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Research report

High density ERP indices of conscious and unconscious semantic priming

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Abstract

The existence of differential brain mechanisms of conscious and unconscious processing is a matter of debate nowadays. The present experiment explores whether conscious and unconscious semantic priming in a lexical decision task at a long prime-target stimulus onset asynchrony (SOA) correlate with overlapping or different event related potential (ERP) effects. Results show that the N400 effect, which appeared when words were consciously perceived, completely disappeared when primes were masked at a level where the ability of participants to detect the prime was near chance. Instead, a rather different set of ERP effects was found to index unconscious semantic priming. This suggests that the processes at the basis of conscious and unconscious semantic analyses can under some circumstances be rather different. Moreover, our results support the notion that conscious and unconscious processes are at least partially separable in the brain.

Theme: Neural basis of behaviour

Topic: Cognition

Keywords: Consciousness; Unconscious priming; N400

1. Introduction

The extent to which unconscious stimuli are able to modulate our behavior has been a recurrent topic of research since the beginning of experimental psychology (i.e., Refs. [39,54]). Among the vast amount of studies exploring unconscious information processing there are those showing that semantic information can be accessed without conscious awareness of stimuli. For example, Marcel [51] proved in his now classic studies that undetectable masked words were able to semantically prime other words presented afterwards in a lexical decision task (LDT), thus showing that the meaning of stimuli can be accessed without conscious experience of these words (see also Refs. [3,33]).

One of the main concerns in the study of unconscious processing was how to make sure that reported effects were not actually due to residual consciousness of the stimulation [38]. Although in the early studies subjective reports were accepted as good estimators of awareness (e.g., Ref. [71]), it was soon noted that more rigorous measures of consciousness were needed in order to prove that participants had indeed been unconscious of the stimuli [32]. Therefore, the objective threshold of consciousness was defined as the maximum stimulus duration at which participants are at chance in discriminating between alternative stimulus states [32]. Although those alternative states can refer to several stimuli dimensions (such as its lexical or semantic status), the most conservative measure of consciousness tests the ability participants have in detecting whether or not a stimulus has been presented [38]. The subjective threshold, on the other hand, is the maximum stimulus duration at which participants report lack of awareness of the stimulation [13].

Nowadays, several studies using different paradigms have shown semantic priming effects with both subjective and objective thresholds of consciousness (e.g., Refs. [25,35,58]). Usually, the mechanism postulated at the basis of this unconscious processing is the automatic activation

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of word meaning, in contrast to those effects caused by conscious expectation [65] (see Ref. [59] for an overview of the processes at the basis of semantic priming effects). Some authors have argued, however, that instead of being caused by an automatic separate mechanism, unconscious semantic processing could be explained by residual effects of strategic conscious processing of the prime (e.g., Ref. [38]). One of the means to study this issue is to record brain activity during both conscious and unconscious semantic processing. If brain correlates of unconscious semantic priming are the same as those of conscious priming, it could be claimed that the same kind of mechanism is involved in both cases. On the other hand, the separate processes hypothesis would be supported if conscious and unconscious semantic analyses correlate with different brain markers [16].

For a long time, event related potentials (ERPs) have been a fruitful tool for studying the mechanisms of cognitive processing in several domains (see, for example, Refs. [49,68]). The high-temporal resolution they provide for measuring brain activity allows researchers to obtain a detailed index of the processing chain from stimulation to response that isolated response time (RT) data cannot offer. Language comprehension tasks are one of those suitable for study with this methodology, and one of the most studied ERP components in this field is the N400, which is a negative-going deflection that appears around 400 ms after stimulus onset.

The N400 is an ERP generated by any content word, and it is sensitive to the ease by which a stimulus is integrated with its preceding semantic context [49], possibly reflecting concept activation. It is not unique to the visual modality of stimuli presentation [37]. The distribution and magnitude of the effect may be dependent on the specific task subjects are performing and the recording reference employed [49]. Kutas and Hillyard [48] were the first authors to describe the N400. In their original reading experiments, sentences that ended with semantically anomalous words generated a more negative N400 component than those ending in a congruent manner. The N400 effect, i.e., the amplitude difference between these two conditions, soon was found in other language tasks. Bentin et al. [7] were the first to show this effect in a semantic priming paradigm. In a lexical decision task, word targets that were related to their primes generated a N400 of smaller amplitude than unrelated ones. Since then, the sensitivity of the N400 to conscious semantic relatedness has been replicated in several studies (see Ref. [49] for an overview). Regarding the cognitive processes the N400 reflects, a debate exists on whether it is sensitive either to both strategic and automatic factors in language processing [59] or only to the former.

On the one hand, the N400 modulation by attentional instructions, or controlled conscious processing, has been proven several times. One of the first researchers to show this was Holcomb [36]. In a lexical decision task, this author manipulated at the same time both the percentage of prime-target related pairs and the instructions to either attend or ignore the primes. A N400 effect was evident in both low and high proportion of related pairs, but its magnitude was larger under instructions to attend to the prime. Therefore, it seemed that the N400 was sensitive to automatic propagation of activation, although this effect was enhanced by attention. In a similar way, Kutas and Hillyard [47] showed that even in tasks in which it was not needed to process the meaning of words (i.e., where attention should be paid to the orthographic structure of stimuli) the N400 effect appeared (see also Ref. [5]).

