Research report

Item-related versus task-related activity during encoding and retrieval in verbal and non-verbal episodic memory: an event-related potential study

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Abstract

In the past 10 years, functional neuroimaging studies have elucidated the role of the prefrontal cortex in memory encoding and retrieval. However, it is still unclear whether these activations reflect item- or task-related activities. In the present study, Event-Related Potentials (ERPs) were used to distinguish item-related activity from task-related activity in both encoding and retrieval processes. This activity was assessed with both verbal and non-verbal material. A recognition paradigm with words or random shapes was administered to 12 young participants. Memory elicited ERPs were compared to those evoked by control tasks that used similar material. The distribution of the N400 was found to be larger on left frontal than right frontal areas for verbal material, however, this was the case in the control and memory conditions as well. This finding likely reflects the sensitivity of this component to processing verbal material. The LPC amplitude was greater in the non-verbal encoding than the non-verbal control condition, whereas in retrieval it was larger than the control condition for both verbal and non-verbal material. Thus, item-related activity is determined by an interaction between properties of the material and the task instructions. Task-related activity was found for non-verbal material: compared to the control condition, the memory condition of non-verbal material elicited bilateral and right frontal activity in encoding and retrieval processes. No task-related effect was reported with the verbal material. Material differences in eliciting task-related effects are discussed in terms of their relation to elaborative and effortful processes.

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1. Introduction

Episodic memory refers to memory for events that are encoded within their temporal and spatial context \cite{75–77}. Episodic memory involves successive stages of encoding, storage and retrieval. Encoding corresponds to processes leading to the formation of new memory traces, storage relates to the maintenance of memory traces over time, and retrieval refers to processes that allow the access of stored memory traces. These processes have been dissociated at the neural level with the use of brain imaging techniques (for reviews see Refs. \cite{9,17,53}). However, experiments that assessed encoding and retrieval processes with brain imaging techniques have typically confounded processes that act on each individually presented item (item-related processes) and more general or strategic processes that act over the entire experimental task (task-related processes). The goal of the present study was to assess item-related and task-related processes in encoding and retrieval processes of episodic memory using event-related potentials.
activation of cerebral areas during the task. For example, used the fMRI technique, a recent study used PET and EEG signals time-locked to the stimulus, response or any increased blood flow in the left medial temporal lobe.

ERPs are the averaged raw Electroencephalographic signals at the posterior electrodes and was associated in PET with the late positive component (LPC) over the left hemisphere. These activations are implicated in the retrieval of verbal information and may depend on the transient context. Finally, successful verbal encoding has been shown to correspond to a neurocognitive set operating independently of item-type [29]. In previous research, a large number of neuroimaging studies used blocked experimental designs with large recording-windows and in which the activation was averaged over a large number of successive trials. This has been the case, for example, in PET (positron emission tomography) and non event-related fMRI (functional magnetic resonance imaging) studies. Because these paradigms obtain their activation over blocks of items, they cannot separate the activation related to the encoding or retrieval of particular items from the activation related to the encoding or retrieval state.

The use of event-related fMRI or ERP techniques renders it possible to obtain information at both the task and individual item level. ERPs reflect the brain activity produced by post-synaptic firing of a neuron group. The ERPs are the averaged raw Electroencephalographic (EEG) signals time-locked to the stimulus, response or any significant event requiring attention or other cognitive processes [60,61]. ERPs do not have the fine spatial resolution obtained with event-related fMRI. However, ERPs have the temporal resolution necessary to assess the activation yielded by processing individual items, and thus can dissociate it from task-related processes.

