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On the Origin of the N400 Effects: An ERP Waveform and Source Localization Analysis in Three Matching Tasks

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Abstract The question of the cognitive nature and the cerebral origins of the event-related potential (ERP) N400 component has frequently been debated. Here, the N400 effects were analyzed in three tasks. In the semantic task, subjects decided whether sequentially presented word pairs were semantically related or unrelated. In the phonologic (rhyme detection) task, they decided if words were phonologically related or not. In the image categorization task, they decided whether images were categorically related or not. Difference waves between ERPs to unrelated and related conditions (defined here as the N400 effect) demonstrated a greater amplitude and an earlier peak latency effect in the image than in semantic and phonologic tasks. In contrast, spatial correlation analysis revealed that the maps computed during the peak of the N400 effects were highly correlated. Source localization computed from these maps showed the involvement in all tasks of the middle/superior temporal gyrus. Our results suggest that these qualitatively similar N400 effects index the same cognitive content despite differences in the representational formats (words vs. images) and the types of mismatch (semantic vs. phonological) across tasks.

Keywords Event-related potentials · Source localization · Semantic judgment · Image categorization · Rhyme detection

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Introduction

The event-related potential (ERP) N400 component, described in relation to semantic incongruities during sentence reading (Kutas and Hillyard 1980), was first interpreted in terms of "reprocessing of the semantic anomalies". Subsequently, the presence of N400-like responses was reported in various language and non-language tasks. For instance, an N400-like response was observed in lexical decision, semantic, orthographic, morphologic and repetition priming tasks (Bentin et al. 1985; Holcomb and Grainger 2007; Khateb et al. 2003; Martin and Thierry 2008; Ritter et al. 1983; Rodriguez-Fornells et al. 2002; Rugg 1985) but also in phonological and orthographical matching of words, non-words and pictures' names (Barrett and Rugg 1990a; Khateb et al. 2007; Kramer and Donchin 1987; Rugg 1984a, b), as well as in category matching of pictures, faces, letter or numbers (Barrett and Rugg 1989, 1990b; Munte et al. 1998; Szucs et al. 2007).

In language tasks, the negative response that characterized for instance ERPs to non-rhyming words as compared to rhyming ones during phonological matching peaked around 450 ms and was initially termed the "N450" component (Rugg 1984b). Due to its time of occurrence

and its centro-parietal scalp localization, this "N450" was immediately linked to the semantic N400 (Kutas and Hillyard 1980, 1982). However, the fact that the "N450" could also be evoked by non-rhyming non-words (Rugg 1984a), led first to the hypothesis that modulation of such N400-like response might not depend necessarily on the semantic aspects of the stimuli. Such a hypothesis was since then abandoned in view of the evidence showing that non-words (pseudo-words) looking like words will at least partially activate (both lexically and semantically) actual words with which these pseudo-words show phonological overlap. Regarding the latency differences of the N400 responses, other subsequent studies showed that they might depend on the type of stimuli (words, pictures or faces), the presentation modality (visual or auditory) or the task at hand (phonological and semantic in words and images but also identity and expression in face matching tasks) (Ganis et al. 1996; Munte et al. 1998; Perez-Abalo et al. 1994). Hence, it was suggested that the "N400s" latency in such matching tasks might be determined as a function of the availability of the relevant information (semantic, phonological etc.…) for the task at hand.

Since these early studies, the most longstanding view is that the N400 reflects the process of semantic integration of a critical word within the working context (see Hagoort 2008; Kutas and Federmeier 2000; Lau et al. 2008; van den Brink et al. 2001). This hypothesized post-lexical access mechanism allows for the on-line appraisal of the semantic goodness-of-fit of the encountered word with the ongoing context. Also, it is supposed to explain the N400 effects in semantic priming studies where the prime is viewed as the 'context' into which the target word is integrated. In a similar manner in rhyme detection (phonological) tasks, the prime is hypothesized to pre-activate phonologically similar words in the lexical system, and these will partially activate the representations with which they are linked at the lexico-semantic level. Then, compared to a phonologically unrelated target, a phonologically related target will lead to a facilitated access to its lexical representation due to the pre-activation induced by the phonologically similar prime. According to this facilitated lexical access view (Kutas and Federmeier 2000), this will result in a stronger N400 for the phonologically unrelated condition compared to the related condition. Similarly in the semantic integration hypothesis (Brown and Hagoort 1993; Holcomb 1993; van den Brink et al. 2001), a phonologically related prime will partially pre-activate the semantics of the target word and thus makes semantic integration easier in such a condition as compared to an unrelated one.

Previous studies comparing the N400 components induced by different stimulus types, in particular in the sentence context, suggested that semantic integration might be only partly independent of the representational format.

