Is the N400 category-specific? A face and language processing study

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N400 event-related potential (ERP) components have been observed during semantic incongruity detection in language, face identity and/or expression. However, it is still unclear whether semantic processing is functionally equivalent, since no study has directly investigated within the same participants the occurrence of the N400s for language and faces. We recorded ERPs while subjects performed incongruity detection on words, facial identities and facial expressions, with conditions matched to involve context integration. N400s were identified on central-parietal electrodes only for language and face identity processing. Scalp topographies of these N400s differed but a LORETA inverse solution identified a common functional generator in the left lateral frontal cortex, suggesting a general role of this brain region in selecting and contextually integrating semantic information. *NeuroReport* 15:2589–2593 © 2004 Lippincott Williams & Wilkins.

Key words: Event-related potentials; Face processing; Language processing; N170; N400; Source localization

INTRODUCTION

The N400 is an electrophysiological signature of semantic processing that has been widely investigated in the language domain (for review see [1]). This negative-going ERP component is maximal over centro-parietal electrode sites and emerges about 250 ms after stimulus onset, with a maximum that peaks at around 400 ms post-stimulus. In the seminal study by Kutas and Hillyard [2], participants silently read sentences which ended with a congruent or an incongruent word. The N400 was larger for incongruent (e.g., the hen laid an oven) than for congruent words (e.g., egg). The better the semantic fit between a word and its context, the more reduced is the amplitude of the N400 [3].

N400-like components have also been identified for non linguistic visual stimuli, especially for face processing, and related to general contextual integration [4,5], similar to the linguistic N400 [5]. Several N400-like effects have been found during matching tasks in which participants had to decide whether or not two faces depicted the same identity [6] or the same facial expression [7–9]. N400-like components have been inconsistently observed only for identity at around 350 ms in fronto-central sites [7], across all the scalp [6] or for identity and expression between 350 and 550 ms in parietal sites [9] or at around 400 ms but with different topographies over the right temporal regions [8]. It is worth noting that little is known about whether all the N400s, enhanced during semantic incongruent information processing, elicit common or distinct neuroanatomical substrates as a function of the visual category of the stimulus (words or faces). Indeed, none of the reported studies could determine the exact relationship between the N400 and the N400-like, as these components were not studied within the same participants.

The aim of this study is to unravel the precise nature and relationship of the N400 components by exploring their occurrence among the same participants during language and face processing, with the face tasks designed to involve context integration in order to give the best match to sentence reading. Since differences between visual categories have been identified for the N170 component [10,11], its time course for incongruity detection was also investigated. Finally, a LORETA inverse solution was applied to define the neuronal substrates involved in all the conditions.

MATERIALS AND METHODS

Subjects: Fifteen right-handed native French speakers voluntarily participate in the study, which was approved by the ethical committee of the University of Geneva.

Stimuli and procedure: Participants performed a semantic incongruity detection task with three conditions (word, identity and expression).

Word stimuli: A total of 140 French congruent sequences (mean ($\pm$s.d.) length 7.5 ± 1.5 words) were devised. The mean frequency of the final words was 52 per million (Frantext database – http://www.atilf.fr) and their mean length of letters was 6.2 ± 1.9 with a cloze probability of 70% or higher, covering a visual angle of $\sim 1.43 \times 2.6°$. Semantic incongruent sentences were obtained by randomizing the final words. All the sentences and final words were counterbalanced and presented as congruent and incongruent trials across all the subjects.