Recent studies have attempted to distinguish item- and task-related memory processes using the event-related fMRI technique with mixed event-related and block-designs. In verbal retrieval, Donaldson et al. [28] showed that recognition depends on three classes of processing. Transient activity was found in the anterior left frontal cortex, medial parietal and lateral parietal regions. This activity reflected item-related processing associated with ‘retrieval success’. Sustained activity was found in the bilateral parahippocampal cortex (decrease) and bilateral frontal operculum regions (increase), reflecting state-related processes associated with ‘retrieval mode’. Finally, concurrent sustained and transient activity, which reflects a combination of state- and item-related processing, was observed in the left middle frontal gyrus, bilateral frontal operculum and medial frontal gyrus. Also in verbal retrieval, Dobbins et al. [27] found activations in the lateral prefrontal and parietal cortices that distinguished source recollection from judgments of relative recency, independently of retrieval success. These areas may be involved in a cognitive mode related to source retrieval and recency judgment. In contrast, medial temporal lobes structures (the hippocampus and parahippocampal gyrus) were differentially more active during successful recollection of the encoding context. Finally, successful verbal encoding has been shown to depend not only on transient neural activity but also on sustained neural activity throughout the task, especially in the left prefrontal cortex and in the inferior medial parietal region [55]. Although previous research used the fMRI technique, a recent study used PET and ERPs techniques successively with the same verbal episodic retrieval protocol. Düzel et al. [30] reported right PFC activations with the former technique and a sustained right fronto-polar positive long-term activity with the latter technique. These activations were absent in semantic retrieval. Right PFC activity was found even when old and new words were presented during the retrieval phase, and thus this activity was independent of the memory status of the items. The activity was interpreted as reflecting a ‘retrieval mode’ or a neurocognitive set of retrieval attempts that covered the entire task period. This cognitive state was present irrespective of whether retrieval cues resulted in successful episodic recollection. In the same study, item-related activity was indexed by comparing hits and correct rejections on the recognition task. As hits correspond to items that were recognized correctly, their related cerebral activity should reflect successful retrieval, or ephory. Item-related activity was apparent in ERPs on the late positive component (LPC) over the left hemisphere at the posterior electrodes and was associated in PET with an increased blood flow in the left medial temporal lobe.
[30]. In comparison to words correctly judged to be new, the ERPs elicited by correctly detected old words revealed a greater LPC [1]. The ERP old/new effect, beginning at approximately 400 ms post-stimulus, is attributed to successful retrieval of items [10,63].

In summary, there are indicators suggesting that verbal recognition memory tasks depend on a combination of state- and item-related processes and that these processes have different neural correlates. Nevertheless, these studies have focused on retrieval processes and solely on verbal material. Indeed, there is a paucity of empirical data on the distinction between cerebral activities related to the neurocognitive set and operations that act on individual items. In the present study, we attempted to demonstrate empirically the distinction between task-related and item-related processes. Our first goal was to assess whether the task-related and item-related distinction that was used for retrieval can also be applied to encoding. In other words, we examined whether there is an ‘encoding mode’ that reflects a state of intentional encoding. In episodic encoding, we expected left asymmetry in encoding for verbal material and right or bilateral distributed activities for non-verbal material. Secondly, there are some indications that the nature of the material to be memorized can be critical for the lateralization of encoding/retrieval effects [11,45,52,80]. As mentioned previously, only verbal material has been used in studies that dissociated item-related and task-related effects. It is crucial to assess whether this distinction generalizes to other types of material. Thus, both verbal and non-verbal material was used in the present study. As we expected that the nature of the material acts at the item-related level, we expected to observe left and right lateralized effects in the electrophysiological components for the verbal and non-verbal material, respectively.

In our study, activities linked to items were dissociated from task-related activities by using ERPs. Task-related activity was estimated by sustained activity, which leads to a change in the baseline level of the cerebral activity upon which individual items are processed [29]. In contrast, item-related activity, which acts at the level of the individual item, could not interfere with task-related activity, since this type of activity varies at the baseline level [29]. To differentiate between the task-related activity and the item-related activity, we manipulated the size of the recording windows. As in Düzel et al. [29–31], task-related activity was assessed using a large 10-s window, whereas item-related activity was indexed using each item-elicited waveform. This was done during the encoding and retrieval phases. One methodological addition to our procedure was the inclusion of a non-memory control condition as a comparison task. The control condition involved the presentation of similar materials to those that were employed in the memory conditions, with the exception that subjects were not instructed to memorize them. In the tradition of functional neuroimaging studies, a control condition was used to separate the cognitive components involved in processing the information (perceptual analysis, phonological analysis) from those involved in encoding or retrieval. Thus this technique provides an interesting neural index of the target encoding and retrieval processes.