Thus, while Nigam et al. (1992) reported that the N400s to pictures and words in sentence ending were comparable in terms of amplitude, scalp distribution, and latency, Brandeis and colleagues (1995) analyzed the N400 time window using map series segmentation methods (or microstate topographical analysis) and found some topographical differences between verbal and non-verbal sentence endings. More recently, Willems et al. (2008) have analyzed the N400 induced by words and pictures in a sentence context and showed a similar N400 effects both in terms of latency and amplitude. Furthermore, their fMRI analysis conducted in the same study showed overlapping activations to both pictures and words in the left inferior frontal cortex but with additional specific activations for words in the left superior temporal cortex (Willems et al. 2008). The authors thus concluded that despite the differences in representational format, semantic information conveyed by pictures and words in the sentence context is integrated in similar ways. Furthermore, the comparison of fMRI and source localization maps contrasting incongruous and congruous sentence endings (i.e. N400 effect) showed converging EEG and fMRI results. In particular, they observed fMRI activation in the left inferior frontal and superior temporal cortex and consistent left anterior source localization during the N400 effect. Partly concordant with these localization data, a recent review (Lau et al. 2008) of functional studies suggested that the temporal areas were the most consistently activated during experimental conditions manipulating the N400 effect.

In a recent study, we have re-analyzed the time course of the phonologically induced N400 component (Khateb et al. 2007) and estimated its cerebral generators. We observed that, similar to the semantic N400 component, the N400 induced by phonologically unrelated words in a rhyme detection task was subtended by temporal areas, as suggested by various functional brain imaging studies (reviewed in Lau et al. 2008). We hypothesized that such qualitatively similar N400 responses occur in relation to cognitive mismatch in primed contexts, a view that is also compatible with the semantic integration and lexical access accounts as well as with the contextual integration hypothesis (Rugg and Coles 1995; see also Munte et al. 1998). In this study, our aim was to assess the comparability of the N400 effects (see methods below) in two verbal and one non-verbal (pictorial) matching tasks in the same subjects using ERP and source localization analysis. In the semantic matching task, written word pairs were presented sequentially and subjects judged whether words in each pair were semantically related or not. In a similar but phonologic task, they decided whether words in each pair were phonologically related (i.e. rhymed) or not. In the image categorization task, they decided whether two sequentially presented images were categorically related or

not. Based on previous results, our prediction was that (i) unrelated conditions will produce more negative responses in the 400 ms time range and, that (ii) depending on the context (semantic, phonological or pictorial), the amplitude and the peak latency of the N400 effects (as assessed by the difference waves between unrelated and related conditions) might differ across tasks but that (iii) they will share common neural substrates and thus be qualitatively comparable across tasks.

Materials and Methods

Subjects

Twenty-two French-speaking subjects (11 women, age 23 ± 2 years) participated in this study. They were recruited from the University and were all right-handed (laterality quotient $= 84 \pm 21$). They had normal or corrected-to-normal vision, with no history of neurological or psychiatric diseases. They gave their informed written consent as recommended by the Research Ethical committee and were paid for participation.

Stimuli and Procedure

The methods (and part of the data) have already been presented elsewhere; they will be presented briefly here. Words were French, concrete, imaginable, high frequency (logarithmic class of word frequency >300, see Content et al. 1990), of 4–7 letters nouns (see Khateb et al. 2003, 2007). In the semantic judgment task (referred to here as the semantic task, Khateb et al. 2003), the words in SR pairs were either categorically (*apple-grape*) or associatively (*sky-cloud*) related ($n = 80$ pairs). In SU pairs, the primes of related pairs were replaced by other unrelated words, while targets remained the same ($n = 80$). A filler condition was also created by repairing the primes of SR and SU pairs ($n = 80$ pairs) but was not further analyzed. Thus, each word was repeated once either as prime or as target. In the rhyme detection task (referred to here as the phonologic task, Khateb et al. 2007), the stimuli were composed of orthographically dissimilar word pairs that were either phonologically related (PR, i.e. rhyming (*tabac* = [taba] − *bras* = [bRa], $n = 40$ pairs)) or unrelated (PU, i.e. non-rhyming, $n = 40$ pairs). Again here, the primes of PR pairs were replaced by other non-rhyming words to create PU pairs. A filler condition was again created by the primes of PR and PU pairs ($n = 40$ pairs). In the image categorization task (referred to here as the image task), the stimuli were selected from Snodgrass's pictures (Snodgrass and Vanderwart 1980). Images that were related (IR) were composed of drawing representing either

manmade (*pipe-cigar*, $n = 30$ pairs) or natural (*camel-elephant*, $n = 30$ pairs) objects. As in previous tasks, the prime images of IR pairs were replaced by other unrelated ones to create the unrelated images (IU, $n = 60$). Here again, a filler condition was established by re-pairing the prime images in IR and IU conditions. Thus, for the semantic task, a total of 240 trials was obtained and randomly distributed in thee equivalent experimental blocs. In the image task, a total of 180 trials was obtained and randomly distributed in two experimental blocs. For the phonologic task, a total of 120 trials was obtained and randomly distributed in two experimental blocs. For all tasks the order of experimental blocs was counter-balanced over the subjects. Notice that in all tasks each stimulus was repeated once and that the proportion of the related targets was 1/3.