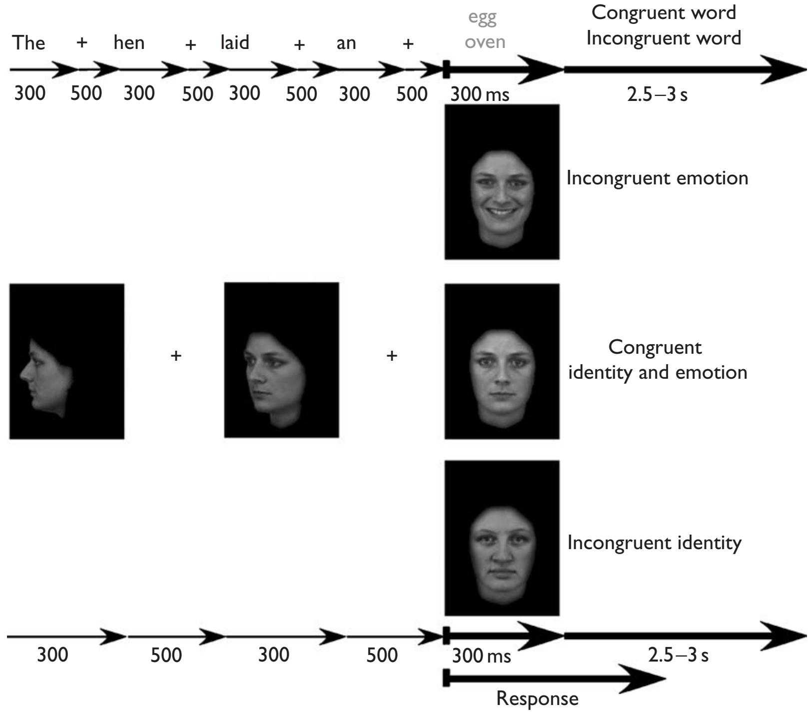

Fig. 1. Top: experimental design used for the word condition. Centre: experimental design used for the identity and expression conditions; congruency depends on the instruction given (identity *vs* emotion incongruity detection).

Word incongruity detection condition: Participants silently read 140 sentences (half congruent) presented one word at a time in black on a white background on a computer monitor 120 cm away. The final word appeared in red, indicating to the subjects to decide whether or not the sentence was semantically congruent (Fig. 1).

Face stimuli: Seventy unfamiliar face identities (35 female, 35 male) each posing with a neutral, happy and fearful expression (Karolinska Directed Expressional Faces set, Lundqvist, D., Flykt, A. and Ohman, A., 1998) were used for creating identity and expression incongruity detection conditions in sequences of one by one face presentations: profile, three-quarter and full frontal views (Fig. 1). External features (e.g. hair) were removed, and the images occupied a visual angle of $\sim 4.29 \times 2.62^{\circ}$. Congruent sequences ($n=70$) consisted of the presentation of faces with the same identity and the expression. In the incongruent identity list ($n=70$), a change of identity, but not gender and expression, occurred during full frontal face presentation. In the incongruent expression list ($n=70$), a change of expression, but not identity, occurred during the full frontal face presentation. The nature of the expression was counterbalanced across lists and conditions.

Identity and expression incongruity detection conditions: For each full frontal face presentation, in their respective condition, participants had either to decide whether the depicted identity or the expression was congruent or incongruent with previous presented faces.

All the sequences were interleaved with a randomized interval between 2 and 2.5 s during which a fixation cross was presented on all trials.

The order of the experimental conditions and the labels of the keys (congruent or incongruent) used for the responses were counterbalanced across subjects.

Behavioural analysis: Mean reaction times and the percentage of errors were statistically analysed using repeated measures ANOVAs.

ERP recordings and analysis: EEG was continuously recorded from 64 Ag/AgCl electrodes. A left mastoid electrode was used as a reference. Ocular artefacts were monitored and vertical blinks were corrected off-line by an automatic algorithm. The recorded signal was low-pass filtered at 30 Hz and rescaled across the average reference. EEG epochs were baseline corrected to the first 200 ms. Finally, all the epochs resulting in a correct answer were carefully scanned and remaining artefacts were rejected before being averaged to give individual and grand-mean ERPs.

In order to investigate the N400, the electrode showing the largest effect for the language condition was selected and repeated measures ANOVAs were performed, for time windows of 50 ms each, on the amplitude with condition (word, identity *vs* expression) and semantic congruency (congruent *vs* incongruent) as factors. The N170 component was investigated by analyzing ERP peak amplitudes and latencies on the P7 and P8 occipito-temporal electrode sites between 140 and 190 ms. A repeated measures ANOVA was performed with condition (word, identity *vs* expression) and semantic congruency (congruent *vs* incongruent) and hemisphere (left *vs* right) as factors.

Greenhouse-Geisser adjusted degrees of freedom are reported.

Table I. Mean (±s.e.) reaction times and percentage of errors for all the conditions.