2. Materials and methods

2.1. Participants

Twelve healthy students (six women and six men) were recruited at the University of Montreal. Their mean age was 21.25 years (S.D. 1.5) and ranged from 19 to 24 years. They had completed an average of 14.5 (S.D. 1.3) years of formal education (range: 13–17). All participants reported normal or corrected-to-normal vision and spoke French as their first language. Participants were classified as right-handed on the basis of the Edinburgh Handedness Inventory [54]. The mean of the laterality coefficient was 0.72±0.25 (range: 1–0.53). None of the participants reported a history of psychiatric or neurological diseases (e.g. stroke, head injury). Also, none of them were receiving anxiolytic or antidepressant treatment. All subjects gave written consent for the testing procedures. Each subject was remunerated at the rate of Canadian$6.00 per hour.

2.2. Materials

All stimuli were displayed in black on a white screen. Each stimulus was unique. Complete details of the stimuli are available in Blanchet et al. [8]. The verbal stimuli were four- and five-letter nouns drawn from the Brulex database [21]. They were displayed horizontally in Dixon 60-point font. Their lexical frequency varied between 400 and 11 000 occurrences per 100 000 000. Stimulus imageability was evaluated in a preliminary study in which 64 students had to score 664 nouns following the procedure used in Hogenraad and Orianne’s study [39]. For the experimental trials, we used 438 words ranging in imageability between 2.42 and 5.54 (on a 7-point scale). For the training trials, the imageability of the 48 words ranged from 1.88 to 5.96.

The non-verbal stimuli were chosen from a set of 486 complex random shapes (Fig. 1). They were designed to be neither figurative nor verbalizable. Each list was comprised of various shapes that were highly dissimilar and easy to distinguish from one another.

For the encoding condition, for each type of material, there were a total of 160 targets to encode. For the retrieval condition, for each type of material, the number of trial-targets to be recalled was 160, and the number of trial-distractors was 160. Each control condition consisted of 112 trials for each type of material.

2.3. Procedure

The experiment was conducted in a single session lasting approximately 3 h (including electrode application).
The tasks consisted of a long-term memory task and a control task that were crossed with the type of material (random shapes, words). The memory task was a yes/no recognition task with lists of 16 targets to memorize. Testing took place in a dimly lit room. The stimuli were presented on a monitor (19-inch Viewsonic PF790) 80 cm in front of the subject.

2.3.1. Memory tasks

In the study phase, the targets were presented successively in the center of the computer screen. Each target remained on screen for 1000 ms. The consecutive targets were separated by intervals of 2500 ms. The study phase was separated from the recognition phase by a gray screen that lasted 2000 ms.

In the recognition phase, probes corresponding to the target stimuli and mixed with the same number of distractors were displayed successively in the center of the screen. Each item was presented for 500 ms. Subjects were required to respond within a time limit of 2000 ms. The elapsed time between two successive probes was 2500 ms. The screen was blank during the inter-stimulus interval. To avoid the serial position effect, the position of the targets in the recognition phase was pseudo-random. Each list was separated by a black screen that lasted for a duration of 10 s.

For each type of material, memory was evaluated with 10 lists of 16 target items split into two experimental blocks and the blocks were separated by a pause. Prior to the experiment phase, participants were trained on two lists of eight items. Participants were required to re-start the training again if they made too many eye movements or did not understand the rules.

The experimenter instructed subjects to memorize the items (random shapes or words) in order to recognize them later from a set of items. The instructions were given prior to training, and repeated before and during each experimental block. The instructions also appeared prior to each list to elicit task processes. The instructions were presented for 5 s prior to the encoding and retrieval phases. Participants responded by pressing a key indicating whether they had or had not seen the item. Participants were required to respond as quickly and accurately as possible. Half of the participants were instructed to press the right key with the index finger of the right hand for a previously seen item and the left key with the index finger of the left hand for an item not seen previously. The response side was reversed for the remaining participants. To reduce artifacts on EEG recordings, the experimenter emphasized the importance of fixating on the center of the screen and relaxing the facial muscles during all of the stimuli presentations.

2.3.2. Control tasks

In the non-verbal control task, participants were instructed only to look at the random shapes, without memorization instructions. In the verbal control task, they were asked only to read the words in their minds. Items were presented successively in the center of the screen; each one for a duration of 1000 ms. The inter-stimulus interval was 2500 ms, filled by a blank screen. Seven lists of 16 items were used for each type of material. A black screen that lasted 10 s separated the different lists. To ensure that subjects complied with the procedure, the instructions appeared on the screen 5 s prior to the presentation of each list. For each type of material, participants were trained on two lists of eight items.