However, those studies did not prove the sensitivity of the N400 to purely automatic processes, given that the tasks used did not prevent the conscious semantic analysis of stimuli. Indeed, the insensitivity of the N400 component to the automatic component of semantic processing was suggested in another series of studies. For example, Bentin et al. [6] presented two lists of related and unrelated words and pseudowords, one in each ear, in a dichotic listening task. Participants had to attend to and remember words presented in one ear while ignoring words in the other ear. A clear N400 effect appeared for stimuli presented in the attended channel, but this effect was missing in the unattended one. Two post-hoc tests (a comparison between false alarms to attended and unattended semantically related words and a repetition priming task) proved that the meaning of unattended stimuli had been processed. Hence, the N400 was insensitive to whatever mechanism was generating this non-controlled analysis of word meaning. In a similar line, Chwilla et al. [14] showed that when attention was not directed to the meaning of stimuli, the N400 was insensitive to semantic relatedness between words (see Refs. [42,55] for converging results). Thus, from these studies it seemed that the N400 amplitude is not modified by an automatic semantic analysis that is not contaminated by controlled strategies.

Masking has been another technique used to study the sensitivity of the N400 to the automatic mechanisms of semantic processing. With this masking procedure it has been proven several times that stimuli that are rendered unconscious by means of a mask are still able to prime responses to another words semantically related to them (e.g., Refs. [25,35,51]). Brown and Hagoort [9] reported that masked semantic priming did not modify the amplitude of the N400, while unmasked priming did. These authors set the threshold where recognition performance for masked words was near chance and then used this value to measure semantic priming for unconscious words. Although both conscious and unconscious words facilitated responses to semantically related stimuli, the N400 amplitude was only modified by primes consciously perceived. However, null results in this study could be questioned given that recognition threshold setting and behavioral semantic priming measures took place in a different group of participants than those from whom ERP were recorded. Thus, it is possible that between group threshold variability made subjects in the ERP group not to show semantic priming at all, which is reinforced by the fact that neither the N400 effect nor any other correlate of semantic analysis appeared. As no behavioral priming was measured in this ERP group, this is an open question.

Indeed, recent investigations have questioned this early masking result. Deacon et al. [21] measured the semantic priming effect in the N400 generated by words preceded by two more words, the second of which could be either masked or not and could be semantically related with the third word or not. ERP results revealed a N400 effect that had the same magnitude and topographical distribution in both conscious and unconscious semantic priming (see also Ref. [69]). Kiefer and Spitzer [44] results corroborated the sensitivity of the N400 to masked semantic priming. These authors showed that primes that could not be identified did modify the N400 amplitude at a short prime-target stimulus onset asynchrony (SOA; 67 ms). On the other hand, when targets followed masked primes after 200 ms of SOA, the N400 was not modulated by semantic relatedness, as in Deacon et al.'s [21] experiment (see also Ref. [43]).

However, neither of the previous reports investigated any other possible correlates of unconscious semantic priming in those conditions in which the N400 was not modulated by this effect. Although in Brown and Hagoort's [9] study there was no correlate of unconscious semantic priming, Kiefer and Spitzer [44] found a frontal ERP modulation in the long SOA condition when semantic priming did not modify the N400. Therefore, in those cases where the brain processes indexed by the N400 are not at the basis of unconscious semantic priming, other electrophysiological markers could signal the activity of the brain regions in charge of such unconscious semantic analysis. Pilot results in our laboratory [77] as well as brief reports in previous literature (e.g., Refs. [44,61,72]) led us to the hypothesis that unconscious semantic analysis could correlate with electrophysiological markers with a more left frontal topography and earlier time course than those of conscious semantic priming.

Therefore, the present study was aimed at studying the differential electrophysiological correlates of conscious and unconscious semantic priming. As previous results in the literature have shown that the prime-target SOA plays a crucial role in determining the N400 sensitivity to unconscious priming [44], we decided to adopt the long SOA interval Marcel [51] used in his study, given the similarity between this paradigm and ours. The finding of differential electrophysiological correlates of semantic priming would suggest that under certain circumstances conscious and unconscious semantic analyses are supported by *partially* distinct brain mechanisms, thus adding support to those theories proposing different mechanisms for conscious and unconscious semantic priming [59,65] in the brain.

With this goal we measured high density ERP (HDERP) correlates of masked and unmasked semantic priming after setting for each participant the subjective (ST) and objective thresholds (OT) of consciousness (see Refs. [13,38]). Moreover, the same stimulus display, materials and subjects were used in both threshold setting and priming phases, and the OT was measured again after the priming phase to ensure individual threshold did not change during the session. This all warranted that perceptual stimulation was the same in both phases and that our results at the OT were due to purely unconscious semantic analysis instead of residual conscious processing of the prime [38].

2. Materials and methods

2.1. Subjects

Forty-five students from introductory courses in psychology (33 female) gave consent for participating in the experiment in exchange for course credits. They all had Spanish as their first language and had normal or corrected to normal vision. All subjects participated in both phase 1 and phase 2 of the experiment.

2.2. Material

A total of 45 associatively related pairs of Spanish words[1], from four to seven letters, were used as stimuli. These words, extracted from a database [73], were used to construct nine different experimental lists. In order to do so, the 45 pairs were divided into three groups, which had similar length and familiarity [12]. From each group three variants were obtained, the first of it by maintaining the pairs semantically related, the second by intermixing words in pairs for them not to be semantically related and the last one by constructing a pseudoword from the second word in pairs not semantically related. Pseudowords were created by changing one vowel or consonant in each word following orthographic normative restrictions in Spanish. Nine sublists were obtained by mixing these three variants, taking five related pairs from one variant, five unrelated from the other and five pseudoword pairs from the variant left. For each participant, three different sublists were used to create the experimental word lists. All participants saw all words, which where counterbalanced across conditions between subjects. Thus, words were repeated eight times for each participant in the whole experiment. In practice

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[1] Mean word familiarity was 5.86. This index represents subjective familiarity as estimated by a Likert rating scale ranging from 1 (poorly familiar) to 7 (highly familiar). The associative strength was calculated by asking a group of participants to generate the first word that comes to mind after reading a prime word (see Ref. [12]). All target words used in this experiment were generated within the first three positions, the average generation position being 1.4.

trials, a different set of words was presented with similar length and familiarity as experimental stimuli. All participants viewed the same words in practice trials.