	Word		Identity		Expression	
	Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent
Reaction times	777 (47)	822 (50)	628 (41)	836 (46)	719 (33)	806 (36)
Errors	0.55 (0.2)	0.55 (0.2)	3.9 (1.15)	26 (2.3)	1.5 (0.3)	9.1 (1.5)

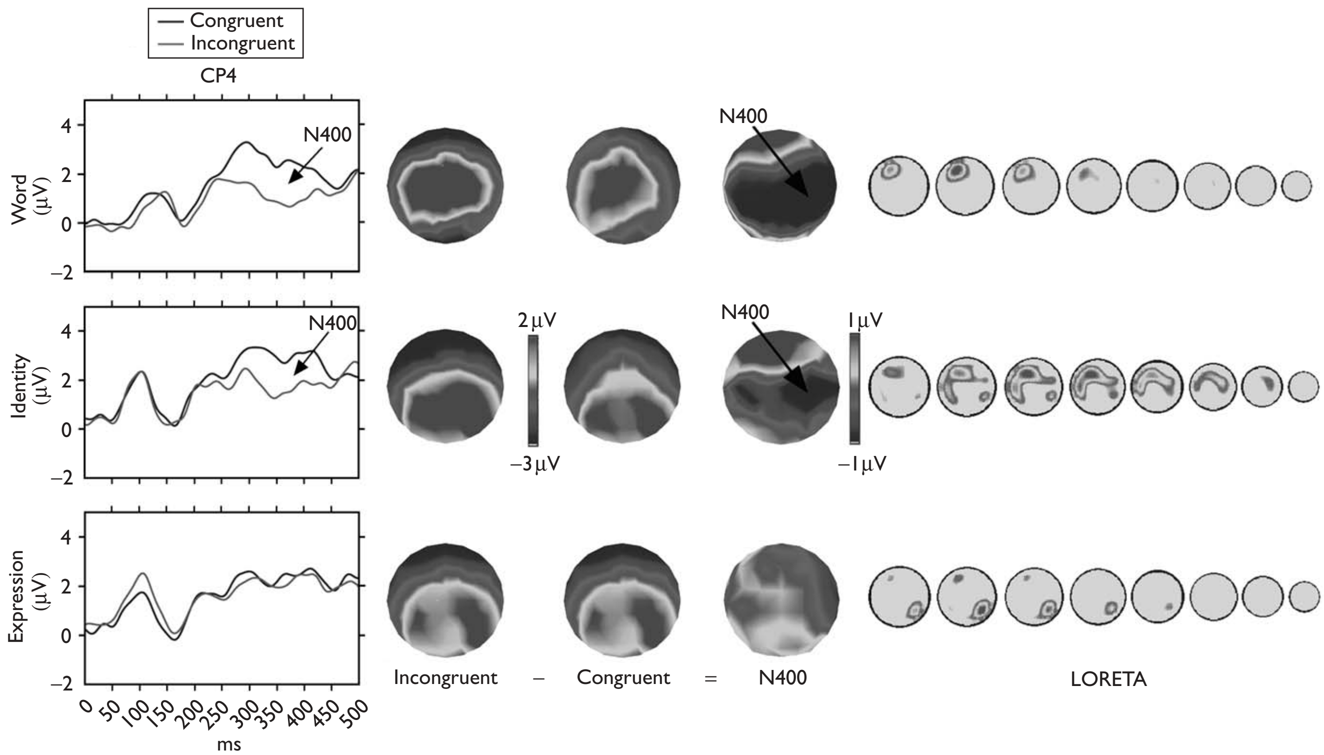

Fig. 2. Left: grand-averaged ERP waveforms recorded at centro-parietal electrode (CP4) in response to word, identity and expression processing. Positive values are up. Centre: map topographies from 300–400 ms for all the conditions and their subtraction. Right: 3D brain activity estimated for the surface maps. Solutions are represented in eight transverse slices through the spherical head model with the lowest slices to the left (nose up, left ear left).

Source localization: To estimate the brain activity underlying the ERP signal, inverse solutions were calculated with LORETA [12].

RESULTS

Behavioural results: Mean reaction times and the percentage of errors for each condition are shown in Table 1. Statistical analysis revealed a significant effect of the semantic congruency factor ($F(1,14)=32.37$, $p<0.001$): congruent trials were faster processed than the incongruent trials. A significant interaction effect was also found ($F(1.34,18.76)=11.52$, $p<0.001$), showing faster processing for the identity in the congruent situations. Regarding the percentage of errors, a significant interaction was found between the conditions and the semantic congruency ($F(1.58,22.24)=45.67$, $p<0.001$). Identity and expression conditions induced more errors than words, especially in the incongruent situations.