To avoid the use of verbal strategies for the random shapes, subjects began with the random shapes control task, followed by the memory test for random shapes. This was followed by the verbal control task and the verbal recognition task. At the end of the experiment, participants were debriefed about the strategies that they used during the memory and control tasks.

2.4. Electrophysiological recording

Electroencephalograms (EEG) were recorded from 60 tin electrodes embedded in a commercially available cap (Electrocap International). Recording locations were based on the guidelines for standard electrode position by the American EEG Society [5]. The montage included eight midline electrodes (Afz, Fz, FCz, Cz, CPz, Pz, POz Oz,), and 26 electrodes over each hemisphere (left/right: AF3/AF4, AF7/AF8, FP1/FP2, F1/F2, F3/F4, F5/F6, F7/F8, FC1/FC2, FC3/FC4, FC5/FC6, C1/C2, C3/C4, C5/C6, CP1/CP2, CP3/CP4, CP5/CP6, T7/T8, FT7/FT8, TP7/TP8, P1/P2, P3/P4, P5/P6, P7/P8, PO3/PO4, PO7/PO8, O1/O2). All electrodes were referenced to linked earlobes and their impedance was kept below 5 kΩ. The electro-oculogram (EOG) was recorded using four 9-mm tin external electrodes. For the horizontal EOG, electrodes were placed at the outer canthus of each eye, and for the vertical EOG infra- and supra-orbital to the left eye, in line with the pupil when looking straight ahead. The EOG was corrected for EOG artifacts in the frequency domain with the Woestenburg method (InstEP; TALO B.V.; [87]) and averaged time-locked to the stimulus. The EEG and EOG were amplified through a bio-electric amplifier (SA Instrumentation, San Diego) with a respective gain of 10 000 and 3500. The filter bandpass ranged from 0.02 to 30 Hz.
The electrophysiological signals were filtered at a rate of 250 Hz. Trials containing large artifacts (>600 µV) were rejected on-line. The electrophysiological signals were filtered at a rate of 250 Hz. For short windows, trials with remaining artifacts (e.g. head or body movements; amplifier saturation) were rejected off-line during the averaging procedure (±150 µV at EOG electrodes, and ±100 µV at EEG scalp electrodes) after EOG correction. For short window ERPs, digital filtering was conducted off-line with a bandpass of 0.08 Hz for 3 dB and 0.10 for 12 dB for low frequencies, and 10.00 for 3 dB and 12.00 for 12 dB high frequencies.

2.5. Behavioral data analyses

Different response indices were utilized to assess memory performance and strategies. First, the reaction time for hits was considered. We also took into consideration the hits, false alarms (FA) and response biases. To ensure that the subjects discriminated correctly between the targets and the distractors, we calculated a discrimination rate (Hits−FA) that was required to be above chance level (δ). To evaluate subject’s strategies, an index of response bias was calculated as follows: \( Br = FA / [1−Hit−FA] \). This formula of two level thresholds allows for an independent examination of discrimination and response biases [70].

2.6. Extraction of ERP data

2.6.1. Item-related activity

In the encoding conditions, we averaged the trials related to successfully encoded items, corresponding to items in the study phase that were subsequently identified correctly in the recognition phase. In the retrieval conditions, we averaged the trials of hits, which corresponded to the old items recognized correctly in the recognition phase. In both the shape control and verbal control conditions, all of the trials were averaged. Within an individual participant, the averaging was trial-weighted, that is to say, each participant contributed equally to the grand mean waveforms when combining data across participants. To maintain an acceptable signal/noise ratio, a lower limit of 16 artifact free trials per subject per response category was set. After EEG artifact rejection, the percentage and standard deviation of trials going into the and encoding (e.g. Refs. [14,33,37,43,56,62] ).

To evaluate subject’s strategies, an index of response bias was calculated as follows: \( Br = FA / [1−Hit−FA] \). This formula of two level thresholds allows for an independent examination of discrimination and response biases [70].