The experiments were carried out in an isolated, electrically shielded room. For the semantic and phonological tasks, the words were written in black letters using "Times" font on the centre of a light-gray screen with their borders subtending up to 2.5 degrees laterally. For the image categorization task, the stimuli, 4×4 cm black and white drawing, were also presented centrally. For each trial (total duration of 3.4 s), the stimulus pairs were presented as follows: (i) a fixation cross appeared for 1000 ms; (ii) the prime (word or image) was shown for 150 ms; (iii) followed by an inter-stimulus interval of 500 ms (thus an SOA of 650 ms); (iv) then the target stimulus for 150 ms and finally (v) a blank screen of 1600 ms allowed the for subjects' responses.

The subjects were seated 120 cm from the screen and asked to fixate the central cross, read word pairs silently, and indicate after the presentation of the target word whether the two words were SR or not in the semantic task, or whether the words rhymed or not in the phonological one. In the image task, they indicated whether or not the images were categorically related or not. They responded as quickly and accurately as possible using the middle (for related) and index fingers (for unrelated) of their right hand. They all underwent a training session consisting of 15 trials for each task. Due to the different natures of the tasks, all subjects first underwent in a counter-balanced (half of the subjects started with the image task and the other with the semantic task) order the semantic and the image tasks (both involving semantic aspects) and then the phonological one. The behavioral data were analyzed here in each subject to provide a global measure of reaction time (RT) and accuracy by task (related and unrelated conditions collapsed), but these results are not further discussed. This analysis showed that the mean RT ($\pm$SE) was of: 639 ± 21 ms for the semantic task, 585 ± 24 ms for the phonological task and 586 ± 25 ms in the image task. The mean accuracy was of $94 \pm 0.7\%$, $95 \pm 0.7\%$ and

95 ± 1.2% respectively in the semantic, phonological and image tasks.

EEG Recordings and Analysis

The EEG was recorded (using a 64-channel system, M&I Ltd., Prague, Czech Republic) from 47 equidistant electrodes placed manually all over the scalp according to the extended 10/10 system (for recording sites see Khateb et al. 2007). The EEG signals were recorded at 500 Hz referenced to Cz and re-computed off-line against the average reference. Filter settings were from 0.15 to 250 Hz and impedance was kept below 5 kΩ. A bipolar vertical EOG monitored eye-movement artifacts. The 3-dimensional positions of electrodes were measured for each subject using a 3-D digitizer (ISOTRACK®, Polhemus Inc., Colchester, VT).

The EEG was analyzed using the Cartool software (v3.3, http://brainmapping.unige.ch/cartool.htm). ERP epochs were separately averaged for related and unrelated targets (words/images) for each task, starting at −100 ms before stimulus onset to 800 ms post-stimulus. Epoch averaging was performed after: (i) eliminating sweeps with amplitude exceeding ± 100 μV in any of the channels, (ii) excluding trials containing eye-movement artifacts, (iii) discarding trials with false responses and filtering each epoch between 1 and 30 Hz. Before computing the grand-mean ERPs for each condition, individual ERPs were baseline-corrected (using the 100 ms pre-stimulus) and spatially standardized by interpolating the subject's electrode positions to a general electrode array using the 3D spline interpolation method (Perrin et al. 1989) implemented in the Cartool software.

We first assessed the presence of the N400 component as expected in this type of paradigms. For this purpose, point-wise t-tests compared for each task the individual ERPs to unrelated and related conditions over all time frames (from −100 ms to 800 ms post-stimulus) and for all recording sites separately. To illustrate the time periods where reliable response differences occurred and define the time window for the analysis of the N400's effects, we retained in this analysis only the significant t-values at $P < .01$, during at least 10 consecutive time frames (20 ms). In the second step, we analyzed the amplitude of the N400 effect (defined hereafter as the difference wave between ERPs to unrelated minus related condition) and its peak latency in each subject and each task and compared them statistically. For this later analysis, we first computed the N400 difference waves for each subject in each task. The individual difference waves were then low-pass filtered at 5 Hz to avoid the selection of spurious peaks as in Moreno and Kutas study (2005). Based on the t-tests analysis, we determined for each subject the amplitude and

the latency of the most negative time point between 250 and 500 ms from the difference wave at Cz. The choice of Cz is due to the fact that highest t-values were observed on (or around) this site in all tasks. The amplitude values and the latency times were then statistically compared across tasks using one way analysis of variance (ANOVA) with 3 levels representing the tasks. In addition, a spatial correlation analysis (Brandeis et al., 1992; see also Khateb et al. 1999) was performed on the topographic maps computed from the peak of the averaged N400 effects in each task to assess the qualitative similarities across tasks. Finally, a topographic ANOVA (TANOVA, Kondakor et al. 1995; see also Murray et al. 2008) was performed between conditions on the maps computed from the N400 peak effect in individual difference waves to test if these peak maps differed between tasks in terms of their field configurations (i.e. topographical organization).

