From Perception to Recognition Memory: Time Course and Lateralization of Neural Substrates of Word and Abstract Picture Processing

Louis Maillard[1,2,3,4], Emmanuel J. Barbeau[5], Cedric Baumann[3],
Laurent Koessler[3,4], Christian Bénar[1,2], Patrick Chauvel[1,2,6],
and Catherine Liégeois-Chauvel[1,2,6]

Abstract

■ Through study of clinical cases with brain lesions as well as neuroimaging studies of cognitive processing of words and pictures, it has been established that material-specific hemispheric specialization exists. It remains however unclear whether such specialization holds true for all processes involved in complex tasks, such as recognition memory. To investigate neural signatures of transition from perception to recognition, according to type of material (words or abstract pictures), high-resolution scalp ERPs were recorded in adult humans engaged either in categorization or in memory recognition tasks within the same experimental setup. Several steps in the process from percep-
tion to recognition were identified. Source localization showed that the early stage of perception processing (N170) takes place in the fusiform gyrus and is lateralized according to the nature of stimuli (left side for words and right side for pictures). Late stages of processing (N400/P600) corresponding to recognition are material independent and involve anterior medial-temporal and ventral prefrontal structures bilaterally. A crucial transitional process between perception (N170) and recognition (N400/P600) is reflected by the N270, an often overlooked component, which occurs in anterior rhinal cortices and shows material-specific hemispheric lateralization. ■

INTRODUCTION

Visual recognition memory is defined as the ability to judge that a stimulus event has been encountered previously. One major dissociation separates the domains of verbal and visuospatial memory. This model, on the basis of the earliest observations of memory deficit after temporal lobe surgery (Milner, 1971), proposed that left and right medial-temporal lobes (MTLs), respectively, mediate verbal and visuospatial memory. Subsequent neuropsychological studies of MTL epilepsy patients supported this view: Left (language-dominant) MTL surgical removal can cause selective impairment of verbal memory (Alpherts et al., 2006; Jones-Gotman et al., 1997), whereas right MTL removal can cause deficits of visual spatial memory (Spiers et al., 2001; Jones-Gotman et al., 1997). However, recent studies (Glikmann-Johnston et al., 2008; Lee, Yip, & Jones-Gotman, 2002) of MTL epilepsy have shown that right MTL epilepsy/surgery do not consistently cause visuospatial memory loss. These results clearly cannot be accounted for by a model in which all components of verbal and spatial memory are lateralized to left and right hemispheres, respectively.

In healthy subjects, fMRI studies comparing nonnameable items and words during the encoding phase (Powell et al., 2005) demonstrated that encoding stimuli (faces and scenes) with an intermediate level of verbalizability resulted in approximately symmetrical activation in MTLs and prefrontal cortices, whereas encoding of abstract, nonnameable patterns and words elicited clearly lateralized activation (left for words and right for abstract patterns). Numerous neuroimaging studies have also shown that this material-dependent asymmetry coexists with "task-dependent" asymmetry. This dissociation has been found to depend upon the different stages of memory processes, regardless of the material, with encoding being found to rely more on the left pFC and retrieval more on the right (for a review, see Habib, Nyberg, & Tulving, 2003). Overall, these results suggest that the effects of material and task may be confounding factors when the issue of hemispheric specialization is being addressed.

The cognitive pathway from visual perception to recognition consists of multiple stages: assembling a representation based on perceptual attributes, relating representation to preexisting lexical (in case of words) and semantic representations, and constructing or reactivating episodic memory traces (Halgren et al., 2006; Poldrack & Gabrieli,

1998). Early parts of this pathway dedicated to object and word identification are found in the ventral visual pathway located in the inferior temporal lobe (Nobre, Allison, & McCarthy, 1994); later stages are dedicated to memory and primarily involve the MTL. The whole process occurs in a narrow time window (within 600 msec) after the onset of stimulus presentation. Electrophysiological methods are therefore particularly appropriate to study the temporal dynamic of this multiple stage process.

Scalp ERPs have been extensively used in recognition memory studies (for a review, see Rugg & Curran, 2007). The most common paradigm is a continuous recognition task. This consists of random presentation of items (words/pictures) within the subject's visual field, within a single session, comprising target items (presented twice) and distracters (presented once). In this paradigm, encoding and recognition processes are not clearly dissociated: Once the stimulus is seen, an initial process of "checking" occurs to establish whether it has been previously presented, and if not, the item must be immediately encoded for possible future recognition. Other paradigms rely on dissociating the recognition phase from the previous learning phase, allowing characterization of the so-called "old/new" effect. In the encoding phase, subjects are exposed to a series of items that they must learn. After some delay, subjects are asked to recognize these "old" items randomly intermixed with new items. Such paradigms, in discriminating between encoding and retrieval phases, can allow better understanding of the relations between these processes. In general, correct responses to old, previously viewed items ("hits") elicit more positive-going ERPs than correctly rejected new items. A frontal old/new effect (300–500 msec) referred to as the "N400" or "FN400" has been shown to index familiarity (Rugg & Curran, 2007; Woodruff, Hayama, & Rugg, 2006). A somewhat later (400–800 msec) component, also termed the *late positive component* (LPC), maximal over (left) parietal electrodes, is thought to index recollection (e.g., Ally & Budson, 2007; Woodruff et al., 2006; Friedman & Johnson, 2000; Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997). The latter effect is greater for items correctly identified as having been previously encountered and is relatively insensitive to modulations of familiarity (Woodruff et al., 2006; for a review, see Rugg & Curran, 2007).

Intracerebral data obtained from presurgical temporal lobe epilepsy patients have provided direct evidence of the contribution of MTL structures to different memory potentials. Using visual recognition memory paradigms, the constant main components recorded from the MTL across studies and patients are N2-like (200–300 msec): N400-like and P600 (Allison, Puce, Spencer, & McCarthy, 1999; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994; Puce, Andrewes, Berkovic, & Bladin, 1991; Smith, Stapleton, & Halgren, 1986). The N2-like component has been shown to be insensitive to mnesic manipulation and could reflect high-order visual processing driven by the perirhinal cortex (Barbeau et al., 2008; Halgren et al., 2006). Within the anterior MTL structures, the N400 (AMTL-N400) is also modulated according to repetition during recognition (Elger et al., 1997; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994). Within the hippocampus, a large positive potential peaking between 300 and 600 msec (hippocampal P600) has been shown to be especially activated in conscious recognition tasks (Grunwald et al., 2003).

The comparison of word and picture recognition has been addressed in several scalp ERP studies (Ally & Budson, 2007; Van Petten & Senkfor, 1996). Ally and Budson (2007) showed that pictures elicited a greater parietal P600 during study and test conditions, whereas words elicited a greater frontal N400. They suggested that words had a greater ability to elicit familiarity whereas images had a greater ability to elicit recollection. Neither study showed any hemispheric asymmetry. However, like most previous scalp ERP studies of recognition memory, these works concentrated on the late semantic and episodic components and did not investigate the earlier time course of material specialization, especially during the transition from high-level visual perception to recognition memory *per se* (that probably occurs during the N2-like component). Recent ERP studies investigated the hemispheric specialization during verbal encoding and during verbal recognition (Evans & Federmeier, 2007, 2009), comparing left and right hemifield presentation of words. They showed that the old/new effect for words was influenced by the side of hemifield presentation during encoding but not during recognition.

Other electrophysiological studies (Rossion, Joyce, Cottrell, & Tarr, 2003; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999) have concentrated on the stages involved in perception of printed words: these showed an early perceptive material specialization consistent with a left (dominant) hemisphere advantage for words and a right hemisphere advantage for pictures. A left posterior temporal (LPT) negative peak around 180 msec has been identified in response to prelexical visual analysis of printed words (Rossion et al., 2003; Cohen et al., 2000). Dipole source localizations and intracranial recordings (Allison et al., 1999) localized the generator of this component within the left fusiform gyrus. This region has been referred to as the visual word form area (Cohen et al., 2000). Visual presentation of faces also evoked a scalp N170 over temporal-parietal electrodes. Using source models, this N170 was localized within the right fusiform gyrus (Rossion et al., 2003).

Following this perceptive component, language-related tasks have evoked a negative peak between 200 and 350 msec, with highest amplitude in temporal or temporo-parietal electrodes. This could reflect an early lexical access (Marinkovic et al., 2003; Bentin et al., 1999; Paller & Gross, 1998). Similarly, face and image processing have evoked a negative peak between 200 and 300 msec, which could reflect structural information processing (Federmeier & Kutas, 2002;

McPherson & Holcomb, 1999). Source localization data have pointed toward the left inferior temporal region for words (Marinkovic et al., 2003) and to bilateral occipito-temporal regions for faces (Schweinberger, Huddy, & Burton, 2004). However, this potential is not usually individualized during scalp ERP studies of recognition memory, being rather included in the classical FN400 old/new effect.

In summary, electrophysiological studies focusing on perceptual stages of word/picture visual identification have suggested an early material-specific hemispheric specialization. Studies focusing on late semantic and mnemonic stages of word/picture recognition have not displayed a clear material specialization. The transition between perceptual and cognitive stages remains to be investigated.

We therefore compared in the same experimental setting the whole sequence of word and abstract image recognition using scalp ERP. To avoid the possible confounding effect of task (encoding vs. recognition effect) on hemispheric specialization, we implemented an experimental design that dissociated the recognition (test) from the encoding phase (study). As control tasks, we used identification of color and gender categorization (thus reflecting pure structural or semantic encoding) to identify and to dissociate the processes that were common to, from those that were specific for, mnemonic processes.

