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Research report

Asymmetric hemispheric contribution to ERPs in associative memory indexes goal relevance and quantity of information

Giulio Pergola[a,c,d,*], Michele Trotta[b], Boris Suchan[c,d]

[a] Cognitive Neuroscience Sector, International School for Advanced Studies (SISSA-ISAS), via Bonomea 265, I-34136 Trieste, Italy
[b] Faculty of Psychology, Padua University, I- 35122 Padua, Italy
[c] Department of Neuropsychology, Institute of Cognitive Neuroscience, Ruhr-University Bochum, D-44780 Bochum, Germany
[d] International Graduate School of Neuroscience, Ruhr-University Bochum, D-44780 Bochum, Germany

HIGHLIGHTS

- Fifteen participants encoded and retrieved picture pairs while ERPs were recorded.
- Retrieval cues yielded either one or two associations, only one of them being goal-related.
- Asymmetric frontal negative peaks dissociated goal-related from unrelated associations during encoding.
- Late right frontal negativity discriminated recall from no-recall trials when multiple associations were available.
- This evidence suggests that asymmetric ERP component play a role in goal-related modulation of associative memory.

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ABSTRACT

Explicit encoding requires humans to select the information relevant to their goals, yet not all irrelevant information is discarded. The present study addressed how different quantity and relevance of information modulate the electrophysiological activity during the encoding and retrieval phases of a recognition memory task.

Subjects learned associations between two semantically unrelated pictures, and then performed a recognition judgment. After recognition, subjects were asked to recall the associated picture by using the recognized image as a cue. Cues yielded either high quantity of information (the cue evoked two associations, only one of them being relevant to the task), or low quantity of information (the cue evoked a single, relevant association).

At encoding, a negative peak (400 ms) showed reduced negativity at left sites for the associative trials compared to the non-associative ones, while at right frontal sites the peak was more negative for goal-unrelated associations, compared to goal-related ones. Late right negativity during the test phase (800–1000 ms) discriminated hits followed either by correct or by no recall, but only when the cue evoked multiple associations.

Frontal electrophysiological asymmetry at encoding was affected by the behavioral goal, i.e. activity reflected goal-related encoding on the left and goal-unrelated encoding on the right. The late right effect at retrieval suggests a link between this activity during encoding and the evaluation of the higher quantity of information in light of the behavioral goal during retrieval. Overall, the results indicate that different mechanisms and/or neuronal populations are involved in goal-related versus goal-unrelated association.

Abbreviations: H^+, hits followed by correct recall of the uniquely paired associate; H^0, hits followed by no recall of the uniquely paired associate; HERA, Hemispheric Encoding-Retrieval Asymmetry; HQ, high quantity of information, i.e., items yielding multiple associations; LQ, low quantity of information, i.e., items yielding single associations.

* Corresponding author. Current address: International School for Advanced Studies (SISSA-ISAS), via Bonomea 265, 34136 Trieste, Italy. Tel.: +39 3408223991/040 3787861; fax: +39 040 3787615.
E-mail addresses: giuliopergola@yahoo.it (G. Pergola), quisutdeus@hotmail.it (M. Trotta), boris.suchan@rub.de (B. Suchan).

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1. Introduction

Frontal electrophysiological activity is consistently found during episodic memory encoding as well as retrieval. It is not yet clear, however, how laterality of event-related potentials (ERP) is related to explicit memory processing. Two lateralized effects show a remarkable consistency across studies: a late right frontal old/new effect during retrieval [1–6] and a left negativity followed by a sustained positivity during associative encoding [4,7–12]. The next paragraphs will shortly outline the models put forward to explain these effects.

The HERA model (Hemispheric Encoding-Retrieval Asymmetry; Tulving and coworkers [13]) proposed that activity at left frontal sites indexes episodic encoding, whereas right-lateralized activity is a correlate of episodic retrieval. This interpretation has been supported by Düzel and coworkers [14,15] and further evidence [9,16]. It has been proposed that left frontal activity plays a role in selection of information during episodic encoding [17], although other views favor a role of left lateral frontal activity particularly during semantic retrieval [18], which may be needed for efficient episodic encoding. Other findings are problematic with respect to the HERA model, including evidence of higher left frontal electrophysiological activity during the retrieval phase of source memory tasks [2,19], and evidence of right prefrontal activation during encoding, in late time windows [20]. Hence the functional role of right frontal activity does not seem to be limited to retrieval, as opposed to encoding.