Source Localization Analysis

In this analysis we applied LAURA (Grave de Peralta Menedez et al. 2001), a distributed linear inverse solution, to estimate brain regions that underlie the N400s' effects. LAURA is calculated on a realistic head model including 4024 solutions points (i.e. voxels) equally distributed within the grey matter of the MNI average brain (Montreal Neurological Institute, Montreal, Canada). This technique, previously used in various cognitive tasks (see Khateb et al. 2007), is similar to other distributed inverse solutions which deals with a priori unknown number and location of active sources in the brain. In order to characterize brain areas underlying the elicitation of the N400 effect in each task, we first applied the LAURA inverse solution to the topographic maps computed, in each task, from the peak of the group-averaged N400 effect. Afterwards, we applied LAURA to the individual N400 topographic maps (extracted from most negative time point between 250 and 500 ms of the difference wave at Cz) and statistically compared the individual inverse solutions between conditions (using t-tests on all solution points, i.e. voxels). Only significant differences at $P < .05$ corrected for the number of electrodes ($N = 47$, i.e. $P < .001$) are reported here.

Results

Figure 1a–c illustrates for the different tasks a superimposition of the grand-mean ERP waveforms to unrelated (red traces) and related (black traces) targets from a selected subset of 9 central electrodes around Cz. As expected in this type of paradigms, it shows that unrelated targets induced more negative responses during the 400 ms time period in the semantic (a), phonological (b) and image

Fig. 1 Superimposition of ERP traces (from −100 to 800 ms) from semantically related (SR) and unrelated conditions (SU, **a**), phonologically related (PR) and unrelated conditions (PU, **b**) and categorically related (IR) and unrelated images (IU, **c**). In each panel, the traces display a selected subset of 9 central electrodes around Cz. As expected, unrelated targets evoked more negative responses during the 400 ms time period in all tasks. **d–f**: The graphs depict the *P* values (color scale inset in **f**: *P* < .01 to *P* < .001; green to dark red with highest values) of the point-wise *t*-tests analysis (see "Materials and Methods") performed on all time points from −100 to 800 ms (*x*-axis) and all 47 recording sites (*y*-axis). In all tasks, robust (highest *P* values) and consistent (longest in duration) differences appeared in the 400 ms time window (see *t*-maps in Fig. 2). Notice that black traces in **a–c** refer to related conditions and red traces to unrelated condition. The inset in the upper right graph **d** shows the location of the 9 illustrated sites
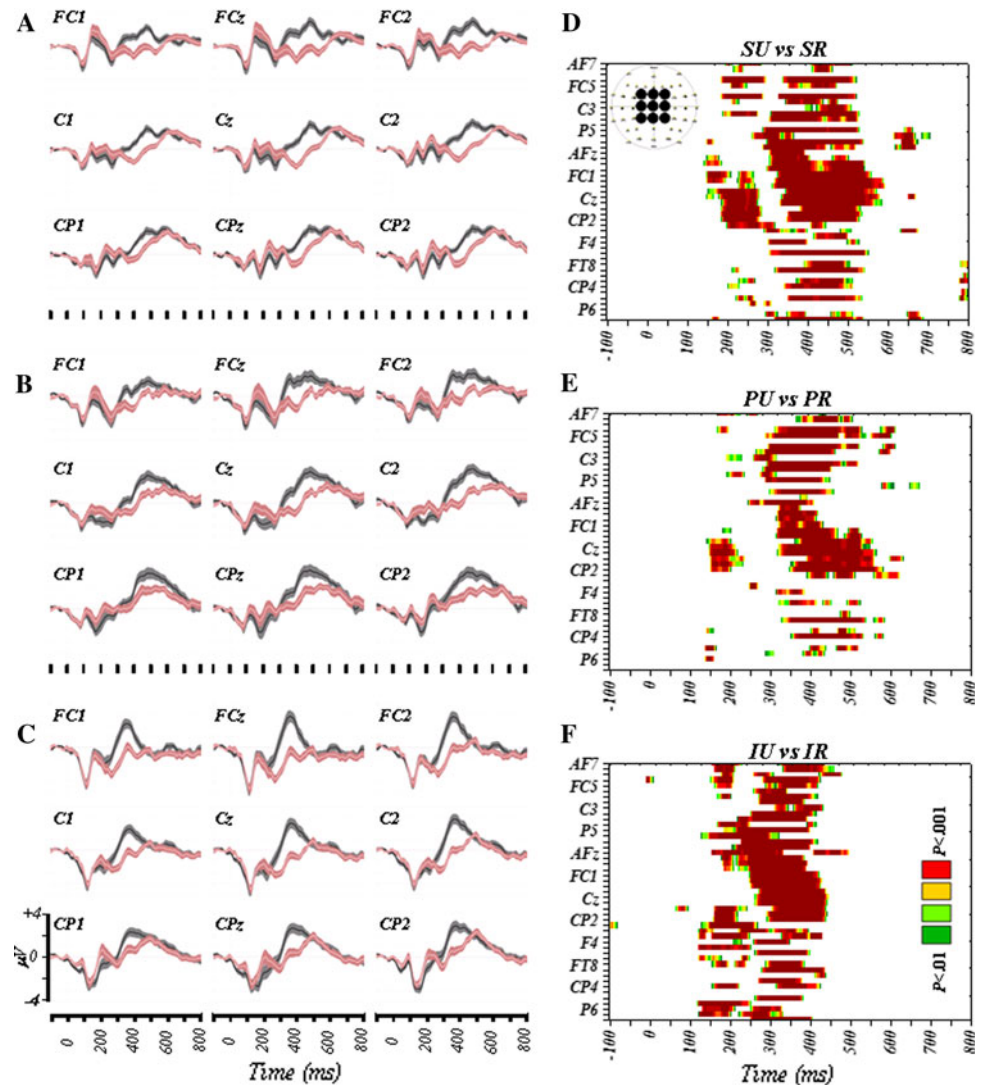