Our primary goal was to assess which stages, during the transition from perception to recognition, are material specific (words vs. pictures). Our secondary goal was to investigate the relation between perception and memory processing addressing the following questions: At which neural level are they distinct? Is there a distinct material specificity at the stages of perception and recognition? As suggested by Evans and Federmeier (2009), the a priori working hypothesis of this experiment was that the earlier perceptive stages, which are more focal, would be specific to the type of material (verbal vs. nonverbal) and the later recognition stages, being related to widely distributed memory processes, would be independent of the material presented.

METHODS

Subjects

ERPs were recorded in 16 right-handed healthy volunteers (mean age = 29 years, 7 women). Informed consent was obtained in accordance with the University Hospital of Marseille institutional review board guidelines. Two subjects were excluded a posteriori: one because of vigilance fluctuation throughout the procedure and the other because of significant EEG artifacts.

Experimental Procedure

The stimuli consisted of 180 frequent concrete French words and 180 color and black and white abstract figures, divided into 60 targets and 120 distracters. This procedure was divided in four blocks of verbal memory paradigm and four blocks of visual memory paradigm (15 targets and 30 distracters per block). The order of verbal and visual blocks was counterbalanced across participants. The design of each block was identical for verbal and visual material (Figure 1) and divided into three phases: a learning phase (encoding phase of 1 minute), an interfering phase (2 minutes), and a recognition phase (3 minutes). Abstract figures were not nameable and were overall difficult to verbalize simply (examples in Figure 1 and available at www.cerco.ups-tlse.fr). Although it may of course have been possible up to a point to verbalize certain images, according to subjects' debriefing this did not appear to be a useful strategy, given that the figures were presented in rapid succession during encoding and recognition phases.

Stimulus presentation was carried out using E-Prime v1.1 software (Psychology Software Tools, Pittsburgh, PA).
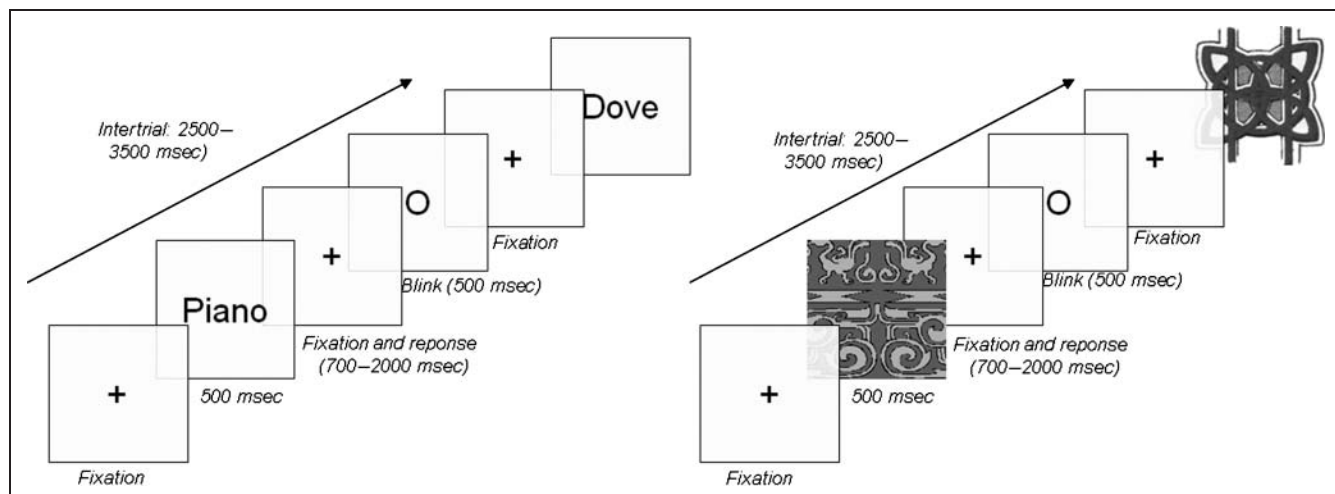

Figure 1. Scheme of the intertrial interval (2500–3500 msec) during recognition tasks of words and pictures. It comprised the following sequence: fixation point, stimulus presentation, fixation point during which the subjects are asked to respond, blinking cue, and fixation point.

Participants were seated in an electrically shielded and sound- and light-attenuated Faraday cage, facing a display monitor (70 cm in front of the subject). Stimuli were presented on the center of the screen with an angular size of about $6° \times 6°$ for pictures and $6° \times 2°$ for words in random order. Intertrial interval comprised the following sequence: fixation point, stimulus presentation (500 msec), fixation point during which the subjects were asked to perform the task, blinking cue, and fixation point again. Intertrial interval ranged between 2500 and 3500 msec depending on the participant's RT when a response was required (Figure 1). During the learning phase, participants were explicitly instructed to memorize the 15 presented stimuli. During the following interfering phase, participants were required to categorize 30 stimuli (color judgment for figures and gender judgment for word) with a two-key pad. Finally, in the recognition phase, subjects were required to recognize the 15 target items among 30 distracters. Participants responded with a two-key pad as to whether the stimuli had been presented previously or not. At the beginning of each phase, participants were reminded of the instructions.

An important feature of this design is that the same kind of stimuli was seen in the interfering task that was therefore used as a control for comparisons with recognition memory tasks. However, all stimuli were trial-unique, except when repeated during the recognition phase.

After a short training session, subjects automatically blinked during the fixation interval, outside the period of signal analysis. Remaining periods with eye movement were further rejected after appropriate analysis.

EEG Recording and Data Processing

EEG was recorded using Neuroscan (El Paso, TX) Synamps DC amplifiers from 64 Ag/AgCl scalp electrodes at standard locations (10–10 system, QuickCap; Compumedics Neuroscan) and referenced to the right mastoid (bandwidth = 0.15–200 Hz, sampling rate = 1000 Hz). Scalp electrode impedances were kept below 5 kΩ. Acquired data were analyzed using Neuroscan Edit software, and off-line processing of EEG data was performed with BrainVision Analyzer® software (Brain Products GmbH, Munich, Germany). Continuous EEG data were filtered digitally (0.15–40 Hz and a roll of 12 and 24 dB/octave, respectively) and rereferenced to an average reference. Epochs were created beginning 150 msec before stimulus onset and lasting until 1350 msec poststimulus. Epochs containing artifacts with a base to peak amplitude exceeding 100 μV on any channel were excluded. The average rejection rate was 10%. ERPs were averaged separately for each block across the four conditions (successful encoding, target recognition, distracter rejection, and categorization) and then grand averaged through the entire session (four blocks).

The early perceptual components were identified visually for both words and pictures: a positive peak around 100 msec (P1) and a negative peak around 160 msec (N1).

They were followed by two bilateral fronto-central and temporal low amplitude negative components peaking around 270 and 400 msec, respectively, and by a bilateral widespread slow and LPC peaking between 500 and 700 msec (corresponding to the P600 or LPC).

Statistical Analysis

To study the time course and spatial localization of material specialization during recognition memory, t statistic mapping provided by BrainAnalyzer® was used on the grand average of the 14 subjects. For each task involved in recognition memory (target recognition and distracter rejection), the effect of material across time was studied by comparing the verbal to the nonverbal condition. A two-tailed paired t test was used with a significant threshold set at 0.05 ($t > 2.145$).

Visual analyses and whole scalp t statistics maps allowed identification of eight sites for further statistical analyses. The analyzed sites were chosen according to previous studies (Ally & Budson, 2007; Rossion et al., 2003; Curran, Tanaka, & Weiskopf, 2002;) and also to cover the peak of each component and to allow comparisons across tasks in the particular setting of our experiment: left and right fronto-central (LFC and RFC, respectively) region, left and right parietal (LP and RP, respectively), left and right anterior temporal (LAT and RAT, respectively), and left and right posterior temporal (LPT and RPT, respectively). The precise time course of the comparison and of the t statistics was then studied in these eight sites. In each site, EEG signals resulted from the averaging of the relevant groups of electrodes: FC1, FC3 for the LFC site; FC2, FC4 for the RFC site; CP3, P3 for the LP site; CP4, P4 the RP site; FT7, FT9 for the LAT basal site; FT8, FT10 for the RAT basal site; TP7, P9 for the LPT basal site; and TP8, P10 for the RPT basal site.

In the sites where a significant material-related effect was observed, we wanted to determine whether this was associated with an effect of the tasks and their potential interactions. Multiway ANOVA was therefore carried out within the specific time window of each potential comprising the factors of "task" (four modalities: encoding, target recognition, distracter rejection, and categorization) and "material" (two modalities: verbal/nonverbal). The amplitude, treated as the dependent continuous variable, was calculated as the average amplitude within the relevant time window of each potential: 130–210 msec for N170, 230–350 msec for N270, 350–470 msec for N400, and 470–810 msec for P600. These time windows were chosen to cover the temporal distribution of each component across task and material.

When the factor task was significant, pairwise comparisons were performed between the relevant tasks. The effect of repetition ("old/new" effect) was defined by a comparison of successful target recognition (hits) to successful distracter rejection (first presentation). The level of type I error used to determine statistical significance was 5%, with

a Bonferroni correction for multiple comparisons. Interaction between the task and the material was considered in the multivariate analysis when both factors were significant simultaneously. Statistical analysis was performed with SAS v9.1 software (SAS Institute Inc., NC, 1997).