Each trial was composed of the following stimuli, all white colored in a gray background. A fixation point 5 mm high by 5 mm wide (0.5°), a prime word made up of four to seven uppercase letters each 8 mm high (0.8°) by 5 mm wide (0.5°) presented between brackets (8 mm high by 1 mm wide, 0.8°) or the same brackets without a prime inside but separated by the same distance as if they had a prime word inside. Four different compound masks were formed by 12 uppercase letters, each 8 mm high (0.8°) by 5 mm wide (0.5°). Finally, a target word with the same characteristics as the primes was presented.

All stimuli were presented on a 17 inch Apple Multiple Scan 1075 monitor, connected to a Power Macintosh 8100/100 AV computer running EGIS [63]. This computer was connected by a serial port to a second computer, same model, recording continuous EEG.

2.3. Design

The experiment comprised two phases. In the first, ST and OT of consciousness were individually estimated for each participant, by means of a descendent methodology (see Ref. [20]). This was done by shortening in a staircase manner the time from prime onset to mask onset. Once each threshold was established, 120 trials were run. Therefore, phase 1 comprised 360 trials [120 where the prime was conscious (CO), 120 presented at the ST and 120 at the OT] plus the trials needed to find those thresholds (variable among participants, with a range of 64–126 trials). Half of trials in phase 1 presented a prime between the brackets and in the other half the brackets were presented alone. In trials where the prime was presented, prime and target were related in meaning in one third of them, in another third they were unrelated and in the remaining trials the target was a pseudoword. Phase 2 followed the same structure as phase 1 except that primes were presented in all trials between the brackets. The proportion of related, unrelated and pseudoword pairs was kept the same as in phase 1. Again in a descendent manner, primes were presented consciously in the first block, and at ST and OT in the second and third block, respectively. Each threshold phase comprised 120 trials.

2.4. Procedure

2.4.1. Phase 1

Subjects carried out a detection task on prime words. After a 500 ms fixation point, a prime was presented into brackets for 13 ms on half of the trials and on the other half only the brackets appeared during the same temporal interval. The time from prime offset to mask onset (ISI or inter stimulus interval) varied depending on blocks. After 1486 ms from prime offset (1500 ms of prime-target SOA), a target word was presented and its offset, 500 ms afterwards, signaled participants they had to respond whether the prime was either present or not by pressing either the X or the M key (see Fig. 1). Each threshold block comprised 120 trials, being the prime present in half of them. In the first block (CO), prime-mask ISI was 483 ms. When this block was finished, the ISI was shortened in a staircase manner, in miniblocks of 18 trials, in order to reduce perceptual quality of the prime (following the sequence 250, 78, 52, 39, 26 and 13 ms). At the end of each miniblock, participants were questioned about the consciousness they had on the prime words. This was achieved by means of a Lickert type scale that varied from 1—prime fully unconscious, to 10—prime fully conscious. The ISI at which participants ranked their consciousness with a 3 or below in this scale was defined as the ST. After this, the ST detection block started, in which participants performed another 120 prime detection trials with the ST ISI. When it was finished, ISI was reduced again in a staircase manner. The experimenter checked the detection

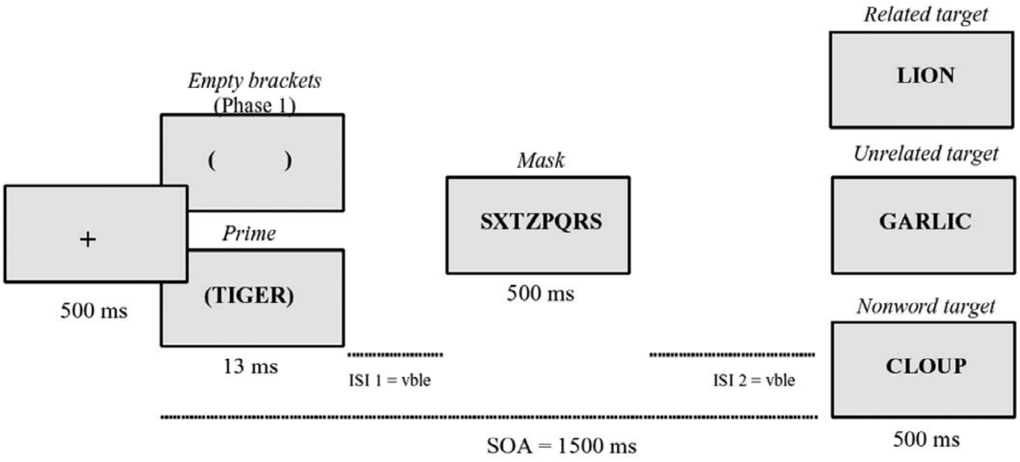

Fig. 1. Experimental procedure in phases 1 and 2.

performance of participants on-line. The criterion for setting one SOA as the OT was either when detection performance was near to chance (i.e., approximately 50% accuracy in the binary detection task) or when the interval could not be shortened anymore (i.e., the SOA was 0 ms). Then, the OT block proceeded for the last 120 trials in phase 1. Participants performed 18 practice detection trials at the beginning of the session with the same structure as CO trials but with a different set of words.