(c) tasks. Point-wise *t*-tests analysis comparing the individual ERPs to unrelated and related targets in each task confirmed that the most significant and reliable differences (i.e. those involving a large number of recording sites for a relatively long time period and with the highest *P* values) were observed at around 400 ms for the semantic (d) and phonological (e) tasks and slightly earlier in the image task (f). As illustrated in these graphs (d–e) which depict *P* values over time and across all electrodes, these differences were the most prominent around the central sites (see centre of each graph), but they also implicated other locations (see Fig. 2).

Figure 2a–c illustrates, using the same 9 recording sites around Cz, the mean across subjects of the difference waves (between ERPs to unrelated minus related targets) for the semantic (a), phonological (b) and image (c) tasks. The comparison of the amplitude of N400 effect, determined in all tasks from Cz (displaying the highest *t*-values in the semantic task), in the period between 250 and

500 ms, showed that the amplitude of the N400 effect varied slightly between tasks ($F(2, 42) = 3.8$, $P < .04$, mean amplitude ± SD = -2.6 ± 0.9, -3.0 ± 1.5 and -3.4 ± 1.6 µV, respectively in the semantic, phonologic and image tasks). Post-hoc comparisons using Fisher's LSD tests showed that this effect was only due to a significant difference between the image and the semantic task ($P < .009$, the image vs. phonologic $P > .14$ and phonologic vs. semantic $P > .22$). Moreover, the comparison of the peak latency (in the individual difference waves on Cz) showed a highly significant effect of task ($F(2, 42) = 24.3$, $P < .000001$). As appearing in Fig. 2a–c (see black arrows on Cz), this effect was due to an earlier peak in the image (350 ± 47 ms) as compared to the semantic (432 ± 43 ms, $P < .000001$) and the phonological task (414 ± 58 ms, $P < .000005$), the later two tasks not differing ($P > .17$).

For illustration purposes only, Fig. 2d–f shows the t-maps and location of all electrodes showing significant