Source Localization

Material specialization and time-specific localization of the different processing stages during recognition memory were also investigated using source localization techniques. MUSIC and equivalent dipole models were applied to the grand average N170 and N270 evoked by word and abstract image recognition. The MUSIC scan method (Mosher, Lewis, & Leahy, 1992) was used first. The MUSIC scan at each point within the brain results in a score of plausibility that this point contains a dipolar source (i.e., a point source); it is therefore better adapted to signals consisting of a few spatially restricted sources. Implementation of MUSIC in ASA® software (ANT, Enschede, Netherlands) was used with one to two components of signal subspace to explain more than 95% of the signal power. MUSIC identified either lateralized deep basal occipito-temporal and temporal sources or medio-basal interhemispheric sources, most probably reflecting bilateral basal temporal sources. On the basis of previous intracerebral studies (Barbeau et al., 2008; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994), we hypothesized that sources of N170 and N270 could result from bilateral coherent sources which could lead to a spurious maximum of the MUSIC scan in the middle of the real sources (especially for pictures). We therefore studied the time course of bilateral rotating dipoles throughout the epoch (Figures 4 and 5 display this time course within 500 msec after stimulus onset): The first dipole was set at the coordinates of the first intracerebral peak explaining 95% of the signal variance given by MUSIC and the second was set at the contralateral and symmetrical coordinates. When the coordinates given by MUSIC were localized in the interhemispheric space (cases of pictures tasks), we successively tested bilateral and symmetrical dipoles along the transverse axis to obtain the best goodness of fit while keeping constant the coordinates given by MUSIC along the posteroanterior and inferosuperior axis. Finally, we analyzed the latency and the amplitude of the peaks (nAmp) of the modeled sources when the goodness of fit was superior to 95% (Table 2). These methods were not applied to the N400 and P600, which have widely distributed generators that are not well represented by point-like dipoles. For N400 and P600, standardized low-resolution electromagnetic tomography (SLORETA) was used, which is more appropriate to multiple distributed generators (Pascual-Marqui, Michel, & Lehmann, 1994). SLORETA is a distributed sources technique, which means that it attempts to estimate the amplitude of a large number of sources distributed uniformly within the cortex all at the same time. Only sources that were stable across the interval of analysis were considered significant. The freeware version of SLORETA was used (available at http://www.unizh.ch/keyinst/NewLORETA/LORETA01.htm).

RESULTS

Behavior

In the word condition, the average hit rate of 83% resulted in an average hit bin of 50; the average correct rejection rate of 90% resulted in an average correct rejection bin of 108. In the picture condition, the average hit rate of 79% resulted in an average hit bin of 47; the average correct rejection rate of 86% resulted in an average correct rejection bin of 103. Response bias was low and comparable for pictures and words (0.4 vs. 0.37, respectively). There was no statistically significant difference between the rate of hits and the rate of correct rejections for words (83% vs. 90%; Student t test, $p = .24$) and for pictures (79% vs. 86%; Student t test, $p = .18$).

Accuracy between words and pictures recognition was not statistically different (73.1% for words and 65% for pictures; Student t test, $p = .28$). RTs were similar for words (1015 ± 183 msec) and pictures (1018 ± 229 msec) recognition. There was no statistically significant difference between word and picture errors ($p = .40$ for false alarms, $p = .76$ for misses). False alarms and misses were excluded from further ERP analysis. Due to the low number of error trials across conditions, ERPs of correct and missed stimuli were not compared.

Event-related Potentials

The grand average ERPs for all hits and correctly rejected distracter words and pictures are shown in Figures 2 and 3, respectively. Both words and pictures elicited early perceptual components: a positive peak around 100 msec (P1) and a negative peak around 170 msec (N1) over bilateral occipito-temporal electrodes (01, 02, 0z, P9, and P10). These early components were followed by two overlapping but distinct bilateral fronto-central and temporal low amplitude negative components peaking around 270 and 400 msec, respectively. A bilateral widespread slow and LPC was observed between 500 and 800 msec (corresponding to the P600). This projected over bilateral fronto-central and temporal electrodes for words and pictures.

Time Course of Word and Abstract Picture Processing during Recognition Memory Tasks

Comparison of the time course and topographies of scalp ERPs elicited by words (dotted line) and abstract pictures (continuous line) recognition on the eight sites of interest (Figures 2 and 3) showed significant differences between 140 and 185 msec (N170) and between 230 and 330 msec (N270). These were lateralized according to the material, with a left hemisphere advantage for words and a right
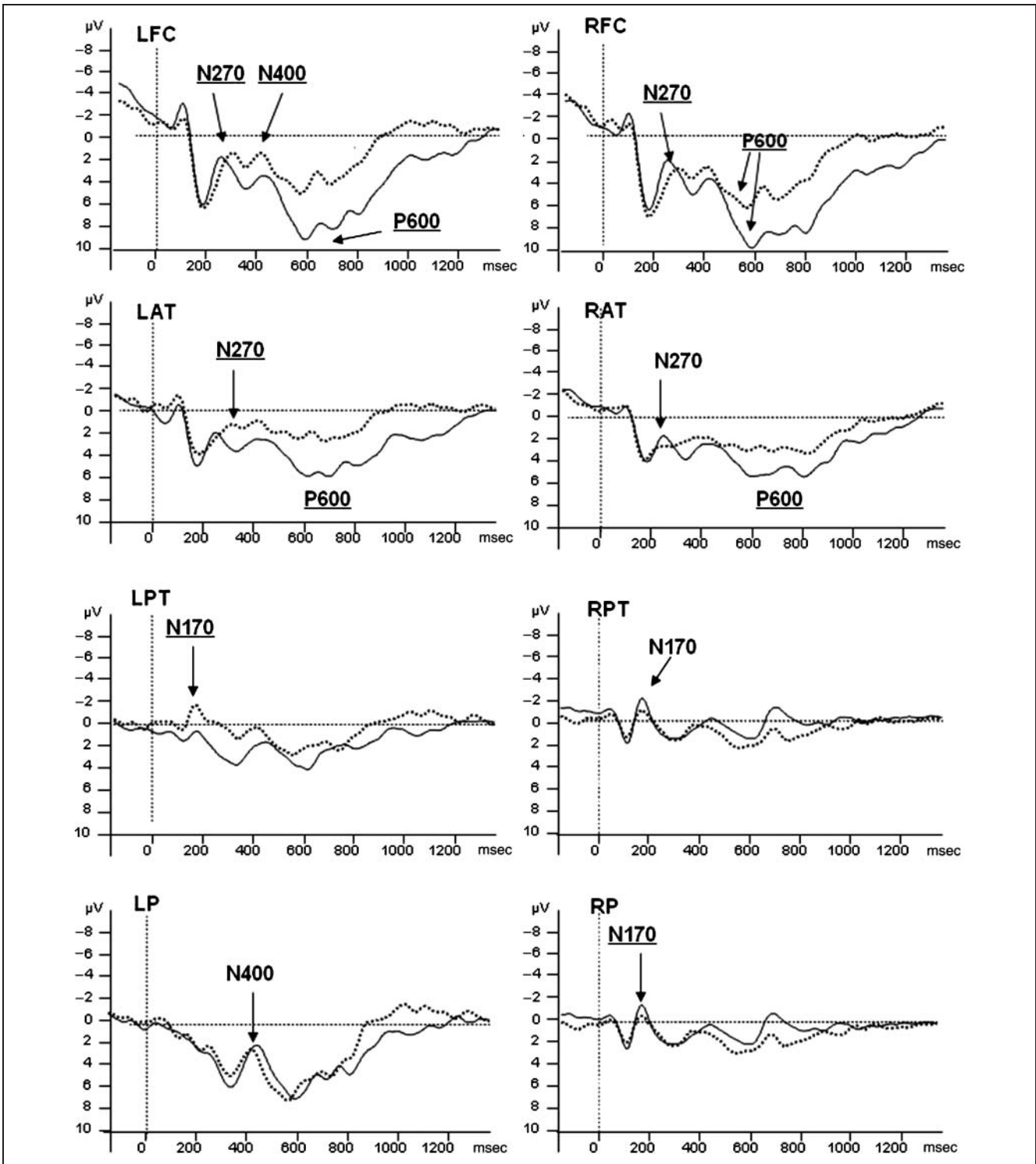
Figure 2. Comparison of successful target recognition (hits) for words and abstract pictures. Overlay plots of the grand average ERPs of hits for words (dotted line) and pictures (continuous line) on the eight analysis sites. Components with statistical difference are underlined. Both conditions elicited the expected early perceptual components. At posterior electrodes, these included a positive peak maximal around 100 msec (P1) and a negative peak maximal around 170 msec (N1). These early components were followed by bilateral fronto-central and anterior temporal negative waves peaking around 270 and 400 msec, respectively. A bilateral widespread fronto-central, parietal, and anterior temporal slow and late positive potential was observed between 500 and 700 msec corresponding to the P600 (or late positive component [LPC]).
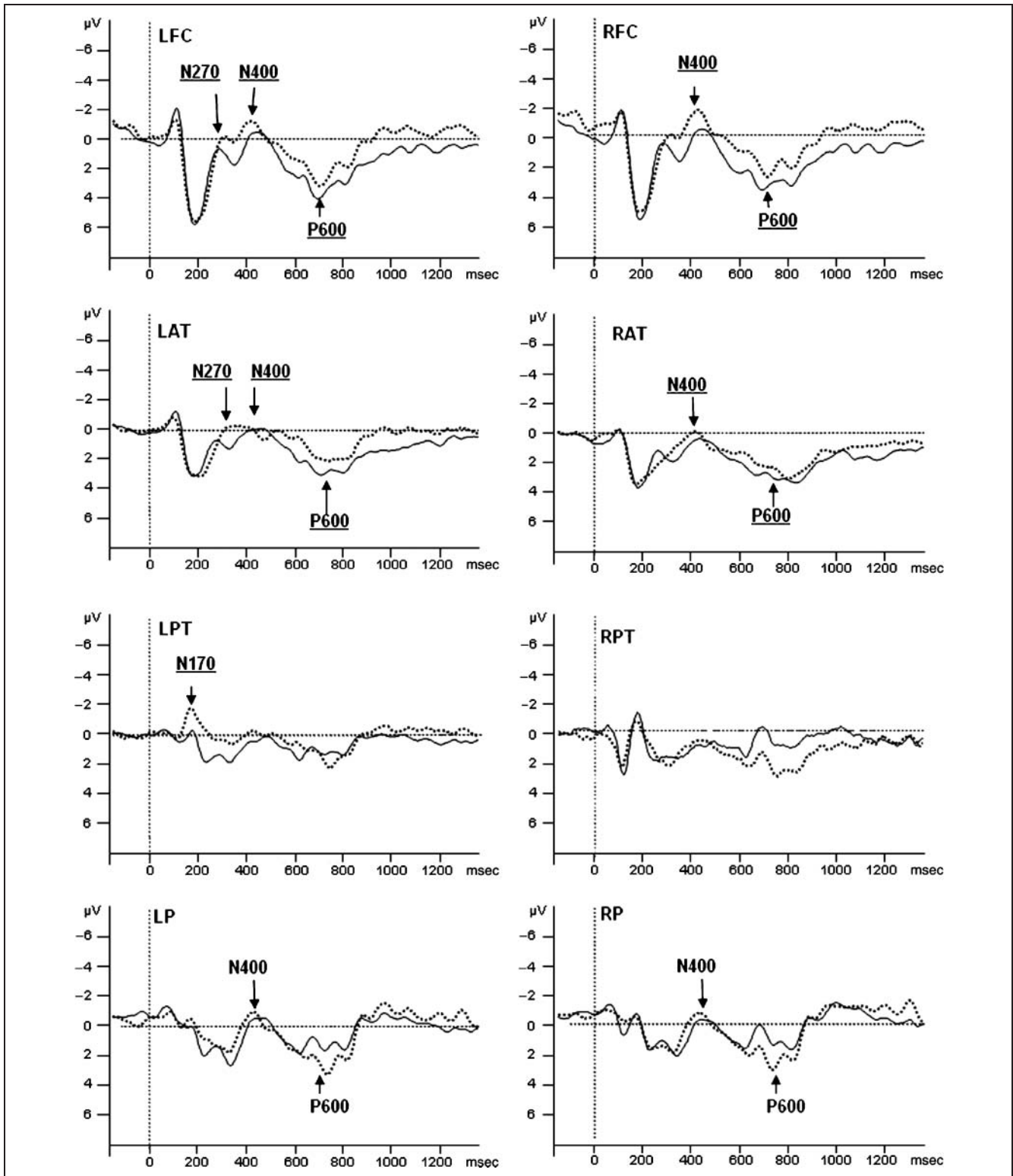
Figure 3. Comparison of word and abstract picture distracter rejection. Overlay plots of the grand average ERPs of correctly rejected words (dotted line) and correctly rejected images (continuous line) on the eight analysis sites. Components with statistical difference are underlined. Both conditions elicited the expected early perceptual components. At posterior electrodes, these included a positive peak maximal around 100 msec (P1) and a negative peak maximal around 170 msec (N1). These early components were followed by bilateral fronto-central and anterior temporal negative waves peaking at 270 and 400 msec, respectively. A bilateral widespread fronto-central, parietal, and anterior temporal slow and late positive potential was observed between 500 and 700 msec corresponding to the P600 (or late positive component [LPC]).