2.4.2. Phase 2

After 2 or 3 weeks from the first session (variable among participants), phase 2 took place. The stimuli display sequence was exactly the same as in phase 1 except that the prime was present in all trials (see Fig. 1). Subjects were to respond, as fast and accurately as possible, to the target with a lexical decision by pressing either the X or the M key depending on whether this stimulus was a real word in Spanish or not. In one third of trials prime and target were semantically related, they were not related in another third and in the trials left the target was a pseudoword. Participants performed 18 lexical decision practice trials with the same structure as the CO block but with a different set of words. As in phase 1, consciousness of the prime was decreased in a descendent manner along blocks. In the first threshold (CO) the ISI was 486 ms. The individual ST was used in the second block for each subject and the OT in the last block. In total there were 360 trials. At the end of the session, participants performed a 120 trials OT detection block, which served as an index of their prime detection in phase 2.

2.5. EEG recording and data analysis

Subjects seated in front of the computer monitor in an electrically shielded room and were instructed to avoid eye blinks and movements during stimulus presentation. Scalp EEG was collected with a 128-channel Geodesic Sensor Net [75] (see Fig. 2) connected to an AC-coupled, 128-channel, high-input impedance amplifier (200 MΩ). Individual electrodes were adjusted until impedances were less than 50 kΩ, as recommended for the Electrical Geodesics high-input impedance amplifiers. Amplified analog voltages (0.1 to 100-Hz band pass) were digitized at 250 Hz (12 bits A/D converter and 0.02 μV minimum resolvable voltage). Recorded voltages were initially referenced to a vertex channel. The EEG was segmented 200 ms before the target word and 800 ms after it and then

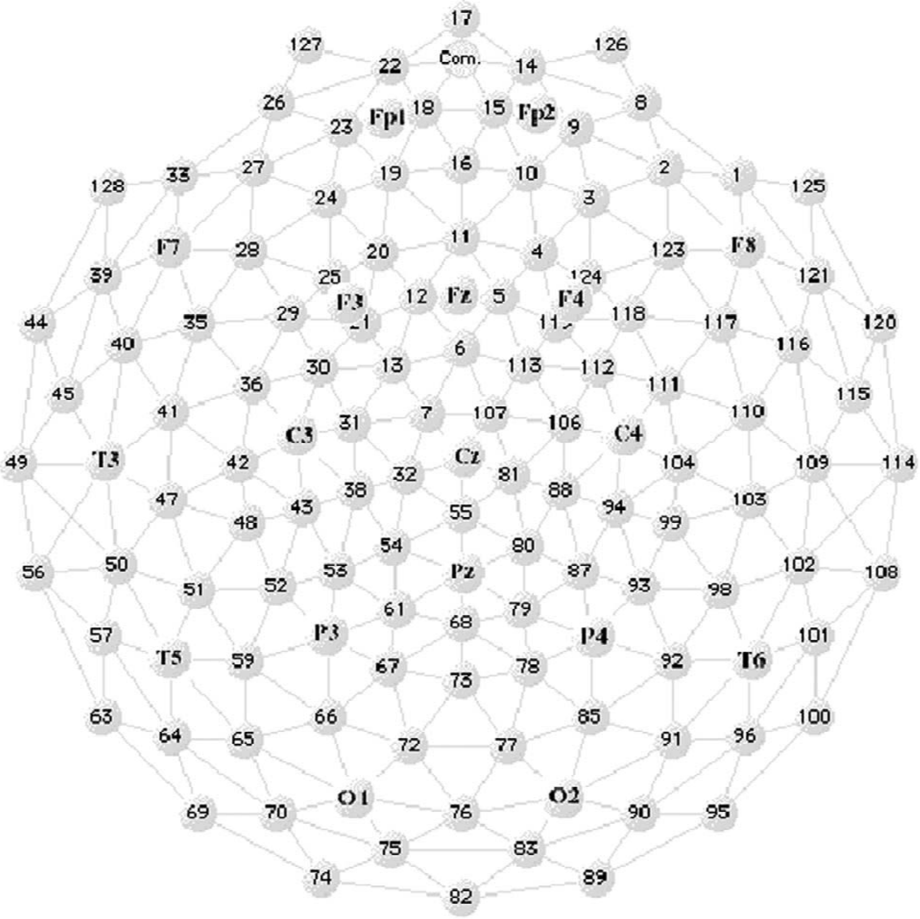

Fig. 2. Layout of the 128-electrode Geodesic Sensor Net.

submitted to software processing for identification of artifacts. Trials containing eye blinks or eye movements (vertical or horizontal electro-oculogram channel differences greater than 70 μV) or more than 7% of bad channels (changing more than 100 μV from one sample to the next, or reaching amplitudes over 200 μV) were not included in the ERPs. Data from individual channels that were consistently bad for a specific subject were replaced using a spherical interpolation algorithm. After incorrect trials and trials containing artifacts were rejected, the mean number of good trials retained for ERP averaging per experimental condition per subject was 32.7 (an average of 18.25% rejected trials). ERPs were re-referenced off-line into an average reference to eliminate the effects of reference-site activity and generate an accurate estimation of the scalp topography of the recorded electrical fields [28,76]. ERPs were baseline-corrected for the 200-ms interval prior to the presentation of the target and digitally band pass filtered from 0.5 to 30 Hz. A final grand average was obtained by averaging across the subject's averages for each experimental condition.