Retrieval effort has been advocated as a functional correlate of late right frontal activity [21]. Another view states that the right frontal activity is a functional correlate of retrieval monitoring, aiming at filtering out illusory memory traces [22]. This theory is consistent with the pattern of impairments observed in patients with right frontal lesions (for a review, see [23]). Insofar as retrieval entailing higher monitoring demands is thought to be more effortful, the theory provides an alternative account for the evidence relating right frontal activity with retrieval effort. Curran et al. [24] for instance found that good, but not poor performers, showed a late [1000–1500 ms] right frontal old/new effect, which suggests a relationship between right late frontal activity and retrieval success.

Dobbins and Han [25] introduced a different view of the right frontal electrophysiological activity, proposing that it covaries with the number of internal decisions required prior to the behavioral response, irrespective of the content, the effort and the accuracy of retrieval. The authors discriminated between an evidence-based and a rule-based account of the right frontal activity, and showed that this activity encompasses mnemonic as well as non-mnemonic tasks. The key variable in their experimental setting was the rule on which decisions were based. This proposal has been supported by Hayama et al. [26], who found the late right frontal old/new effect independently of the retrieval task (semantic or episodic) and concluded that a higher quantity of information (a priori with respect to effort and success) elicited the effect. Hayama and Rugg [27] additionally provided imaging data in support of this hypothesis.

In general, the relationship between the late right frontal electrophysiological activity during retrieval and the electrophysiological activity during encoding has not yet been satisfactorily elucidated, perhaps because neural correlates of encoding have been less extensively investigated compared to retrieval [28]. This issue is one of the aims of the present investigation, i.e., understanding how the late right frontal activity is related to electrophysiological components found during encoding. At least two further issues remain open. First, old/new effects (also including hits vs. false alarms contrasts) compare stimuli which are intrinsically different with respect to the corresponding memory trace (i.e., studied vs. non-studied). This implies a difference in monitoring requirements: old/new effects express the interaction between the nature of the stimuli (old or new) and subject's responses (acceptance or rejection). Associative memory tasks, instead, allow dissociating experimental trials based on subsequent recall to obtain a comparison among hits. Such a comparison is purer and more straightforward to interpret than an old/new comparison (see also [29]). However, this is the second point, recall of a source associated to several stimuli is prone to a generative retrieval strategy, i.e. attempting to imagine the given cue within the different contexts constituting the possible sources (e.g.: remembering the action performed upon the first encounter with the item, where there is a limited set of possible actions – two or three). This feature, depending on task design, may introduce an effect of guessing which is difficult to account for and can limit comparability between conditions. To overcome this issue, Montaldi and Mayes [30] suggested using unique associations to probe recall and exclude confounds due to guesses.

The present study aimed to investigate how the right frontal electrophysiological activity in the post-retrieval phase is affected by the quantity and relevance of information encoded [25]. We shall define "goal-related encoding" the acquisition of information which subjects will be asked to report later in the experiment. By "goal-unrelated encoding" we refer to acquisition of information which will not be required later, but is spontaneously memorized. This sort of encoding cannot be defined "incidental", because subjects are aware that a memory test will follow. The task we developed to differentiate these cognitive operations requires associative encoding and cued recall of pictorial material. During encoding, a set of stimuli prompted two associated representations (high quantity of information: HQ), another only one (low quantity of information: LQ). The HQ pairs were presented immediately after presentation of a picture semantically related to one component of the HQ pair, so that subjects could encode two different associations (one goal-related and one goal-unrelated). In the LQ pairs subjects only encoded the goal-related association. At retrieval subjects were asked to make an old/new assessment and subsequently respond reporting the picture uniquely associated to the recognized stimulus.

We predicted that retrieval of HQ items would elicit increased right frontal activity. Recognition success was matched across conditions; critically, the information associated to the cues was not necessary to solve the old/new test, so that response selection was not affected. We expected an early left frontal effect during associative encoding, followed by a sustained positivity [4,7–9]. We exploratively studied the ERP correlates of goal-unrelated encoding, aiming at establishing a link between electrophysiological activity during encoding and the right late frontal component during retrieval.

2. Methods

2.1. Participants

Twenty-five healthy, right-handed German native speakers participated in the study (eight females; age ranged from 19 to 29 years, mean and standard deviation: 24.1 ± 2.0). Subjects were students of the Ruhr-Universität Bochum recruited by means of advertisements. After artifact rejection in the ERP analysis, only subjects with at least ten trials per experimental condition were included in the final analysis. The exclusion of subjects was a consequence of the high variability of behavioral performance in the memory task. The final sample entailed fifteen participants.

The study was approved by the Ethics Committee of the Faculty of Medicine of the Ruhr-Universität Bochum. All participants gave informed written consent. Subjects received either course credit or 15 € upon completion of the task.

2.2. Stimuli

A set of 350 pictures representing common objects and indoor/outdoor scenes was rated in the pilot phase of the study by a group of 21 subjects, with respect