hemisphere advantage for pictures. Following N270, significant differences were observed for N400 and P600: Words evoked greater N400 whereas pictures evoked greater P600 in both hemispheres.

N170

Both words and pictures elicited a negative wave peaking around 170 msec with maximal amplitude in the bilateral temporal posterior sites. Words evoked greater N170 than pictures in the LPT site only, between 145 and 165 msec after stimulus presentation during hits and between 140 and 185 msec during distracter rejection. Abstract pictures evoked greater N170 than words in the RP site for hits only, from 150 to 184 msec after item presentation.

N270

Following N170, a second negative peak was identified between 230 and 350 msec in both conditions. Its scalp topography was less focal than that of N170. It projected onto the fronto-central and anterior temporal sites. It was elicited bilaterally by both words and abstract picture processing (Figures 2 and 3).

Within the time window of N270, t statistics showed significantly greater amplitude in the LAT, LPT, and LFC sites for words compared with pictures during target recognition and also distracter rejection (Figures 2 and 3). In the LPT site, this effect was observed earlier (230–330 msec) than that in the LAT and fronto-central sites (starting at ~280 msec and lasting until ~330 msec).

The N270 elicited by abstract pictures was more pronounced in the RFC site for hits but not for distracter rejection.

N400

N400 immediately followed the N270 described above. It had a wide bilateral scalp distribution, predominating in the bilateral fronto-central and temporal electrodes but extending to the parietal sites without polarity reversal.

Overall, N400 evoked by words had greater amplitude than N400 evoked by abstract pictures (Figures 2 and 3). In the target recognition condition, this difference was statistically significant in the LFC site from ~360 to 430 msec. In the distracter rejection condition, this difference was more widespread and was statistically significant in the bilateral anterior temporal sites (from ~350 to 390 msec) and in the bilateral fronto-central sites (from ~350 to 440 msec).

P600

Following N400, a late and slow positive potential known as the P600 (or LPC) was identified, peaking between ~560 and ~590 msec in target recognition and between ~660 and ~700 msec in distracter rejection (Table 1). In both verbal and nonverbal conditions, it was widely distributed over the bilateral fronto-parietal and temporal sites, without clear polarity reversal (Figures 2 and 3).

Abstract pictures elicited greater P600 than words in bilateral fronto-central and anterior temporal sites during both target recognition and distracter rejection (Figures 2 and 3). This effect started roughly between 500 and 600 msec after stimulus presentation and lasted at the most until ~1330 msec.

Table 1 summarizes the amplitudes and latencies of each component plotted on the representative electrodes of the eight sites as well as the time interval significance between word and abstract picture processing ($t > 2.145$ or $t < -2.145$ for two-tailed paired tests; "words > pictures" means potential of greater amplitude for words than for pictures and vice versa). One of the characteristics of the N170 and N270 components is their lateralization to electrodes in the left sites (LPT, LAT, LPT, and LFC) of the scalp for word recognition (hits and distracter rejection) and to electrodes in right sites (RP and RFC) only for the hits of abstract pictures. The hemispheric lateralization according to the material is not clear for the latest components. The next step was to explore the time-specific localization of these components (N170, N270, N400, and P600) using source localization.

Source Localization of Abstract Picture and Word Encoding and Recognition Processing

Figure 4 shows the localization and time course of the modeled sources. For the N170, they were localized to occipito-temporal medial junction (presumably the fusiform gyrus). For the N270, they were localized to anterior parahippocampal structures (presumably the rhinal cortex) for the N270 during successful encoding, hits, and distracter rejection. Table 2 summarizes latency and amplitude of the peak of magnitude of the sources calculated on the time interval characterized by a goodness of fit superior to 95%.

N170 and N270

For words, MUSIC consistently localized the sources of the N170 to the left medial occipito-temporal junction (presumably the left fusiform gyrus) and to more anterior left MTL region for the N270. For pictures, MUSIC consistently localized the sources of the N170 and N270 in the interhemispheric medio-basal space (along the medial occipito-temporal structures). Source localization and time course of the bilateral modeled sources allowed separation of the N170 linked dipolar activity predominating in the fusiform gyrus from the N270 linked dipolar activity predominating in the rhinal cortices. Time course of the dipoles also showed asymmetric visual processing of abstract pictures predominating in the right rhinal cortex

at the stage of the N270 and asymmetry of word processing with a left predominance for the N170 and N270 (Table 2; Figure 4).

N400 and P600

As mentioned in the Methods section, MUSIC and dipole models were not appropriate to localize the widely distributed generators of N400 and P600 and were therefore not applied to these waves. SLORETA was used instead, which showed several active regions predominating in bilateral basal temporal and basal frontal sites regardless of the tasks and the material for both potentials (not shown).

In summary, the N170 sources were spatially restricted and consistently localized in medial occipito-temporal junction (presumably the fusiform gyrus), whereas the N270 sources were consistently localized more anteriorly in the medial-temporal structures. Despite bilateral scalp projections, source localizations of N170 and N270 were consistent with early material-specific hemispheric asymmetry: left for words and right for abstract pictures. Sources of N400 and P600 were widely distributed and localized in the bilateral ventro-frontal and anterior basal temporal regions regardless of the task and of the material. Finally, it was important to determine whether this material effect was related to the task (recognition vs. encoding, vs. categorization).