2.6.2. Task-related activity

To investigate task-related activity, ERPs were averaged including a 500-ms baseline prior to the stimulus until 9300 ms after stimulus onset. Consistent with Düzel et al. [30,31], we applied the windows from 4000 to 9300 ms post-stimulus. The absolute areas (AA) below and above the curve and the x-axis were pooled after being used in the statistical analyses. The selected electrodes were C1/C2, C3/C4, C5/C6, CP1/CP2, CP3/CP4, CP5/CP6, P1/P2, P3/P4, P5/P6. Due to our interest in the laterality effect, we focused only on lateralized electrodes that were pooled for each hemisphere, condition and type of material for the statistical analyses.

2.7. Statistical analyses

A two-tailed Student’s t-test was used to determine whether the two types of materials differed on each cognitive index. Univariate repeated analyses of variance (ANOVAs) were conducted separately for each ERP component with the Greenhouse–Geisser correction when applicable for violations of the assumption of sphericity. Significant interactions were examined further with post hoc simple effects analyses. The significance level was set at \( P<0.05 \). The data were analyzed using SPSS statistical software (SPSS 10.0 for Windows).
3. Results

3.1. Behavioral results

Performance on both the non-verbal and verbal recognition tasks is shown in Table 1. RTs were slower for random shapes than words, however, this difference was not statistically significant. Accuracy was significantly higher for words than random shapes ($t(11) = -3.24, P = 0.008$) and the false alarm rate was significantly larger for random shapes than for words ($t(11) = 4.06, P = 0.002$). Furthermore, the discrimination rate was higher for words than shapes ($t(11) = -5.43, P = 0.000$). However, the discrimination rate indicated that subjects responded above chance level for words as well as random shapes. Finally, there was no difference across material type on the response bias index.

3.2. Item-related analyses

Figs. 2 and 3 display ERP waveforms at all site recordings in the encoding, retrieval and control conditions for the verbal and non-verbal material respectively. In the following section, the N400 and LPC components are presented separately. In both cases, ANOVAs were performed independently for each type of material (verbal and non-verbal) and for both memory processes (encoding and retrieval) with Condition (Memory condition (encoding or retrieval), Control condition) and Hemisphere (RH, LH) as repeated factors. This design is similar to that used in PET and fRMI studies. Indeed, in the majority of these studies, the design involved the comparison of blood flow obtained in target-task or target-item and a reference-task or reference-item (for reviews see Refs. [9,17]).

3.2.1. N400 component

3.2.1.1. Words, N400 amplitudes (Fig. 4) revealed a Hemisphere effect ($F(1,11) = 9.98, P = 0.009$), reflecting a larger negativity in the LH ($m = -2.33 \pm 1.82 \mu V$) than the RH ($m = -1.19 \pm 1.34 \mu V$) for both the word encoding and control conditions. N400 latencies yielded a main Condition effect ($F(1,11) = 37.31, P = 0.000$) as the encoding condition elicited longer latencies ($m = 461 \pm 37$ ms) than the control condition ($m = 378 \pm 32$ ms). There was also a main effect of Hemisphere ($F(1,11) = 10.01, P = 0.000$), revealing shorter N400 latencies in the LH ($m = 402 \pm 32$ ms) than in the RH ($m = 438 \pm 33$ ms). For word retrieval
(Fig. 4), N400 amplitudes also revealed a Hemisphere effect ($F(1,11)=12.72$, $P=0.004$), with larger amplitudes in the LH ($m=-2.69\pm1.43 \mu V$) than the RH ($m=-0.88\pm1.97 \mu V$). N400 latencies yielded a main Condition effect ($F(1,11)=4.78$, $P=0.05$), with shorter latencies to retrieval ($m=344.04\pm43.75$ ms) than to the control task ($m=378\pm33.29$ ms).

3.2.1.2. Shapes. No significant main effect or interaction was found in shape encoding on the N400 amplitude (Fig. 4). There was a Condition by Hemisphere interaction ($F(1,11)=4.77$, $P=0.05$) on the N400 latencies. This was due to a Hemisphere effect in the encoding condition, ($F(1,11)=8.40$, $P=0.015$) but not the control condition (see Fig. 5). It is notable that the Condition effect was larger in the right than left hemisphere even when it reached significance in both cases ($P=0.001$ and $P=0.028$, respectively). For shape retrieval (Fig. 4), no significant main effects or interactions were found on the N400 amplitude. N400 latencies yielded a main Condition effect ($F(1,11)=9.49$, $P=0.01$), indicating shorter latencies for the retrieval ($m=327.5\pm39.49$ ms) as compared to the control condition ($m=368.71\pm29.68$ ms).