3. Results

3.1. Behavioral results

In phase 1, mean ISI value for the ST block was 36.4 ms (with a range of 52–13 ms) and 0.57 ms for the OT block (all participants but one had 0 as ISI in OT). Participants responses were classified as hits, misses, false alarms and correct rejections and then transformed to a d' index (see Table 1; d' range was $-0.54-0.75$; 0.39 S.D.). Those values, for each participant and threshold, were introduced into a one-way analysis of variance (ANOVA) (Threshold: CO, ST and OT). d' values were different among thresholds, $F(1,44)=111.47$, $P<0.001$. Moreover, CO d′ was different from d′ in the ST block [$F(1,44)=27.38$, $P<0.001$] and d' in the ST differed from d' in OT [$F(1,44)=73.35$, $P<0.001$]. The mean d' in the OT in phase 1 did not differ significantly from zero (single-sample $t=1.85$, $P>0.05$) and it did not differ either from the d' measured in the detection block that took place after the lexical decision task in phase 2, $F<1$.

In phase 2, only trials in which the probe was a word were analyzed. Furthermore, trials containing a wrong response (1.19%) or those in which RT was shorter than 200 ms or longer than 1065 ms (the mean plus two standard deviations, 3.1% of trials) were rejected from analyses. The mean RT for each participant in the remaining trials (see Table 2) was introduced into a three (Threshold: CO, ST and OT)×2 (semantic relationship: Related and Unrelated) two-way repeated measures ANOVA. There was a main effect of Threshold, $F(1,44)=12.67$, $P<0.001$, a main effect of Semantic relationship, $F(1,44)=12.31$, $P<0.001$ and an interaction between the two factors, $F(1,44)=5.85$, $P<0.005$. The semantic priming effect was significant in the CO threshold (52 ms), $F(1,44)=17.60$, $P<0.001$ and in the OT (19 ms), $F(1,44)=4,32$, $P<0.05$, but not in the ST, $F<1$. The priming observed in the CO threshold (52 ms) was significantly greater than that in the OT (19 ms), $F(1,44)=4.13$, $P<0.05$. The same analysis was performed on error rates. No significant effects were found (all F values<1).

Table 1
Mean d' for participants in CO, ST and OT blocks in phase 1 and in the detection block after TDL in phase 2

	Mean d'
CO block	2.47816
UT block	1.63214
OT block	0.30762
OT after phase 2	0.23576

3.2. Electrophysiological results

Only ERP data from phase 2 are reported in this article. Data from three participants were rejected from analyses due to too many bad channels all over the recording. ERP amplitudes from the rest of participants were first analyzed by means of a sample by sample two-tailed t-test and those ERP sections showing modulation by semantic priming were further analyzed with ANOVAs. Bonferroni corrected degrees of freedom were used in all cases in which no previous hypothesis existed regarding the site of the ERP semantic priming modulations. In order to facilitate comparisons, the same time windows and electrodes were used in the three thresholds of consciousness.

3.2.1. CO threshold

Related and unrelated primes first differed in the time range of the N400 component, starting 352 ms after target onset, in centroparietal electrodes (see Fig. 3; in all the ERP figures, positive is plotted upward). In order to evaluate the statistical significance of the N400 effect, a one-way ANOVA (Semantic relation: Related and Unrelated targets) was performed on the averaged amplitudes of the parietal electrodes noted in Table 3, in a time window spanning from 352 to 492 ms.

The N400 effect was significant in this spatio-temporal window, $F(1,41)=20.64$, $P<0.001$. Related and unrelated ERPs also differed in the LPC over right posterior channels (listed in Table 3), from 556 to 588 ms, $F(1,41)=6.676$, $P<0.05$. No other significant effects were found.

Table 2
Mean RT (in ms) of each experimental condition in phase 2

	CO	UT	OT
Related targets	632.71	618.08	604.74
Unrelated targets	684.384	623.96	623.63
Pseudoword targets	747.02	683.37	694.50

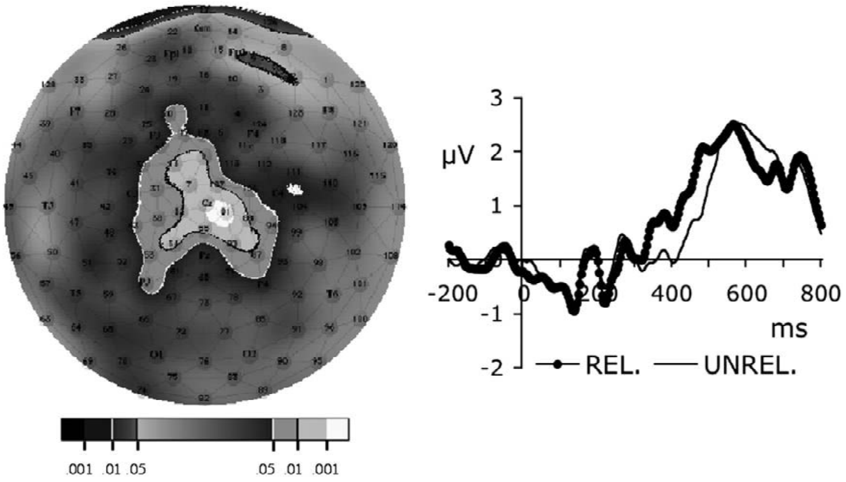

Fig. 3. *t*-Test interpolated map at 484 ms after target onset in CO block. Both the N400 effect topographical distribution and all the epoch (averaged across channels) are shown.

Table 3
Electrodes selected for the ANOVA in CO and OT blocks

CO block	N400	6, 7, 13, 31, 32, 38, 43, 53, 54, 55, 60, 80, 81, 88, 94, 107 129
	LPC	72, 73, 76, 77, 78, 83, 84, 85, 86, 90, 91, 92
OT block	N200	54, 55, 61, 62, 67, 68, 72, 73, 76, 77, 78, 79, 80
	Left frontal	12, 20, 21, 24, 25, 28, 29, 35
	Right frontal	1, 3, 4, 5, 6, 11, 12, 105, 106, 112, 113, 118, 119, 122, 123, 124

3.2.2. ST

Neither the N400 effect nor the LPC were significant (as spatio-temporally defined in the CO threshold; both *F* vaules<1). No other significant effect was found.