ERPs: Figure 2 shows the time course of the N400 on the right centro-parietal electrode (CP4) as well as the topographies and source localizations for all the conditions. Repeated measures ANOVAs were performed on four time windows of 50 ms each, going from 250 to 450 ms. Semantic incongruity elicited larger negativities over all these time periods ($p<0.01$ at least) and no significant differences were observed for the condition as factor. Crucially, however, significant interactions between conditions and semantic congruency were found in two time windows, going from 300 to 350 ms ($F(1.94,27.2)=5.53$, $p<0.01$) and 350 to 400 ms ($F(1.73,24.3)=3.76$, $p<0.05$). *Post-hoc* analysis revealed that this effect was present only for the word and face identity conditions ($p<0.001$). For the word condition, LORETA localized the generators of electrophysiological incongruities in the left lateral frontal cortex. Detection of face identity incongruities involved a more distributed region on the left frontal cortex, accompanied by a right occipito-temporal activity. For face expression, the greatest activity was observed in the right occipito-temporal region rather than in the left frontal cortex.

The time course of the N170 component is reported in Figure 3. A significant interaction was found between the condition and electrodes ($F(1.35,19.01)=26.84$, $p<0.001$),

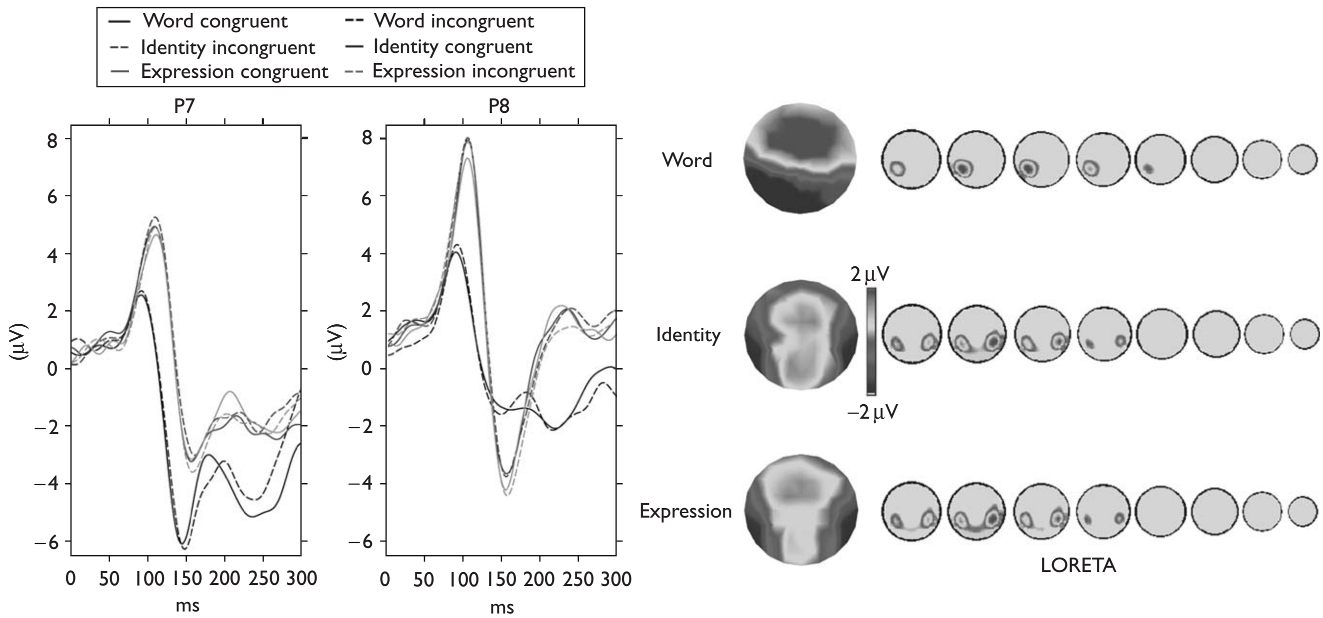

Fig. 3. Left: grand-averaged ERP waveforms for the N170 component recorded at lateral temporo-occipital electrodes (P7 and P8) in response to word, identity and expression. Positive values are up. Middle: map topographies from 140 to 190 ms for the congruent conditions only. Right: 3D brain activity estimated between 140 and 190 ms. Solutions are represented in eight transverse slices through the spherical head model with the lowest slices to the left (nose up, left ear left).