3.2.2. Late positive component (LPC)

3.2.2.1. Words. For word encoding, no significant main effect or interaction was significant on the LPC amplitude. LPC latency yielded a main Condition effect ($F(1,11)=8.71$, $P=0.01$) with longer latencies related to encoding ($m=602.44\pm86.69$ ms) than to the control task ($m=515.8\pm52.86$ ms). LPC amplitudes yielded a main Condition effect ($F(1,11)=16.71$, $P=0.002$) in word retrieval, reflecting greater amplitudes related to retrieval ($m=8\pm4.7 \mu V$) than to the control condition ($m=2.7\pm1.7 \mu V$). LPC latencies did not yield any significant effects or interactions.

3.2.2.2. Shapes. There was a main Condition effect ($F(1,11)=19.64$, $P=0.001$) on the LPC amplitudes in shape encoding, reflecting larger amplitudes for encoding ($m=6.0\pm3.5 \mu V$) than for the control condition ($m=2.4\pm2.3 \mu V$). LPC latencies failed to reach any significant main effects or interactions. In shape retrieval, a main Condition effect ($F(1,11)=30.12$, $P=0.000$) indicated that

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**Table 1**

<table>
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<th>Words</th>
<th>Shapes</th>
<th>t-test</th>
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<td>S.D.</td>
<td>Mean</td>
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<td>7.71</td>
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<tr>
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<td>20.31</td>
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<tr>
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<td>0.44</td>
<td>-0.64</td>
</tr>
<tr>
<td>RT (ms)</td>
<td>736.25</td>
<td>122.98</td>
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</tr>
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</table>

The reaction times correspond to hits. **$P<0.01$; ***$P<0.001$. n.s., not significant.
there were larger LPC amplitudes for retrieval ($m = 8.3\pm 4.1 \mu V$) than for the control condition ($m = 2.4\pm 2.3 \mu V$). On LPC latencies, there was also a main Condition effect ($F(1, 11) = 8.24, P = 0.015$) with shorter latencies for retrieval ($m = 515.6\pm 48.1\text{ ms}$) than for the control condition ($m = 580.9\pm 80.3\text{ ms}$).

3.3. Task-related analyses

ANOVAAs were performed independently for each type of material (verbal and non-verbal) and for both memory processes (encoding and retrieval) with Condition (Memory task, Control task), Hemisphere (RH, LH) and Electrode (2 anterior frontal) as within-subject factors. Fig. 6 shows the sustained activity on the anterior frontal areas for the word and shape encoding conditions and the word and shape retrieval conditions, respectively. This statistical procedure enabled us to compare our data directly to those from functional neuroimaging and electrophysiology experiments.

3.3.1. Words

In word encoding, as well as word retrieval, no significant effects or interactions were found.

3.3.2. Shapes

The sustained activity yielded a main Condition effect ($F(1, 11) = 5.35, P = 0.04$) in shape encoding. It was larger in the encoding than the control condition ($m = 14180.4\pm 5004.63 \ AA$ and $m = 10209.4\pm 5760.2 \ AA$, respectively). The sustained activity indicated a significant Condition by Hemisphere interaction ($F(1,11) = 4.99, P = 0.05$) in retrieval. As illustrated in Fig. 7, RH sustained activity was larger in the retrieval than in the control task, whereas it was roughly equivalent in the LH. Post hoc analyses were not significant.

4. Discussion

Our main goal was to dissociate item-related cerebral activity from task-related cerebral activity in episodic encoding and retrieval processes. This was conducted by manipulating the size of the recording window. We also attempted to dissociate the item- and task-related activities related to memory from those related to the nature of the material. This was achieved using a control task that allowed for the disentangling of memory from non-memory elicited components and by using verbal and non-verbal material. In the following section, we discuss first the item-related activities evidenced by the amplitudes of N400 and LPC components, and by their latencies. We then discuss our findings regarding task-related activities.
4.1. Item-related activity