3.2.3. OT

Related and unrelated waveforms differed from 212 to 248 ms after target onset in posterior medial electrodes (Table 3). This is because the peak of the N200 component is more negative for related targets than for unrelated ones, $F(1,41)=5.52$, $P<0.05$; see Fig. 4.

From 280 to 320 ms after target onset, unrelated targets become more negative in left frontal electrodes (Table 3), $F(1,41)=9,19$, $P<0.005$; see Fig. 5.

Finally, related and unrelated waves differ in right frontal electrodes from 316 to 500 ms (see Table 3),

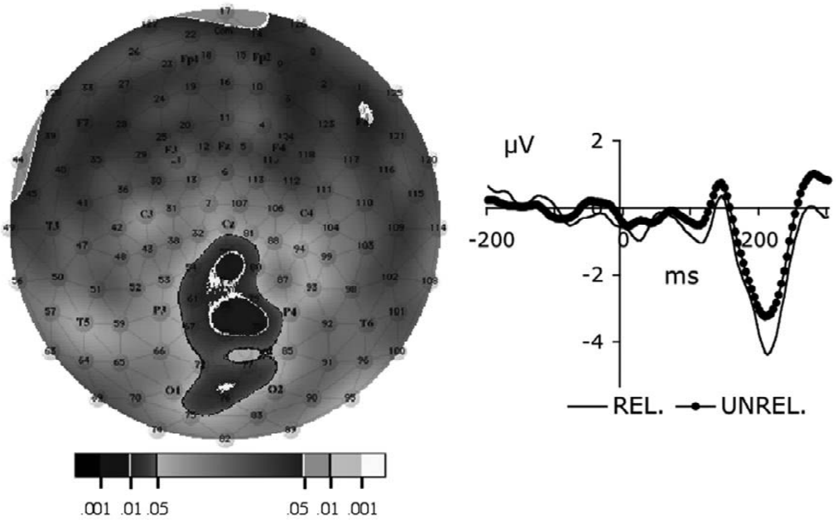

Fig. 4. *t*-Test interpolated map at 220 ms after target onset in OT block. The map shows the distribution of the modulation in the N200 component, and all the epoch is shown averaged across channels showing the effect.

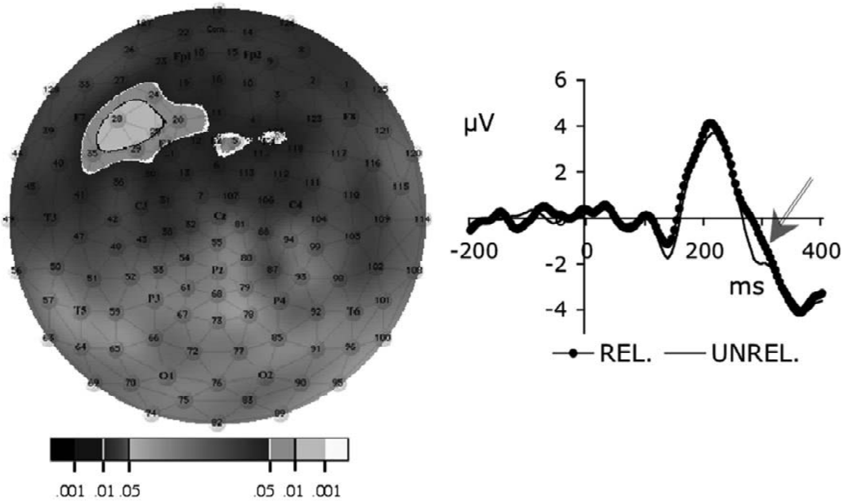

Fig. 5. *t*-Test interpolated map at 292 ms after target onset in OT block. Both the topographical distribution of the left frontal effect and all the epoch averaged across channels are displayed.

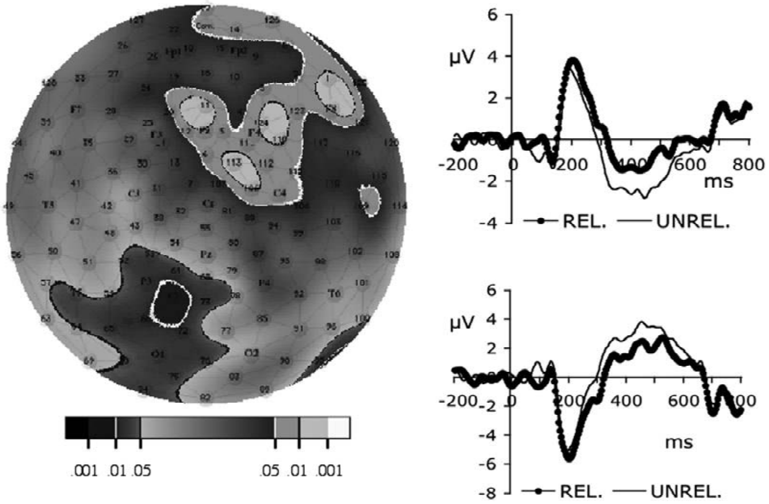

Fig. 6. *t*-Test interpolated map at 332 ms after target onset in OT block. The distribution of the modulation in right anterior and left posterior electrodes is shown, as well as all epoch activity averaged across channels that show the effect.