Fig. 2 Average (±SEM) of individual difference waves between ERPs to unrelated minus related condition in the semantic (a), phonologic (b) and image (c) tasks. Although these waves were qualitatively similar in all tasks, the analysis of the peak (on Cz) amplitude showed slight significant differences in particular between the semantic and image tasks (a and c, see text). The analysis of peak latency in individual waves also on Cz revealed significant differences (indicated here in each panel by a black arrow) due mainly to earlier occurrence in the image task. d–f: Illustration of the 2-D t-maps computed for each task from the time point corresponding to the mean peak latency of the N400 effect (left maps), together with 2-D maps (right) showing in red color all electrodes which in the point-wise t-tests showed significant differences (at P < .01) between unrelated vs. related conditions. Maps are shown from top, with left ear at left and right ear at right. Color scales indicate the respective t-values
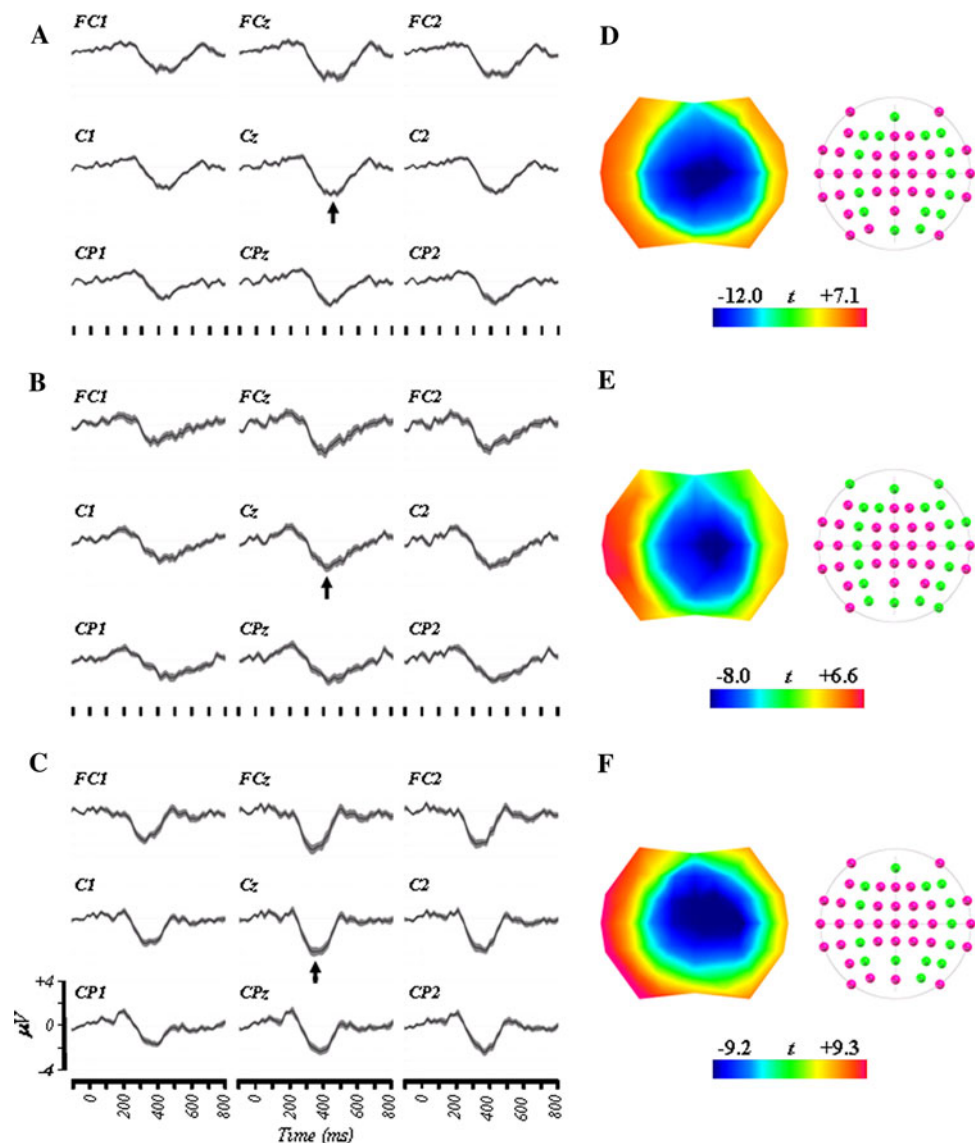
differences during the time moment of the mean peak latency of the N400 effect (indicated by arrows in a–c at Cz). Figure 3 illustrates the topographic voltage maps from this same time point in the averaged difference waves and the source localization images (as estimated by LAURA). A spatial correlation analysis (Brandeis et al. 1992; see also Murray et al. 2008) performed on these grand-mean peak effect maps showed that the map in semantic task (a) correlated at 0.96 with the map in phonologic task (b) and at 0.97 with map in the image task (c), the later two (i.e. b and c) correlating at 0.95. Separate topographical ANON-As (TANOVA, see Murray et al. 2008) were then performed on the individual N400 maps (the maps computed from most negative time point between 250 and 500 ms of the difference wave at Cz, see above and illustration of the individual maps in Supplementary Fig. 1). This analysis revealed that these maps did not differ between tasks

(semantic vs. phonologic tasks P > .08; semantic vs. image tasks P > .25 and phonologic and image tasks P > .16).