Our study revealed a left frontal distribution of the N400 amplitudes for verbal material irrespective of task instruction (i.e. encoding, retrieval, as well as control). Thus, the N400 amplitude was sensitive to the verbal nature of the material but not to the instruction. This is consistent with studies reporting N400 effects with similar topography in different verbal tasks such as lexical processing (see Ref. [46] for a review), successful verbal encoding [48] and verbal episodic retrieval ([25,26]; see also Ref. [34] for a review). It is well known that episodic memory is particularly dependent on semantic memory representations [75]. Thus, it is possible that the left frontal N400 amplitude found here reflects item-related activity associated with activations within lexico-semantic memory generated by words. These activations would occur whether or not subjects are instructed to commit those words to memory. Nevertheless, the N400 latencies appear to be sensitive to memory instructions. In contrast, the N400

Fig. 6. Event-related potential waveforms elicited by lists presented during the encoding condition (dotted and bold line), retrieval condition (filled and bold line) and control condition (filled and thin line) for words (left) and shapes (right). The displayed epoch of 9300 ms encompasses four successive items from the lists, starting at 500 ms before the onset of first item and ending 1500 ms after the presentation of the fourth item. AF3 and AF8, left anterior frontal; AF4 and AF8, right anterior frontal.

Fig. 7. Sustained activity for shapes retrieval and control in left hemisphere and right hemisphere.
amplitude can be sensitive to the contextual constraint [19], to the incongruity and to lexical and semantic deviations (see Ref. [46] for a review). This N400 component appears to be distributed primarily in the centro-parietal areas [19]. Furthermore, we can reject the hypothesis that our component was a N200. Indeed, the negative peak appears later than that of the N200 component (i.e. about 420 ms for encoding, about 350 ms for retrieval, and 380 ms for the control) and is localized differently, as the N200 component is distributed in fronto-central areas. In addition, the N200 component occurs in a cognitive context quite different from our negative component, as it appears to be sensitive to the acoustic analysis and phonological processing of spoken words [18,19].

Verbal encoding was not accompanied by an LPC amplitude effect. This finding contrasts with studies that have reported larger LPC amplitudes in successful verbal encoding [32,58,78,81]. However, there are indications that the LPC effect depends largely on the associative nature of the memory task. For example, the subsequent memory effect on LPC has been reported to be smaller for words encoded in a shallow condition than for words encoded in a more elaborate condition [58]. Similarly, Weyerts et al. [81] reported that the LPC was not found for non-associatively studied word pairs but was found for word pairs encoded associatively. In the present study, the lack of an LPC effect in word encoding can be explained by the use of a paradigm in which words were presented in isolation, thus involving relatively few associative processes. In contrast, non-verbal encoding was accompanied by a greater LPC amplitude than the non-verbal control condition. This may be related to efficient associative and/or contextual encoding which could be particularly important for memorizing random shapes, as these are novel stimuli without pre-existing representation in memory. Thus, the difference in the type of material for the encoding-related LPC amplitude appears to be determined by the degree of elaboration yielded by different stimuli.

LPC amplitudes were larger in both verbal and non-verbal retrieval than in their respective control reflecting item-related activity specific to retrieval. This finding is consistent with numerous studies that found a similar effect with verbal [10,40,44,65,68,69,82–84] and non-verbal recognition paradigms [36,79]. This is likely a reflection of ephory, which refers to processes involved in the retrieval of stored information and translates to correct detection.

For both types of materials, latencies were generally sensitive to the memory condition. For verbal material, the N400 and LPC latencies were longer in the encoding than the control condition. The non-verbal encoding condition also elicited longer N400 latencies than the control condition, however, this effect was found only for the right hemisphere. These longer latencies may reflect the presence of additional or more complex processes involved in committing information to memory. The opposite pattern was found for retrieval. The N400 latencies were shorter for retrieving words than in control condition and the N400 and LPC latencies occurred earlier in non-verbal retrieval than in the control condition. Düzel et al. [30,31] also reported shorter latencies on the same components for old than new items in verbal retrieval. This is typically interpreted as reflecting a repetition effect due to the item’s prior presentation, leading to faster subsequent processing.