$F(1,41)=8.13$, $P<0.01$, with a reversed amplitude effect at left posterior electrodes, $F(1,41)=7.47$, $P<0.01$, see Fig. 6. The N400 effect, as defined in the CO threshold, was not significant ($F<1$)[2] as neither was the LPC, $F(1,41)=3.31$, $P>0.08$. The interaction in the spatiotemporal window of the N400 between the CO and OT is significant; $F(1,41)=3.96$, $P<0.05$. In order to assess whether the right frontal effect in the OT block had the same of different scalp distribution as the N400 in the CO block, the interaction between Threshold, Semantic Relation and Topographic distribution (i.e., sensor group) was computed on normalized ERP data as proposed by McCarthy and Wood [56][3]. The ANOVA shows a significant second order interaction between Semantic Relation, Consciousness Threshold and Sensor Group, $F(1, 40)=9.6$, $P<0.005$.

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[2] As noted by one of the reviewers, it may be possible that a small N400 effect was present in the OT condition but was masked by our high pass 0.5 filtering. However, the same ANOVA performed on 0.1–30 Hz band pass filtered ERPs showed this was not the case ($F<1$).

[3] For each participant, experimental condition and time point, the minimum and maximum value across right frontal and central groups of electrodes (see Table 3) were determined and the normalized value n at each electrode group j was computed according to:

$$n_j(t)=\frac{x_j(t)-\min}{\max-\min}$$

where $x_j(t)$ is the mean potential at sensor group j and time point t.

4. Discussion

The goal of this investigation was to study the extent to which conscious and unconscious semantic priming are supported by overlapping or differential brain mechanisms at a long prime-target SOA. We obtained a behavioral semantic priming effect for both conscious and unconscious priming. Moreover, these two effects correlated with different ERP markers depending on consciousness of the prime. In the first place, our results are in line with previous behavioral research on semantic priming. Conscious stimuli that are presented at a long prime-target SOA are able to semantically prime speeded responses to other words. In addition, unconscious masked words presented at the OT of consciousness are still able to prime words presented after a 1500 ms delay. Although some authors characterize automatic or unconscious effects as decaying fast in time (e.g., Refs. [23,65]), our results show that, at least under certain circumstances, unconscious effects can persist more than one second (see Ref. [22], for converging results). Indeed, early reports of unconscious semantic priming that employed the LDT used a long prime-target SOA (e.g., Refs. [3,33,51]). Therefore, although unconscious semantic priming in the OT is smaller in magnitude (19 ms) than priming in the conscious threshold (52 ms), our results add to the wealth of studies showing that unconscious words, even when presented under strict masking conditions, are able to prime other words related in meaning.

The lack of unconscious priming at the ST, although puzzling, is in the same line as some previous results showing that d' and amount of priming do not correlate or are even negatively correlated in some masked semantic priming procedures [18,30,40,43,46]. That is, it is not always the case that a better perceptual quality leads to a deeper processing of word meaning. There are, indeed, some theories devised to explain phenomena like this one. The center-surround mechanism by Dagenbach and Carr [18] is perhaps the most well known (see also Ref. [30]). These authors proposed an attentional mechanism that helps stimulus recognition by the inhibition of related representations in circumstances in which the experimental setting renders recognition hard to accomplish (like, for example, stimuli masked at the subjective threshold of awareness [19] or very infrequent words whose semantic representations are not well established in memory (see Ref. [18] for more details). Following Dagenbach and Carr [18]), it may be possible that the descendent testing methodology used in this study led participants to narrow down the attentional focus to help identifying the stimuli, and this may have inhibited the semantic associates of word targets and thus make the semantic priming benefit disappear. The fact that this attentional center-surround mechanism does not operate in all circumstances but only when information retrieval is difficult but still possible [18] could explain why semantic priming was found in both CO and OT blocks. However, our investigation was not aimed at exploring this specific question and thus cannot prove this to be the right explanatory mechanism for the lack of priming effects at the ST. Hence, more investigations will be needed in order to shed light on this issue.

On the other hand, our study replicates and extends previous results on the ERP correlates of conscious and unconscious semantic priming. When primes were consciously perceived, ERP to target words show a N400 effect at parietal locations in the scalp together with a later modulation on the LPC. On the other hand, when primes were masked at the OT, the N400 effect disappeared. Instead of it, a posterior N200 effect together with later modulations in left frontal and right fronto-central waves appeared. Our results are in accord with those of Brown and Hagoort [9] who showed a masked priming effect that was not indexed by an N400 effect. Since then, several studies have reported that the N400 can in fact be modulated by the meaning of unconsciously perceived words, given that the SOA between words is short enough [44] (see Refs. [21,43], although see Ref. [24]). This modulation in the N400 is taken to prove that this component is sensitive to automatic mechanisms leading to semantic facilitation effects, which have a fast decay rate after unconscious presentation conditions. However, the N400 is not sensitive to the unconscious semantic priming effect found in our study, although its amplitude was modulated by consciously perceived primes. This means that whatever mechanism is generating our semantic priming effects, it is at least partially different from the one involved in Refs. [21] and [43].

There are some variations among the procedures of the experiments that could be at the basis of the divergence in the results. In the first place, the prime-target SOA used in our study was longer than the SOA in previous reports showing N400 modulation by unconscious semantic priming [22,43,44]. As a matter of fact, Kiefer and Spitzer [44] results suggest the length of the SOA may be the main variable determining the N400 sensitivity to unconscious effects. In their experiment they showed that when prime-target SOA was really short unconscious semantic priming modify the N400 whereas this effect was not found when the SOA was long enough. In order to explain why the SOA at which the N400 is no longer modified by unconscious words varies among studies, these authors claim that the duration of unconscious automatic semantic activation depends on the specific procedure employed [44]. For example, in an attentional blink paradigm [50] this activation must last longer because the N400 is modified even at a 583 ms prime-target SOA [66] whereas in the paradigm employed in [44] it had decayed at 200 ms prime-target SOA.