The sources of activity estimated by the LAURA inverse solution applied to these maps (Fig. 3A₁–C₁) suggested that, despite some variations in the activation strength of certain areas, the N400 effect was subtended by highly similar brain areas across tasks. Particularly, the estimated sources for the three tasks showed all the predominant involvement of the bilateral superior (STG, BA 22/41) and middle temporal gyrus (MTG, BA 37/39). Additional but slightly varying sources were observed in the bilateral middle/superior frontal gyrus (BA 10), left insula (BA 13), right lingual (BA 19), right posterior cingulate gyrus (BA 30) and putamen. In order to assess whether or not these observed sources, in particular the temporal and frontal ones, differentiated tasks, we compared the individual inverse solutions of the N400 effect in the different tasks
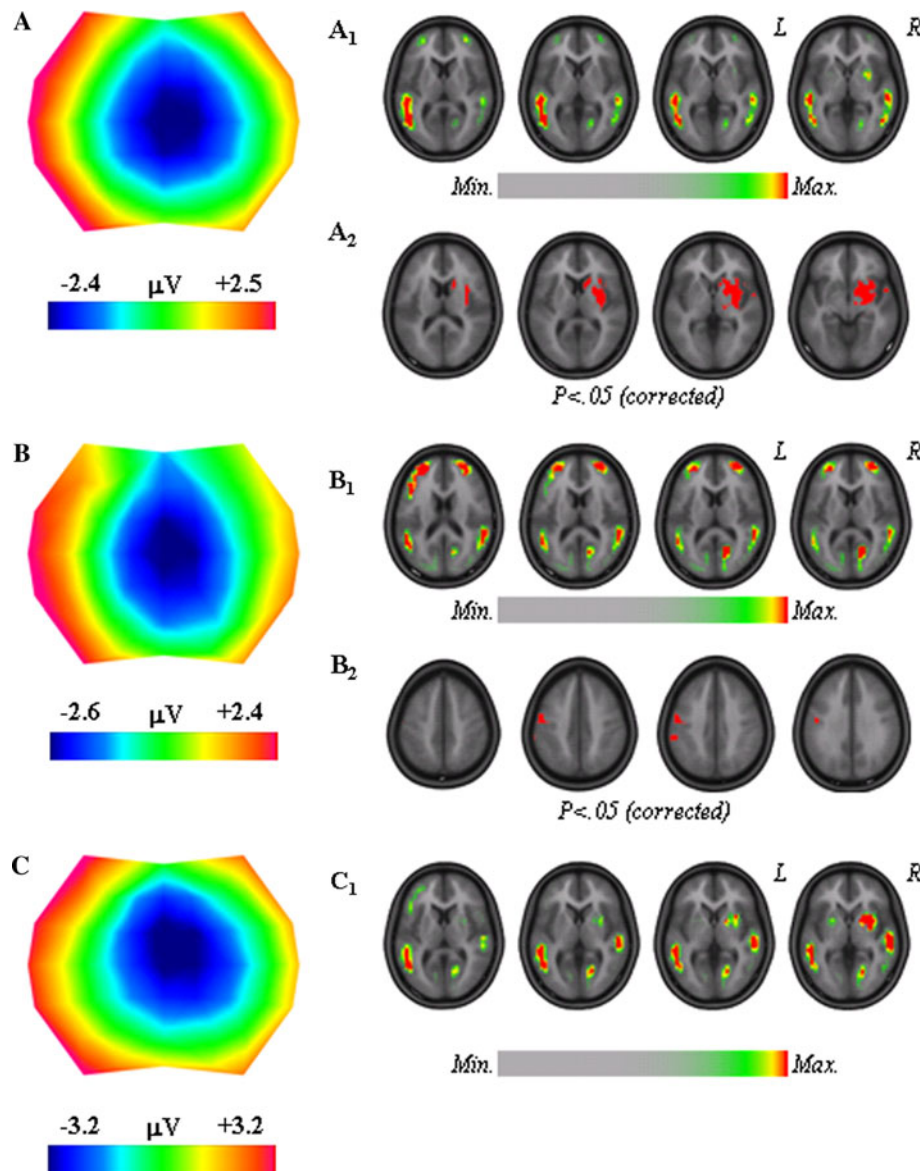
Fig. 3 a–c Topographic maps computed for each task from the group-averaged difference waves during the peak of the N400 effect (see arrows at Cz in Fig. 2). Color scales indicate voltage values and the maps are shown from top, with left ear at left. A_1–C_1: The source localization using the LAURA inverse solution during the same peak effect. LAURA solutions, displayed on four successive MRI slices according to the neurological convention (left is at left, A_1–C_1), showed a relatively similar pattern of activity involving in all tasks the bilateral temporal areas (see text for details). Statistical analysis using t-tests performed on the individual inverse solutions computed from the subjects' N400 maps (maps computed during the most negative time point on Cz between 250 and 500 ms, see Supplementary Fig. 1 for the individual maps) showed only significant difference between the semantic and the phonologic task (A_2) and between the phonologic and the semantic task (B_2, statistics at $P < .05$ corrected). No difference was observed between the image and either task. Note that the inverse solutions are scaled to their maximum. Color scale below C1 indicates the intensity of the current density. Note that the red color in panels A_2 and B_2 corresponds to areas showing statistical differences scaled at $P < .05$ corrected)

(computed on the potential maps illustrated in Supplementary Fig. 1 and extracted from most negative time point between 250 and 500 ms of the difference wave at Cz). This analysis showed that the semantic task relative to the phonologic one exhibited some additional sources around the right parahippocampal gyrus (Fig. 3A2). The semantic relative to image task showed no significant

difference. The comparison of the phonologic and the semantic task showed some additional sources in the precentral gyrus and the inferior parietal lobule (Fig. 3B2). The phonologic relative to the image task, the image relative to the semantic and to the phonologic tasks showed no significant difference. Of particular relevance is the fact that these analyses showed no difference between tasks

with regard to the superior/middle temporal sources, the ones hypothesized to be the most frequently involved in the N400 effects (Lau et al. 2008).

Discussion

In this study, we used classical ERP waveform analysis to compare the N400s' effects in three matching tasks. The ERP waveform analysis performed on all electrodes using time frame-by-time frame *t*-tests between the individual ERPs for unrelated and related conditions in each task confirmed the visually observed response differences between conditions. These differences, appearing in the form of more negative ERPs to unrelated as compared to related conditions in the N400 time range, involved maximally the scalp central sites in all tasks. These findings replicate previous observations showing N400 effects in various priming contexts including semantic and phonological matching of words and pictures (see "Introduction").