Relationship between Material and Task Effects

The overlay of grand average waveforms for words (Figure 5) and abstract picture processing (Figure 6) as a function of task encoding (continuous black line), hits (dotted line), distracter rejection (large dotted line), and categorization (continuous gray line) at the eight sites of analyses shows an effect of task because no P600 was recorded for categorization of words and abstract pictures. Moreover, and in contrast to gender decision, the categorization of pictures did not elicit an N400.

To test the effect of task across the eight sites, taking into account the effect of material for each main component, we conducted multiway analyses of variance with the factor of material (two modalities) and the factor of task (four modalities).

N170

Multiway ANOVA did not show any task effect, $F(3, 39) = 0.89, p = .45$ (Figures 5 and 6), and confirmed an independent material effect in both the left temporal posterior site, $F(1, 39) = 55.5, p < .0001$, and the right temporal posterior site, $F(1, 39) = 23.95, p < .0001$, with a left advantage for words and right advantage for abstract pictures.

N270

In the LPT and LFC sites, the analysis did not show any significant effect of the task, $F(3, 39) = 0.49$ in LPT, $F(3, 39) = 0.84, p = .473$ in LFC. It confirmed a significant and independent material effect, $F(1, 39) = 23.06, p < .0001$ in LPT, and a tendency toward a greater amplitude for words in LFC, $F(1, 39) = 3.07, p = .08$ in LFC.

In the RFC site, the analyses did not show any significant effect of the task either and confirmed a greater activation elicited by pictures, $F(1, 39) = 4.36, p = .039$.

N400

In right and left frontal sites, the analyses, taking into account the material effect, showed an independent effect of the task in the bilateral fronto-central sites, $F(3, 39) = 5.89, p = .001$ in the LFC, $F(3, 39) = 9.33, p < .0001$ in the RFC. Correct rejection elicited greater N400 than hits, consistent with the classical FN400 effect (old/new effect: $t = 3.16, p = .0021$ in RFC; $t = 3.04, p = .0031$ in LFC). These effects were not found in any other sites. It also showed a material effect independent of the task, $F(1, 39) = 6.32, p = .0136$ in the LFC, $F(1, 39) = 8.38, p = .0047$ in the RFC: Words processing evoked a greater N400 than abstract pictures processing, regardless of the task.

Finally, a further post hoc analysis (Student t test) was conducted to compare word and abstract picture categorization because visual analysis strongly suggested a lack of N400 in the color categorization task. This showed a significant greater amplitude for words in bilateral fronto-central sites ($t = 2.54, p < .05$ in LFC; $t = 2.45, p < .05$ in RFC) and in right parietal site ($t = 4.29, p < .001$ in RP).

P600

In bilateral fronto-central sites, there was an independent effect of the tasks, $F(3, 39) = 11.14, p < .0001$ in RFC, $F(3, 39) = 11.4, p < .0001$ in LFC. Hits elicited greater P600 than distracter rejection ($t = 2.59, p = .011$ in RFC; $t = 2.32, p = .0225$ in LFC) consistent with the late old/new effect. Distracter rejection elicited greater positive deflection than categorization in the time window of P600 ($t = 3.16, p = .0021$ in RFC; $t = 3.44, p = .0009$ in LFC) with both words and abstract pictures. It also confirmed a material effect independent of the task in the bilateral fronto-central sites, $F(1, 39) = 5.47, p = .0215$ in RFC, $F(1, 39) = 6.1, p = .0154$ in LFC, showing that abstract picture recognition elicited greater P600 than word recognition.

In both the anterior temporal sites, there was no significant task effect. There was an independent material effect, $F(1, 39) = 8.01, p = .0057$ in RAT, $F(1.39) = 19.58, p < .0001$ in LAT, with a greater P600 evoked by abstract pictures than words.

In parietal sites, there was an independent effect of the task, $F(3, 39) = 10.1, p < .0001$ in RP, $F(3, 39) = 10.4,$

Table 1. Shows for Each Potential during Hits and Correct Distracter Rejection the Site Where the Material Effect Was Significant (Evidenced by *t* Statistics), the Latency and Amplitude of the Peak, and the Nature and Time Range of the Effect

Time	Regions		Target Recognition	Distracter Rejection
N170	LPT	Latency and amplitude of the peak	W: −2.1 μV, 170 msec	W: −2.2 μV, 168 msec
			Im: −0.4 μV, 178 msec	Im: −0.6 μV, 175 msec
		Effect	Words > images	Words > images
		Interval of effect	145–165	140–185
	RP	Latency and amplitude of the peak	W: 0.2 μV, 162 msec	W: −0.6 μV, 169 msec
			Im: −1.2 μV, 168 msec	Im: −0.9 μV, 172 msec
		Effect	Images > words	No
		Interval of effect	150–184	–
N270	LPT	Latency and amplitude of the peak	No peak	No peak
		Effect	Words > images	Words > images
		Interval of effect	230–330	230–260
	LAT	Latency and amplitude of the peak	W: −3.6 μV, 306 msec	W: −3.5 μV, 314 msec
			Im: −3.1 μV, 246 msec	Im: −2.6 μV, 270 msec
		Effect	Words > images	Words > images
		Interval of effect	305–321	280–350
	RAT	Latency and amplitude of the peak	W: −1.3 μV, 250 msec	W: No peak
			Im: −2.4 μV, 246 msec	Im: −2.8 μV, 254 msec
		Effect	No	No
		Interval of effect	–	–
	LFC	Latency and amplitude of the peak	W: −5.0 μV, 292 msec	W: −6.1 μV, 306 msec
			Im: −3.9 μV, 251 msec	Im: −5.25 μV, 273 msec
		Effect	Words > images	Words > images
		Interval of effect	305–335	290–350
	RFC	Latency and amplitude of the peak	W: 4.5 μV, 295 msec	W: −5.5 μV, 350 msec
			Im: 5.2 μV, 254 msec	Im: −5.5 μV, 410 msec
		Effect	Images > words	No
		Interval of effect	230–280	–
N400	LAT	Latency and amplitude of the peak	W: −3.1 μV, 415 msec	W: −3.6 μV, msec
			Im: −3 μV, 410 msec	Im: −2.3 μV, msec
		Effect	No	Words > images
		Interval of effect	–	350–380
	LFC	Latency and amplitude of the peak	W: −4.95 μV, 415 msec	W: −6.5 μV, 420 msec
			Im: −4.3 μV, 417 msec	Im: −5.8 μV, 415 msec
		Effect	Words > images	Words > images
		Interval of effect	367–430	350–440
	RFC	Latency and amplitude of the peak	W: −4.6 μV, 406 msec	W: −7.0 μV, 427 msec
			Im: −4.6 μV, 410 msec	Im: −5.8 μV, 413 msec
		Effect	No	Words > images
		Interval of effect	–	325–445

Table 1. (*continued*)

Time	Regions		Target Recognition	Distracter Rejection
	RAT	Latency and amplitude of the peak	W: −2.1 μV, 402 msec	W: −3.5 μV, 420 msec
			Im: −1.7 μV, 415 msec:	Im: −3.1 μV, 420 msec
		Effect	No	Words > images
		Interval of effect	–	325–395
P600	LAT	Latency and amplitude of the peak	W: 3.9 μV, 560 msec	W: 2.3 μV, 681 msec
			Im: 7.3 μV, 595 msec	Im: 3.6 μV, 696 msec
		Effect	Images > words	Images > words
		Interval of effect	570–1190	499–1183
	LFC	Latency and amplitude of the peak	W: 5.1 μV, 572 msec	W: 4.1 μV, 692 msec
			Im: 9.6 μV, 585 msec	Im: 4.9 μV, 691 msec
		Effect	Images > words	Images > words
		Interval of effect	502–1167	512–1326
	RFC	Latency and amplitude of the peak	W: 6.6 μV, 565 msec	W: 4.2 μV, 707 msec
			Im: 9.6 μV, 580 msec	Im: 4.6 μV, 684 msec
		Effect	Images > words	Images > words
		Interval of effect	568–1040	500–1332
	RAT	Latency and amplitude of the peak	W: 4.2 μV, 580 msec	W: 2.3 μV, 660 msec
			Im: 6.5 μV, 590 msec	Im: 3.2 μV, 660 msec
		Effect	Images > words	Images > words
		Interval of effect	568–845	515–1150

Amplitudes of the N160 and P600 are measured between the baseline and the relevant peak. Amplitudes of the N270 and N400 are expressed as the difference between the relevant peak and the preceding positive peak (corresponding to the anterior counterpart of the N170).

$p < .0001$ in LP, related to a bilateral mnesic effect (distracter rejection vs. categorization: $t = 3.4$, $p = .001$, RP; $t = 3.16$, $p = .002$, LP) and to a left old/new effect ($t = 2.08$, $p = .0405$, LP; $t = 1.94$, $p = .055$, NS, RP). There was no significant material effect, $F(1, 39) = 0.83$, $p = .366$ in RP, $F(1, 39) = 0.08$, $p = .785$ in LP.

DISCUSSION

The primary goal of the present study was to investigate the neural mechanisms underlying visual recognition memory as a function of the nature of the stimulus (words vs. abstract pictures). During the transition from perception to recognition, we observed the following:

1. The first two stages, reflected by the N170 and N270, were lateralized according to material. They were characterized by a left hemisphere advantage for words and a right hemisphere advantage for abstract pictures. Source localization confirmed this early material specific hemispheric advantage and further localized the generators in the medial occipito-temporal junction for the N170 and in the mid- to anterior medial-temporal structure for the N270. The relevant processes were not influenced by the mnesic nature of the task.