Another difference is the task employed to set the OT of awareness. In our study, performance of participants was driven near to chance in a stimuli detection task, whereas the other studies used different criteria (recognition of words, [21]; forced discrimination in Ref. [43]), which some authors have characterized as being less stringent that a pure detection task [38]. Finally, in our paradigm all stimuli were repeated several times for each participant whereas previous studies presented words only once. Thus, although the most likely cause for the absence of unconscious N400 modulation is the long prime-target SOA, we cannot reject the other details as contributors to our results.

On the other hand, our experiment was not designed to explore which are the causes of a lack of N400 modification by unconscious semantic priming. Instead, our aim was to study the electrophysiological markers that do indeed correlate with the unconscious priming that actually appears in those situations in which the N400 is not modulated by unconscious words that still prime other words.

4.1. Novel correlates of unconscious semantic priming

The use of a HDERP recording system allowed us to obtain a more exhaustive sampling of the electrical signal on the scalp and thus to find some novel correlates of unconscious semantic priming. When primes are unconsciously processed, semantically related targets generate a N200, peaking at 212 ms, of larger amplitude than that generated by unrelated targets. Moreover, prime-target semantic relation also modulates ERPs at left frontal electrodes around 280 ms and at right frontal and left posterior locations starting at 316 ms. Although language related left frontal modulations in ERP have been reported several times (e.g., Refs. [8,60–62,79]), the same is not true for the other two ERP modulations revealed by our data. The use of a HDERP recording system with our specific experimental paradigm allowed us to detect some ERP effects which may be harder to find with other ERP recording techniques and references (see Refs. [17,28]).

The modulation in the amplitude of early posterior components by language variables has been reported before. The N170 component, as well as the Recognition Potential [52,67] amplitude, differs depending on whether stimuli are words or pseudowords (see Ref. [79]), and its likely generators have been located in a posterior fusiform area, the so-called visual word form area (VWFA [15,53]). Moreover, Martín-Loeches et al. [53] showed that the Recognition Potential can be modified by semantic factors, which is in line with our results and with other reports of early semantic activation (Dien et al. [29]). This N170 component is also modified by manipulations outside language, like orientation of human faces (e.g., Ref. [31]), and it is also sensitive to the degree of practice participants have with stimuli [74]. Although the maximum peak and topographical distribution of the N200 we measured is slightly different from previous reports [8,15,17], it is likely that its generators are in the VWFA or in close regions, given its sensitivity to language variables. The repetition of words that took place through the experimental sessions could be considered as a sort of practice, what could have boosted this early N200 component sensitive to semantic variables (see Refs. [29,70]).

On the other hand, the modulation of left frontal electrodes is common in different language paradigms (e.g., Refs. [8,61,62,79]), being the N3 the component focus of research. Some authors [60,64] claim that this early frontal effect signals lexical process while later and more posterior ones (i.e., the N400) reflect discourse integration [49]. These frontal ERP modulations could be generated by frontal left hemisphere regions related to language processing [8]. Specifically, there are some regions that seem to be involved in semantic tasks and that show semantic repetition priming in several neuroimaging studies [10,11,26,41,57] as well as ERP studies [64,72]. Moreover, these activations remain in amnesic patients [34], what drives some authors to relate these regions with implicit recollection of semantic information [78]. All this together suggests that the negative deflection that appears for semantically related targets in our ERP data could be generated by modulations in the activity of these frontal left regions involved in semantic processing.

Finally, right frontal electrophysiological effects elicited by language variables although less common than left lateralized effects have been previously reported (e.g., Refs. [1,45]). This right scalp effect we have found may be driven either by some specific characteristic of our lexical decision task or by a more general semantic process, but this issue should be addressed in future research.

4.2. Conscious vs. unconscious semantic priming

The electrophysiological indices of semantic priming in our study were qualitatively different depending on whether primes were either consciously or unconsciously perceived. Targets preceded by conscious primes generated a N400 effect at centroparietal scalp locations. However, when the same targets were primed by unconscious stimuli, the N400 effect completely disappeared and instead of it the N200 and frontal sites were modulated. It may be important to note that perceptual stimulation was exactly the same in both conscious and unconscious target related ERPs (as all the targets words are presented during the same amount of time and after the same prime-target SOA in all conditions), and therefore electrophysiological differences could only be generated by differential consciousness of the prime. The electrophysiological markers of conscious and unconscious priming in our study show that, al least in a long prime-target SOA procedure, the mechanism at the basis of these effects are *partially* dissociable. Therefore, it is not likely that unconscious effects in our procedure are generated by residual conscious expectative but rather by unconscious mechanisms. In general, our results raise more general issues on the relation between conscious and unconscious processing in the human brain.

The fact that electrophysiological indices of semantic facilitation are, at least, partially dissociable suggests that conscious and unconscious processes differ to some extent. Contrary to models which claim that a certain cognitive representation is unconscious because its level of activation has not reached the threshold for consciousness (e.g., Refs. [4,27]), our results rather support those theories that relate conscious and unconscious processes to partially separable brain anatomy and different functions in the cognitive system [2,16,23]. The finding that consciousness of a stimulus qualitatively changes the pattern of ERP effects suggest that, instead of a mere raise in the level of activation of a set of representations, consciousness of stimulation recruits a unique set of brain areas and processes to perform the cognitive functions that are uniquely tied to conscious information processing [16,23].

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