The analysis of the subjects' difference waves to assess the amplitude and latency of the N400 effect in the three tasks indicated that it differed slightly in amplitude across tasks. Moreover, the effect occurred significantly earlier in the image than in the word tasks. The latency effect observed here resembles that previously observed between pictures and words in the sentence context (Ganis et al. 1996). Also, a difference in the N400 latency across linguistic and non-linguistic tasks using different modalities of presentation had also previously been observed between written and auditorily presented words and between words and images and was hypothesized to reflect the availability of the semantic and phonological information during the matching process (Perez-Abalo et al. 1994). In a face matching task, a difference in the peak latency of the N400, together with some topographic differences at the maximal effect, were previously found between identity and expression mismatches (Munte et al. 1998). Although such differences were interpreted as reflecting different processes that rely on separate neural generators, other authors have argued that the presence of certain topographical differences between the N400 effects in such tasks does not necessarily means that they are due to the participation of two (or more) distinct cognitive operations (Ganis et al. 1996; Rugg and Coles 1995). Indeed, it has been argued that, since ERPs are sensitive both to the representational format of the stimuli and to the type of the cognitive operations involved (Rugg and Coles 1995), differences in topography might be observed when the same cognitive operation is applied to process contexts that differ in their cortical representations. In our data, not only did the pattern of the averaged difference waves looked qualitatively

similar but also the topographic maps computed during the peak of the averaged N400 effects were highly correlated. Also, at the individual level, the comparison of the maps computed during the peak of the N400 effect (i.e. difference waves) using topographic ANOVA did not differ significantly between conditions. Taken together, these findings suggest that despite differences in representational formats (images and words), and the involvement of different types of mismatch/incongruency (semantic vs. phonological or categorical), the N400 effects measured here appeared to reflect an invariant process.

Concordant with the qualitatively comparable patterns of difference waves and the highly correlated peak map topographies, the source localization indicated that the group averaged N400 effects were subtended by a pattern of activation that in all cases shared the involvement of the bilateral temporal cortex, together with other areas. Of note is the fact that statistical analysis on individual inverse solutions showed no difference between tasks with regard to the involvement of the middle/superior temporal areas. The participation of bilateral temporal areas in tasks inducing N400 effects has been proposed in various functional brain imaging and electrophysiological studies, including sentence processing with semantic violations and lexical decision tasks (see Khateb et al. 2007; Lau et al. 2008). Taken together, these results thus converge towards the hypothesis that the N400 effects observed in these tasks are closely linked and all appear due to context/semantic integration mechanisms in primed linguistic and non-linguistic tasks. With respect to their neural basis, a recent review by Lau et al. (2008) highlighted the fact that, in fMRI studies, the only area showing consistent priming-related activity (across different SOAs and modalities) is the MTG, although some reports have also, though inconsistently, implicated the STG (probably dependant on specific design parameters). According to the authors, such observations strongly support the idea that this area is involved in generating the N400 effect. The authors also considered, on the basis of various functional and clinical observations, that the posterior temporal cortex (MTG/STG and inferior temporal cortex, IT) is the best candidate for the storage of lexical representations, and hence they proposed that the N400 effects are related to processes involved in lexical access. In this respect, the increased N400 response, in both semantic priming and sentence processing contexts, appears as a consequence of a certain decreased facilitation of lexical access. Such a view is not really discordant with the post-access semantic integration hypothesis (Hagoort 2008) and the contextual integration account (Rugg and Coles 1995). Thus, when a word (or a face) is repeated, its second occurrence can be integrated with less effort (probably due to the pre-activation of the same representation at the lexico-semantic level) and will

lead to the attenuation of the N400 component. The same mechanisms could explain the findings related to the N400s in other linguistic (such as phonological, orthographical and letter matching tasks) and non-linguistic tasks such as pictures and faces where the prime stimulus pre- activates the conceptual representation (such as face expression, identity, gender, occupational category etc.) of the face stimulus on which the judgment has to be made.

In summary, our study allowed the comparison of the N400 effects in three different tasks and showed that these effects were qualitatively comparable. One should note that qualitative similarities and absence of significant statistical differences between topographic maps do not causally involve comparable generator distributions. However, and in line with many functional studies we observed that the source localization of the N400 effects measured here indicated the participation of bilateral temporal areas, although with some differences of activation appearing in other areas. With regard to the temporal areas, no major difference was observed between tasks. Accordingly and in view of multiple experimental functional evidences, we interpret these temporal activations as being related to the invariant content of the cognitive operation involved. Future functional imaging research comparing different linguistic and non-linguistic tasks will be needed to further substantiate these findings and to better assess the influence of the representational formats on the brain patterns of activation which lead to some inconsistent interpretations in this literature.

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