2. Later stages reflected by the N400 and P600 were involved differently in word and abstract picture recognition: Words evoked a greater N400 whereas abstract pictures evoked a greater P600, thus reduplicating the findings of Ally and Budson (2007).

N400 and P600 were best modelled by multiple sources, bilaterally distributed in anterior basal temporal and ventral prefrontal areas. The relevant processes were influenced by the mnesic nature of the task and complied

Figure 4. Localization and time course of the modeled sources (bilateral equivalent dipoles) of the N170 and N270 evoked by successful word encoding, hits, and correct rejection. FG = fusiform gyrus; Rh Cx = rhinal cortex; nAm = nanoAmpere; GOF = goodness of fit.
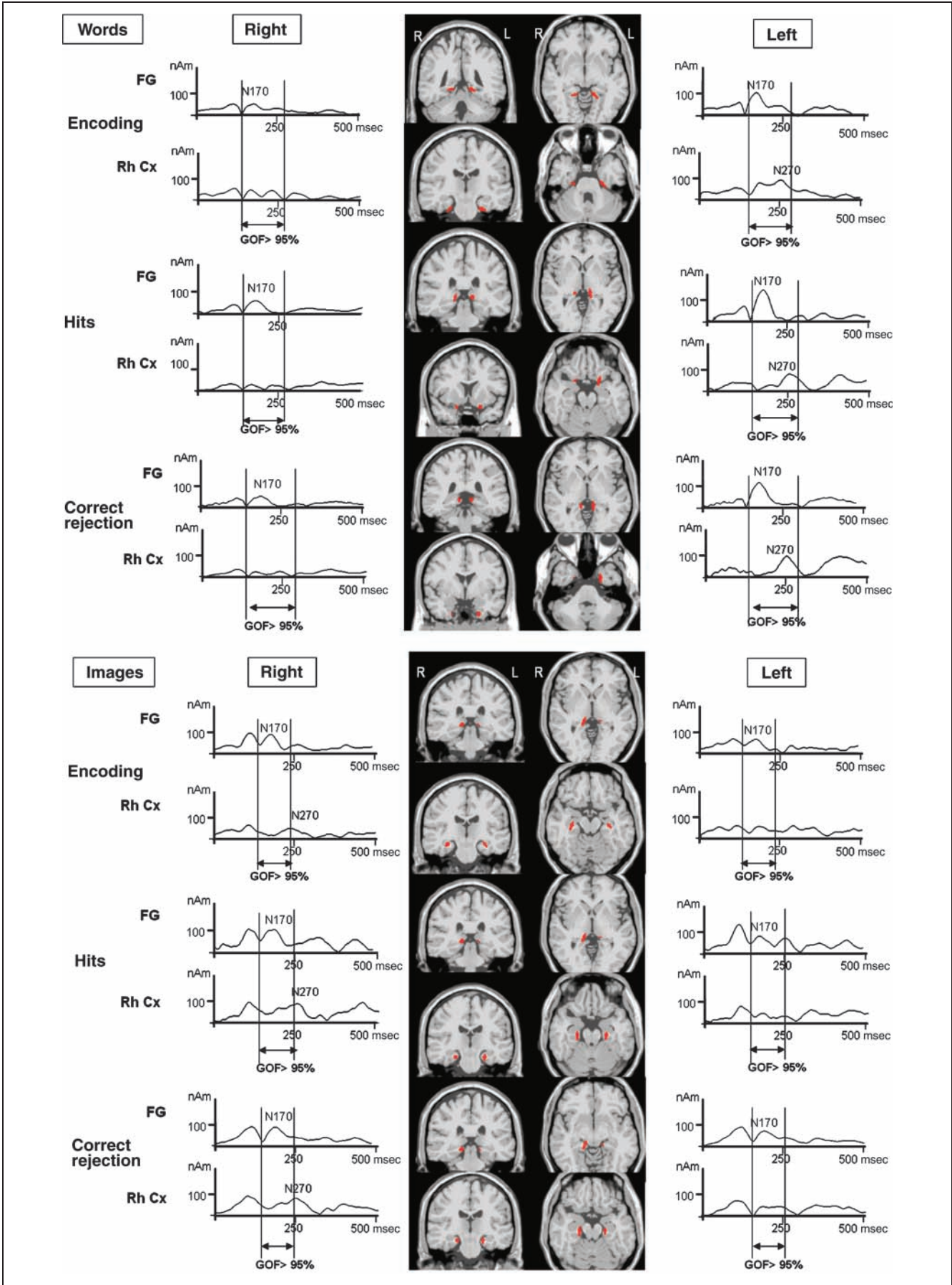
Table 2. Time Course of Modelled Sources of N170 and N270 Evoked by Word and Image Encoding, Target Recognition, Distracter Rejection, and Categorization

Tasks	Dipoles	N170: Fusiform Gyrus		N270: Rhinal Cortex	
		Words	Images	Words	Images
Correct Encoding	Peak latency of the left/right source (msec)	172/168	167/168	251/237	249/249
	Peak Magn (nAm) of the left/right source	109/52	65/94	95/68	39/53
Hits	Peak latency of the left/right source (msec)	176/176	170/170	253/237	250/255
	Peak Magn (nAm) of the left/right source	123/66	85/105	91/71	30/96
Correct Rejection	Peak latency of the left/right source (msec)	166/167	176/176	251/247	249/253
	Peak Magn (nAm) of the left/right source	117/53	70/95	99/29	43/94
Categorization	Peak latency of the left/right source (msec)	172/172	163/168	265/265	249/249
	Peak Magn (nAm) of the left/right source	88/41	50/86	71/58	48/50

Latency and amplitude of the peak of magnitude are measured on the time window associated with a goodness of fit superior to 95% (Magn = magnitude of the dipole).

with the classical old/new effect. Post hoc analyses showed that, contrary to gender categorization, color categorization of abstract pictures did not elicit an N400. The P600 was specific to mnesic tasks.

Perceptive Stages

Following the early low-level visual perception stage reflected by the P1, the first difference between word and picture processing was observed from ~140 to ~180 msec in posterior temporal sites. The time window and the spatial distribution of this effect corresponded to the classical N170. In the LPT site, words elicited a greater N170 than abstract patterns whereas in the right parietal site, abstract pictures elicited a greater N170 than words for hits. This potential has been shown to be the earliest reliable marker of processing difference between faces, pictures of common objects, and words and between linguistic and nonlinguistic visual patterns within the ventral visual pathway (Rossion et al., 2003; Halgren, Raij, Marinkovic, Jousmäki, & Hari, 2000; Bentin et al., 1999). Source localizations were consistently found in the medial occipito-temporal junction regions and more precisely in the vicinity of the posterior collateral sulcus and fusiform gyrus.

Also, the dorso-medial orientation of the dipole suggests an involvement of the collateral sulcus, which is oriented perpendicularly. We cannot exclude that the recorded potential resulted from the activation of a larger area covering the ventral occipito-temporal junction because the dipolar representation of the modeled sources does not allow delineation of the limits of the activated area. However, it is unlikely that it captured variance that would have been more appropriately allocated to other visual regions because the goodness of fit of the dipoles was very high specifically in the time window of the studied potentials and because the time course and localization

of the N170 modeled source were consistent with the time course of intracerebral potentials recorded between 160 and 200 msec in the posterior fusiform gyrus (FG) during face and word processing (Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994; Nobre et al., 1994). The FG belongs to the ventral visual pathway dedicated to visual object identification (Ungerleider & Mishkin, 1982) and could mediate structural encoding processes (Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994; Nobre et al., 1994). Notably, it showed clear asymmetry of word processing characterized by a greater left source. This asymmetry was less marked for the abstract pictures. In both cases, although asymmetric, left and right sources seemed coherent suggesting a hemispheric advantage rather than a clear left/right words/pictures separation of processing. This activity was not modulated by the mnemonic nature of the task nor by the repetition of the stimuli, which is consistent with a purely perceptive function. For words, the identified area is very close to the so-called visual word form area (Cohen et al., 2000).

