence for the view that the former type of processes is mediated by the medial frontal lobes (i.e. the rostral and caudal ACC), whereas the latter might be realized by medial and lateral posterior parietal cortices.

This functional account and the proposed neuroanatomical correlates are necessarily preliminary and coarse in nature. Several issues remain open and need to be addressed by future experimentation. For example, while the abovementioned proposal implies that the LPN should vary in topography as a function of material or modality queried during retrieval, the data at hand do not allow an examination of fine-grained differences in scalp topography. Conversely, it could be argued that the posterior parietal cortex, as a multi-modal association area (Nieuwenhuys et al., 1988), may bind attributes across modalities into sensory-unspecific representations. This view is supported by the consistent scalp distribution of the LPN across different tasks and stimulus modalities. Further experimentation will also be required to resolve this sensory-specificity versus multi-modality issue.

Source models with equivalent dipoles suggest that a medial neuronal source in the ACC and bilateral and posterior sources in the posterior parietal cortex could generate bilateral distributed negative slow wave activity (Nunez, 1981; M. Scherg, personal communication, October, 17, 2002). Nevertheless we would expect subtle topographical differences between the LPN associated with action monitoring and the retrieval of attribute conjunctions. Hints towards functionally relevant topographical differences of this kind are provided by Fig. 1B and Fig. 3, displaying a more posterior distribution of the LPN in the Johansson et al. (2002) study requiring the retrieval of word-picture associations than in the Nessler and Mecklinger (2003) study. In a similar vein, the only three studies of associative retrieval included in Table 1 showed a right lateralized LPN (Donaldson and Rugg, 1998, 1999; Rugg et al., 1996). In addition, subtle differences in topography might be obscured by the involvement of temporally overlapping response-locked factors. Consequently, it would be informative to compare the distributions of the negative-going old/new effects associated with old items from different modalities after the included trials have been matched with respect to response latencies.

Another open issue concerns the relationship between retrieval-related late slow wave activity arising from the PFC and the LPN. In some studies there is a close temporal and functional relationship between both ERP components, whereas in others it is more tentative than real. The available data do not allow us to be more specific about this cross-study pattern of results and the nature of the interaction between the late frontal slow wave and the LPN. As noted above, any interpretation is rendered difficult by the components' opposite polarities and overlapping temporal distributions. We have tentatively argued that the LPN may reflect processes related to forming and holding a representation of a conjunction of attributes that specify the prior study episode. Given this, it is conceivable that frontal slow waves reflect sustained top-down signals emanating in the PFC that select the task-relevant attributes to search and to bind with the recognized item (cf. Miller and Cohen, 2001; Shimamura, 2000) and, further, processes that evaluate the resulting representation (cf. Allan et al., 1998; Rugg et al., 2000). This is not only supported by the reciprocal nature of the connections between the PFC and posterior parietal regions (Petrides and Pandya, 2002), most models of executive control would also be consistent with the general notion that the PFC exerts a top-down influence on early and higher sensory areas to maintain goal oriented behavior in different task environments. However, the nature of this top-down processing should be different in the case of response conflict than in the case of retrieval of attribute conjunctions. In any case, elucidating the precise nature of the interaction between the frontal slow wave and the LPN in memory retrieval tasks remains an important objective for further research.

Finally, the relationship between encoding and retrieval-related ERP activity also remains an open issue. The retrieval account implies some topographical resemblance of study- and test-phase ERPs. As none of the studies reviewed has reported such a comparison (with the exception of Gonsalves and Paller, 2000b), we could only speculate on this issue. Further recognition studies focusing on temporal and topographical similarities between study- and test-phase ERPs will be required. Taken together, we hope that this review and preliminary proposal will stimulate fruitful research endeavors and, ultimately, help to elucidate the brain mechanisms underlying episodic memory retrieval.

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Experimental Neuropsychology Unit, Department of Psychology, Saarland University, 66123 Saarbrücken, Germany. Electronic mail may be sent to m.johansson@mx.uni-saarland.de. We are grateful to Monica Fabiani and two anonymous reviewers for their valuable comments on an earlier version of this paper.

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