words eliciting a larger negativity on the left (−7.25 μ *vs* −3.9 μ for faces) and faces on the right hemisphere (−4.9 μ *vs* −3.35 μ for words). A trend was observed for the same interaction on latencies ($F(1.31,18.47)=2.57$, $p=0.094$). In this time period, LORETA identified bilateral generators in the occipito-temporal regions, dominant in the right hemisphere for face conditions, and only a left unilateral source in the same region for words.

DISCUSSION

Behavioural results showed that congruent detections are processed faster than incongruent detections for all conditions. Word processing induced considerably less errors than face processing, with face identity being the more difficult condition [5,9]. Recognition of unfamiliar faces relies mainly on the external features [13], removing such facial information increased the difficulty for the identity condition and provide an explanation of the observed results.

Regarding ERPs, three important results were established. First, a classical N400 was identified between 300 and 400 ms at the central-parietal sites during semantic incongruity detection in the word condition [1–3]. In the same period and location, a N400 component was also identified for identity [5,7,9], but not in the expression condition [7]. It is worth noting that using unfamiliar faces did not influence the occurrence of the N400 for incongruent identities [6,8]. These observations provide direct evidence that this component is not category-specific (words *vs* faces), but instead condition-specific (word and identity *vs* expression). Scalp topographies of the N400s and LORETA source localizations refined these observations at the functional level. LORETA identified an activity in the left lateral frontal cortex (lFC) for the N400 elicited in the word condition. A recent fMRI study [14] identified an increase of the responses in the left inferior frontal gyrus (lIFG), a region within the lFC, for semantic incongruities occurring on the last word of a sentence. Thus, a critical contribution of the lIFG [14], within the lFC activity defined by LORETA, can be inferred. For face Identity condition LORETA identified a widespread activity over the lFC, in line with fMRI studies on face working memory tasks showing left prefrontal [15] or frontal [16] activations accompanied by face-sensitive responses [15] in the fusiform face area (FFA) [17]. Crucially, the lFC was activated in both of our ERP conditions. The functional role of the left prefrontal cortex for faces [15] or language (for review see [18]) has been related in selecting semantic knowledge from a set of alternatives. Thus, our findings posit the lFC as a critical candidate in controlling and integrating semantic information independently of the visual category at hand (words or faces) during context integration.

Second, critically, the lFC was sensitive to the nature of the handled information (word, identity *vs* expression), since only weak activations of the lFC and no enhanced N400 were observed for face expression incongruity. This finding confirms that identity and expression processing are subserved by different neural pathways [7,9], and indicate that expression incongruity detections take part in other regions of the brain, most likely in the amygdala, a structure highly involved in emotion processing (for recent review see [19]). However, because the activations arising from the amygdala are not directly recordable with the ERP technique, future fMRI studies are planned to define where expression incongruity detection occurs in the brain.

Third, regarding the category-specific N170 component, no differences between the conditions were found for the detection of incongruities at the semantic level. However, in line with recent findings [11], the N170 component was larger on the right hemisphere for the faces, and in the left for the words, suggesting a functional difference between these categories during this time period. LORETA inverse solution refined these findings by defining a bilateral pattern of activity in the FFA regions for faces [10], with a right hemisphere advantage. For words, a unilateral source of activation in the left part of the occipito-temporal cortex was observed [11,20]. These findings complete the knowledge, established by using the LORETA algorithm, of the neuronal structures engaged in this critical time period of high-level visual categories processing (for a detailed review on faces and objects see [10]).

CONCLUSION

Larger N400s, but with different topographies, were evoked for incongruent trials during language and face identity processing. Such enhanced negativities were absent for facial expressions processing. Although the N400 for words and faces elicited distinct semantic pathways, they recruited a common generator in the left lateral frontal cortex, reflecting a functional involvement of this brain region in selecting and integrating information at the semantic level. Altogether, these observations indicate that the N400s are sensitive to the nature of semantic information processing, rather than the visual categories *per se*.

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