Transition from Perception to Recognition

In the usual time range of the FN400 (200–500 msec), we identified a first negative peak around 270 msec, which could be dissociated from the subsequent FN400. First, the N270 was evoked by all the tasks involving words and pictures and especially by categorization of abstract pictures which did not evoke any N400. Secondly, contrarily to the N400, the material effect observed in the time window of the N270 was clearly lateralized, showing a word advantage in the left temporal and fronto-central sites and an advantage for abstract pictures in the right
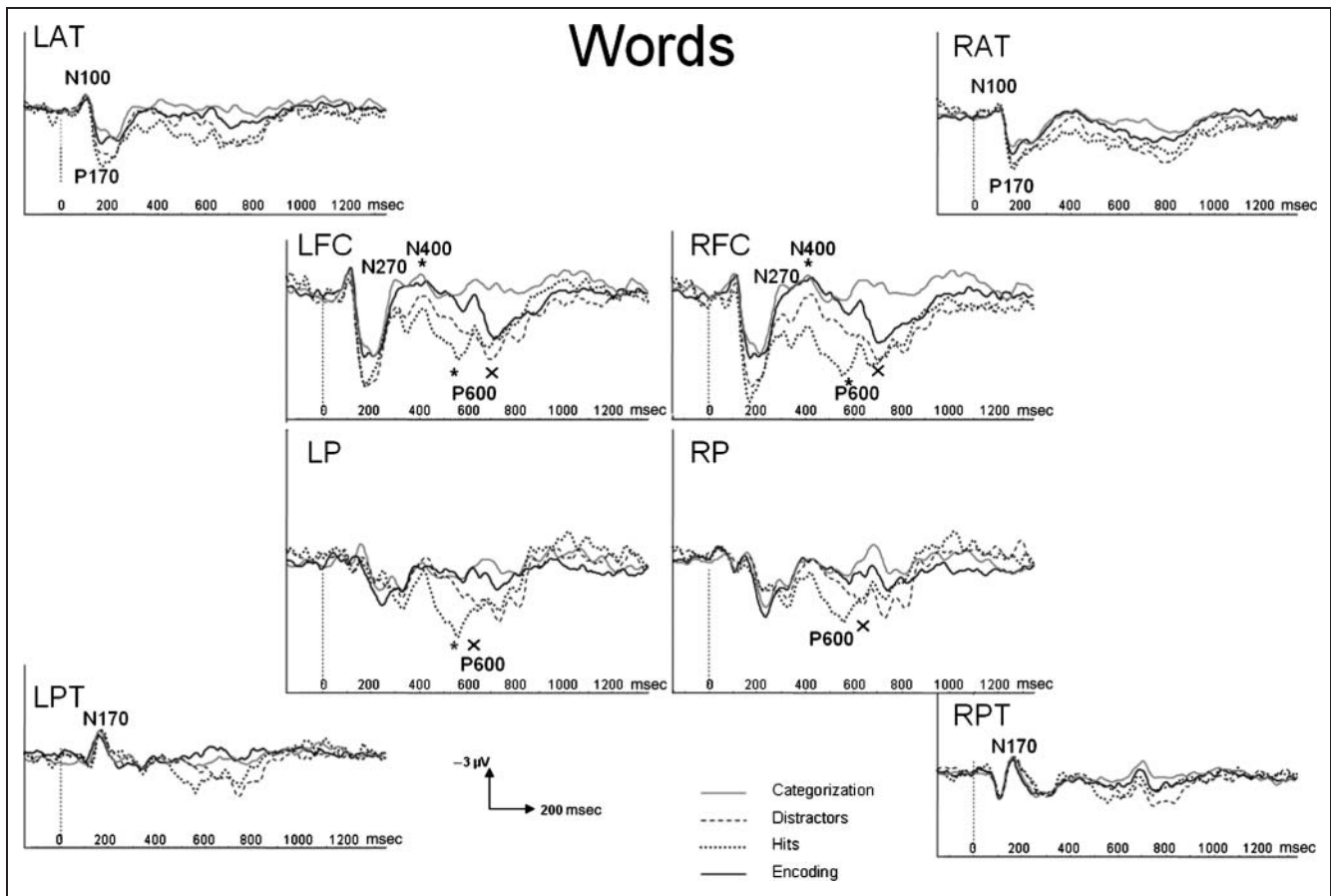
Figure 5. Overlay plots of the grand average ERPs recorded in the eight sites of interest evoked by successful verbal tasks: encoding (black), target recognition (dotted line), distracter rejection (large dotted line), and gender categorization (gray). It shows a significant old/new effect (comparison of target versus distracter recognition) on the frontal N400 (but not on the N270) and on the fronto-parietal P600 and the lack of P600 evoked by the categorization task. Potentials involved by significant old/new effect are marked by a "*", those involved by significant mnesic effect (difference between distracter rejection and categorization) are marked by a "×".

fronto-central site. This pattern of hemispheric asymmetry for words and pictures processing was confirmed by source localization. Thirdly, contrarily to the N400, the amplitude of the scalp N270 was not influenced by the nature of the task, in particular mnesic processes (no old/new effect). These results seem to contradict previous scalp ERP studies of recognition memory that did not individualize this potential. In these studies, the evoked electrical activity between 200 and 300 msec was considered as the beginning of the midfrontal N400 (Groh-Bordin, Zimmer, & Ecker, 2006; Rugg et al., 1998; Düzel et al., 1997; Van Petten & Senkfor, 1996; for a review, see Rugg & Curran, 2007).

However, other studies provide three lines of evidences supporting the existence of a distinct stage of processing between 200 and 300 msec. First, several scalp studies, which explored semantic memory and contextual integration, also identified two distinct negativities peaking around 300 and 400 msec, respectively (Marinkovic et al., 2003; Federmeier & Kutas, 2002; McPherson & Holcomb, 1999). In these studies, these two components were differentially sensitive to hemifield presentation, semantic

variables, and object structure information, suggesting that the first peak reflected high-level visual representation of objects or a transitional stage between perceptual and conceptual representation. The N270 identified in the current study can also be compared with the N250r component, evoked by faces and also by other objects (Schweinberger et al., 2004), which is thought to reflect the activation of a complex familiar visual representation (such as that of a familiar face; Tanaka, Curran, Porterfield, & Collins, 2006). The second line of evidence comes from intracerebral studies exploring the whole time course of word and face recognition in various sites within the ventral visual stream and MTL. First, Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al. (1994) and Halgren, Baudena, Heit, Clarke, Marinkovic, and Clarke (1994) identified a negative peak around 240 msec in a sequence of three events (N130–P180–N240), most prominent in the basal occipito-temporal cortex. This was evoked by both face and word processing. It is important to note that for technical reasons, the rhinal cortex and the most anterior part of the collateral sulcus were usually not explored at that time. In a more recent intracerebral study of face recognition, the same team,

this time exploring the anterior collateral sulcus, clearly identified a similar negative peak around 240 msec within the middle fusiform gyrus, posterior para-hippocampal gyrus, perirhinal cortex, and medial-temporal pole (Barbeau et al., 2008). Interestingly, the same abstract stimuli were used in this last study as in the present one to serve as control stimuli. These abstract stimuli clearly evoked an N240 most prominent in the anterior visual pathway, which could thus be related to the N270 reported in the present study. According to its morphology and source localization, the scalp N270 resembles an analogue of this intracerebral N240: The two dipoles model constrained by the results of MUSIC localized the sources of the N270 in the vicinity of the anterior collateral sulcus, consistent with a generator within the rhinal cortex. This is consistent with the posterior-anterior stream of information within the ventral visual pathway from fusiform gyrus toward the perirhinal cortex as shown also by the time course of the dipoles within this time frame (Figures 4 and 5). Thirdly, it is noteworthy that studies investigating the first moment

at which brain activity for a previously encountered item differs from that for new items have found that divergence occurs around 250 msec. This latency has mainly been identified for faces (Schweinberger et al., 2004; Bentin & Deouell, 2000; Eimer, 2000), possibly because there are many more neurons specialized for faces (and persons) than for the type of abstract, previously unseen pictures or words, which were used in our study. However, the fact that such a phenomenon has been identified in the time window of the N270 further strengthens the idea that this period is critical for perceptivo-mnesic processes. Indeed, the fact that the N270 was most prominent in anterior temporal lobe structures and that these structures are involved in declarative, conscious memories suggests that the N270 could reflect a mandatory process for overt recognition.

In our study, the process reflected by the N270 was not influenced by the old/new effect, suggesting that it reflected a high-level perceptive process rather than a recognition process. However, the old/new effect identified
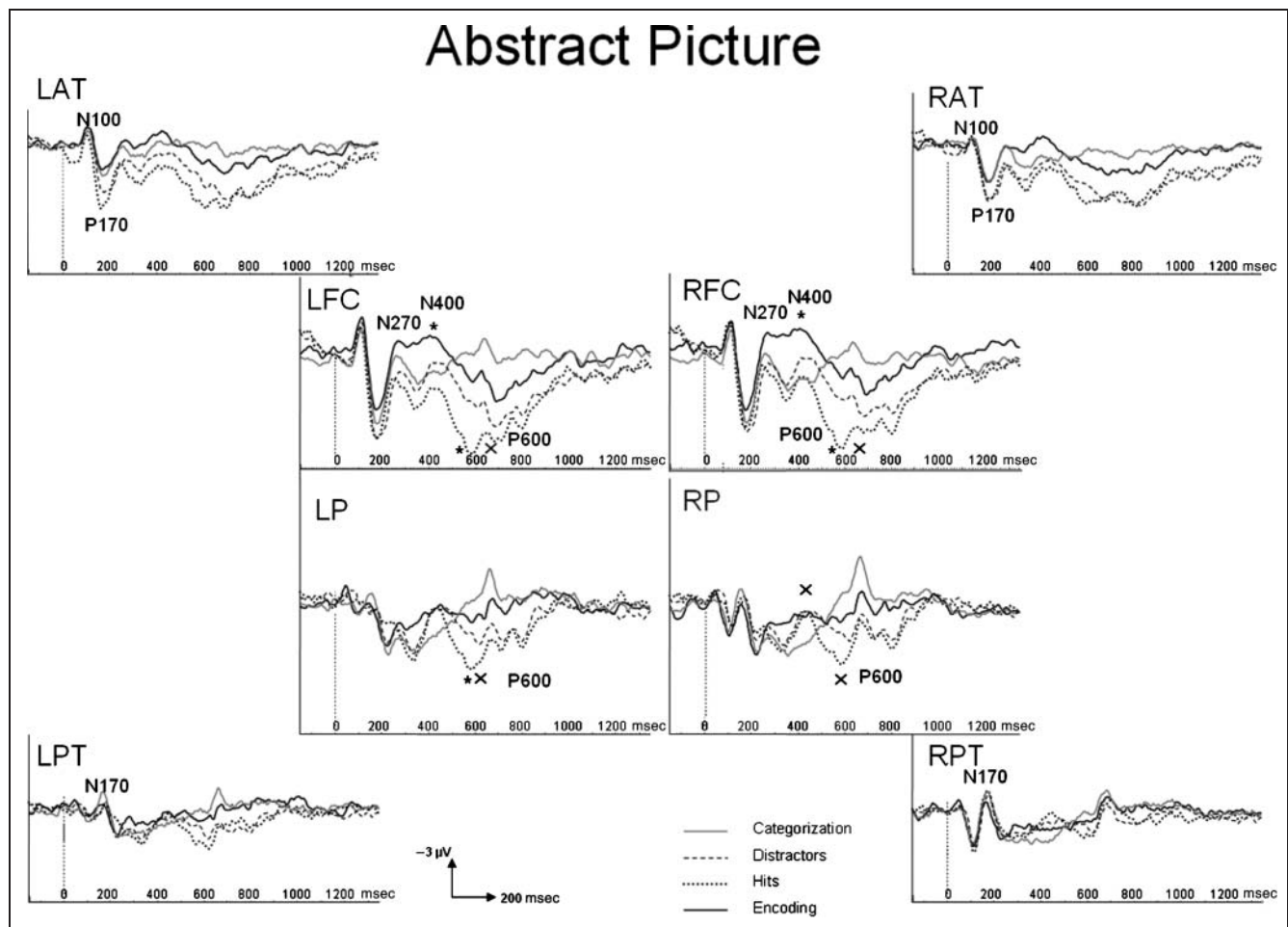