In summary, the analysis of item-related activities indicates that the amplitude of the N400 is sensitive to the verbal nature of the material but not to the memory condition when using reading as a control task. This suggests that the cognitive processes indexed by this component may not be specific to memory, but instead implicate mechanisms that are homologous to language processing systems. In contrast, the LPC amplitudes were sensitive to the memory comparison of our paradigm, particularly for non-verbal material at encoding and retrieval and for retrieval of verbal material. Our difficulty in finding amplitude components that distinguish memory and language processes, particularly at encoding, is consistent with ‘process views’ of memory which consider storage and processing to reside in the same neural units [2,6,20,22–24,49–51,71]. Our data suggest that encoding and retrieval of complex material may require additional processes, such as executive and attentional processes. It would be interesting to examine this hypothesis by manipulating the attentional demand in encoding and retrieval processes with different types of material.

4.2. Task-related activity

One of our major goals was to extend the hypothesis of task-related activity to encoding and to non-verbal material. We were only partially successful in this endeavor. Our paradigm was unsuccessful in demonstrating task-related activity for verbal material at either encoding or retrieval. This finding is surprising, particularly for retrieval, as Düzel et al. [30] and Donaldson et al. [28] found task-related activity in the right frontal areas for verbal retrieval. The lack of task-related activity in this study may be due to differences in methodology between our study and those mentioned above. For example, in the study by Donaldson et al. [28], subjects had to make semantic associations between pairs of words before proceeding to word-pair recognition. This paradigm may have led subjects to develop more intensive search sets compared to those in the present study, in which subjects were presented with isolated words. This retrieval effort may increase the right anterior PFC activity [42,64,66]. The finding of task-related activity may thus depend largely on the effortful nature of the task. This hypothesis is consistent with our finding for random shapes. Indeed, we found strong task-related activity for the retrieval and encoding of non-verbal material. In particular, sustained activity in the bilateral anterior frontal regions was greater in the encoding than the control condition. The effect was
lateralized in the non-verbal retrieval condition: frontal sustained activity tended to be greater for retrieval than for the control condition in the right hemisphere only. First, non-verbal material, such as random shapes, is likely to solicit effortful retrieval because it does not have a pre-existing representation to support encoding and retrieval. Second, the fact that performance was poorer in the non-verbal than verbal condition suggests that encoding and retrieving random shapes was more difficult and more effortful. Overall, the likelihood of finding task-related activity may be associated with differences in retrieval effort, with verbal material resulting in less retrieval effort than non-verbal material. The retrieval mode has been referred to as the process of ‘thinking back’, which corresponds to auto-noetic effort [29,86]. Thus, our task-related activity may implicate auto-noetic consciousness and may be related to auto-noetic effort.

Our data seem to validate the pertinence of assessing task-related activity. The findings of the present study also extend task-related activities to encoding processes and to non-verbal material. One remaining question relates to the nature of this process and its mechanisms. Prior to discussing this aspect, it is important to note the potential limitations of comparing the two types of material. First, it is difficult to match verbal and non-verbal material on meaningfulness. The majority of verbal material is characterized by its familiarity, notably because of its preknowledge in semantic memory. Use of familiar visuo-spatial material (for example, images of objects) always leads to the risk of subjects using verbal labels. Use of pseudo-words rather than words for verbal materials may have helped circumvent this problem; however, this would have made it more difficult to compare the present study with previous research. Thus, it is important to exercise caution when comparing the two types of material used here. Another potential limit in comparing the different material is that our verbal and non-verbal memory tasks had different overall difficulty levels, since word recognition performance was better than performance on random shape recognition. This difference likely accounts for part of our effects. In particular, visuo-spatial recognition measured in our paradigm probably involves effortful and attentional processes to a larger extent than verbal material.

We hypothesized that task-related activity is linked to the elaborative or effortful nature of the encoding and retrieval processes. These effects were obtained only with visuo-spatial material that may be more difficult to memorize than words. Moreover, the effects may implicate executive processes that are involved in monitoring the task or in initiating processes involved in creating new links within representational systems. These executive functions may be interrelated with episodic memory [86]. As random shapes have no pre-existing representations, auto-noetic awareness may be important for this material to access past random shapes in their spatio-temporal context.

5. Conclusions

Using an ERP paradigm to dissociate task-related effects from item-related activity, our data revealed task-related activity associated with non-verbal material. In contrast, item-related activity was determined by the interaction between properties of the material and task instructions, since the N400 and LPC amplitudes varied according to material and condition. In sum, encoding and retrieval should be conceptualized as the outcome of interacting processes that include task-related strategies, item-related strategies (particularly for retrieval or for material that is difficult to encode), and processes related to the information processing systems at encoding.

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