Figure 6. Overlay plots of the grand average ERPs recorded in the eight sites of interest evoked by successful nonverbal tasks: abstract pictures encoding (black continuous line), hits (dotted line), distracter rejection (large dotted line), and color categorization (gray). It shows a significant old/new effect on the fronto-central N400 and on the fronto-parietal P600 but not on the N270. It also shows the lack of N400 and P600 evoked by the color categorization task. Potentials involved by significant old/new effect are marked by a "*", those involved by significant mnemonic effect (difference between distracter rejection and categorization) are marked by a "×".

intracerebrally during the N240 was of low amplitude compared with the following effects during the AMTL-N400 and could be attenuated when measured on scalp electrodes. The absence of old/new effect at the stage of the scalp N270 could also represent a "cancelling out" of the signal because of opposing effects of repetition, the pattern of neuronal activation being influenced both positively (repetition enhancement) and negatively (repetition suppression) within a restricted anatomical area and brief timeframe. Indeed in a recent study, microelectrode recordings in the anteroventral temporal lobe of an epileptic patient showed a temporally close, antagonistic effect of word repetition on either side of the collateral sulcus, within the ento- and the perirhinal cortices (Halgren et al., 2006). The perirhinal cortex along with the parahippocampal cortex has been shown to provide the main inputs to the entorhinal cortex, which is in turn the main gateway to the hippocampus (Suzuki & Amaral, 2004). Anatomically, it is at the interface of the ventral visual pathway and medial-temporal memory structures (Bussey & Saksida, 2007). Lesion studies in primate have clearly demonstrated the role of perirhinal cortex in recognition memory (Meunier, Bachevalier, Mishkin, & Murray, 1993; Zola-Morgan, Squire, Amaral, & Suzuki, 1989). More recent studies of memory and perception in primate have also revealed that the perirhinal cortex does not contribute exclusively to memory but also to abstract visual perception (Buckley, Booth, Rolls, & Gaffan, 2001). It has led to construction of a new model that represents the ventral–visual–perirhinal stream as a hierarchically organized continuum (the perceptivo-mnemonic model; Bussey & Saksida, 2007). The scalp N270 could reflect both perceptive and mnemonic processing and be the hallmark of the transition from the earlier perceptive phase to the later mnemonic phase within the inferotemporal–perirhinal stream. Interestingly, a recent intracerebral study by our group evidenced widespread parallel processing within the ventral pathway during the N240, implicating both posterior perceptive areas and anterior perceptivo-mnesic areas (Barbeau et al., 2008). This result further emphasizes the possible role of the N270 as a key point between perceptive and mnesic stages. The fact that mainly anterior sources, rather than parallel sources, were identified in the present study may be related to the source models being more sensitive to the high amplitude sources of anterior areas whereas these sources may be overshadowed by the N170 in posterior areas. At this stage, there still persists a material-specific hemispheric asymmetry with a left advantage for words and a right advantage for nonnameable pictures. It is also consistent with a recent event-related fMRI study (Powell et al., 2005), which showed predominant activity in the rhinal cortices when contrasting successful recognition of pictures and faces versus words. Lesion studies in human have long emphasized the importance of hippocampal removal in generating material-specific memory deficits after MTL surgery (for a review, see Lee et al., 2002). Our results suggest that the material specificity of memory deficits could be related to lesions of inferotemporal and perirhinal cortices rather than the hippocampus proper.

Recognition Stage

Following the N270, the N400 and the P600 characterize the recognition phase. These both embody processes consistent with the classical "old/new" effect (Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001; Rugg et al., 1998; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994; for a review, see Rugg & Curran, 2007).

The experimental design of our study comprised a greater number of distracters than target items. It slightly favored the "new" response when participants did not have an accurate memory and had to guess the response (as shown by the calculated response bias). Such a response bias has been associated with a marginally greater old/new effect at anterior sites in the time window of the FN400 (Azimian-Faridani & Wilding, 2006; Windmann, Urbach, & Kutas, 2002). Therefore, the actual old/new effect could reflect both an accuracy-related and a bias-related effect. However, we believe that the bias-related effect should be marginal here because the bias effect was reported mainly in prefrontal sites (Windmann et al., 2002), whereas the old/new effect reported here was observed mainly in fronto-central and parietal sites.

In our experiment, the FN400 effect for words could reflect recognition processes on the basis of both familiarity (Woodruff et al., 2006; Rugg et al., 1998; Düzel et al., 1997) and conceptual priming (Van Petten & Senkfor, 1996) because the control task of gender categorization evoked a similar N400 reflecting the activation of semantic representations (Kutas & Federmeier, 2000). In the contrary, the FN400 effect observed for abstract pictures could primarily reflect a familiarity-driven recognition process because the control task of color categorization did not elicit any N400, showing that the presented pictures did not elicit automatically a semantic representation. This is in line with previous intracerebral (Puce et al., 1991) and scalp ERP studies showing that recognition based on familiarity does not necessarily require to link the studied item to preexperimental semantic knowledge (Voss & Paller, 2006; Van Petten & Senkfor, 1996) and could also rely on perceptual similarities (Groh-Bordin et al., 2006). These distinct processes could account for the different amplitude of activation evoked by words and abstract picture recognition at the N400 stage.

In our experiment, the P600 was also greater for hits than for distracters (late old/new effect). In contrast to the N400, it was specifically evoked by mnesic tasks. The late old/new effect is thought to reflect the last and hierarchically highest stage of recognition (Rugg & Curran, 2007; Woodruff et al., 2006; Friedman & Johnson, 2000; Rugg et al., 1998; Düzel et al., 1997). This so-called "recollection" stage corresponds to the building and retrieval of a memory trace,

which combines the representation of the item to be re-membered and other associated features related to the encoding context. Interestingly, the late old/new effect was not restricted to the LP site usually implicated in verbal material recollection but was also observed in bilateral fronto-central regions, especially for abstract pictures. In the same region, the P600 also had greater amplitude for images than for words. This is consistent with a recent study that showed a late (450–700 msec) old/new effect for congruent (same color) as opposed to noncongruent abstract images in left frontal and mid-fronto-central regions (Groh-Bordin et al., 2006) and suggested that it could reflect a specific recognition strategy on the basis of the association of perceptual attributes. Generators of these potentials were best modeled as distributed sources localized in anterior basal temporal and ventral prefrontal regions. The low resolution of the method does not allow for better accuracy. Nevertheless, these localizations are consistent with the results of intracerebral ERPs showing that the N400 and the P600 are recorded in widely distributed sites in bilateral temporal and frontal lobes. These sites include inferior temporal cortex, medial-temporal structures such as the perirhinal and entorhinal cortices for the N400, hippocampus for the P600, OFC, and anterior cingulate gyrus for both potentials (Barbeau et al., 2008; Grunwald et al., 2003; Elger et al., 1997; Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, et al., 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Clarke, 1994). It is unclear, however, whether the hippocampal P600 is the same as the LPC recorded from neocortical areas, particularly from the point of view of the surface because the hippocampus could be a closed electric field. The distributed source localizations suggest that at these late integrative stages, both pictures and words are ultimately processed by the same system, without hemispheric asymmetry.

Conclusion

In contrast to previous scalp ERP studies of verbal recognition memory, we identified a negative component around 270 msec that could be functionally and anatomically individualized from the N400. This N270 originated in the rhinal cortices and could embody both perceptive and mnemonic processing at the transition between these two phases. Up until this transition from perception to recognition, words and pictures would be processed preferentially and respectively in the left and in the right ventral visual stream and rhinal cortices. After this transition, in the higher stages of recognition and recollection, both words and pictures would be processed by the same bilateral medial-temporal and ventral prefrontal structures.

Acknowledgments

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