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Author(s): Kujala, A., Alho, K., Service, E., Ilmoniemi, R. J., & Connolly, J. F.

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Activation in the anterior left auditory cortex associated with phonological analysis of speech input: localization of the phonological mismatch negativity response with MEG

Kujala, A.[a,b,*], Alho, K.[c], Service, E.[c,d], Ilmoniemi, R. J.[b,e], & Connolly, J. F.[d,f,g]

[a] Cognitive Brain Research Unit, Department of Psychology, University of Helsinki, P.O. Box 9, FIN-00014, Finland

[b] Helsinki Brain Research Center, University of Helsinki, P.O. Box 9, FIN-00014, Finland

[c] Department of Psychology, University of Helsinki, P.O. Box 9, FIN-00014, Finland

[d] Cognitive/Clinical Neuroscience Unit, Department of Psychology, Dalhousie University, Halifax, NS, Canada

[e] BioMag Laboratory, Engineering Centre, P.O. Box 340, Helsinki University Central Hospital, FIN-00029 HUS, Finland

[f] Department of Psychiatry, Faculty of Medicine, Dalhousie University, Halifax, NS, Canada

[g] Department of Pediatrics, Faculty of Medicine, Dalhousie University, Halifax, NS, Canada

[*] Corresponding author. Cognitive Brain Research Unit, Department of Psychology, University of Helsinki, Siltavuorenpenger 20 C, P.O. Box 9, Helsinki FIN-00014, Finland. Tel.: +358 9 191 29459; fax: +358 9 191 29450. E-mail address: anu.kujala@helsinki.fi (A. Kujala)

Abstract

The spatio-temporal dynamics of cortical activation underlying auditory word recognition, particularly its phonological stage, was studied with whole-head magnetoencephalography (MEG). Subjects performed a visuo-auditory priming task known to evoke the phonological mismatch negativity (PMN) response that is elicited by violations of phonological expectancies. Words and non-words were presented in separate conditions. In each of the 318 trials, the subjects first saw a word/non-word (e.g., 'cat') that was soon followed by a prime letter (e.g., 'h'). Their task was to replace mentally the sound of the first letter of the word/non-word with the prime letter, thus resulting in a new word/non-word (e.g., 'hat'). Finally, an auditory word/non-word either matching or mismatching with the anticipated item was presented. In most subjects, a PMNm followed by a later, N400m-like negativity was obtained in the left hemisphere to the mismatching auditory stimuli. A similar response pattern was obtained in the right hemisphere only in a few subjects. Source localization of the N1m, an index of acoustic analysis, and the PMNm and N400m-like responses was performed using L1 minimum-norm estimation. In the left hemisphere, the PMNm source for the words was significantly more anterior than the source of the N400m-like response; for the non-words, the PMNm source was significantly more anterior than the sources of the N1m and the N400m-like response. These results suggest that the left-hemisphere neuronal networks involved in sub-lexical phonological analysis are at least partly different from those responsible for the earlier (acoustic) and later (whole item) processing of speech input.

Keywords
Auditory word recognition; Phonological processing; Lexical processing; Phonological mismatch negativity (PMN); N400; Magnetoencephalography (MEG)

1. Introduction

Auditory word recognition requires multiple processing steps before the meaning of the speech signal is perceived and, further, integrated into a sentence context [7]. Mapping the input onto the corresponding lexical entry occurs, due to the nature of speech input, in a cascading manner, with the number of lexical candidates diminishing with time [19]. Phonological analysis is required before semantic evaluation; this analysis is extended when the input does not agree with preactivated candidates (normally triggered by a constraining context). Accumulating evidence suggests that this effort is reflected in event-related potentials (ERPs) in the form of the phonological mismatch negativity (PMN [2– 4,8,31]), which peaks between 200 and 350 ms after stimulus onset. The PMN thus precedes the N400 [17,18], which apparently indicates the semantic processing of sentence-primed spoken or written words (a process that peaks approximately 400 ms after word onset).

Both the PMN and N400 have larger amplitudes (i.e., increased negativity) to stimuli that mismatch compared with those that match the anticipated stimuli or sentence context. However, the critical feature to which the violation occurs differs between these brain responses. In the experiment of Connolly and Phillips [2], the PMN was isolated from the adjoining N400 by modifying the spoken sentence ending words. The phonologically mismatching (unexpected initial phoneme) but semantically matching (appropriate within the sentence context) words elicited the PMN, whereas no N400 response was obtained in this condition (e.g., When the power went out the house became quiet— 'dark' being the high cloze probability ending). In contrast, semantically incongruent words that began with the expected phoneme elicited the N400 but no detectable PMN (e.g., The gambler had a streak of bad luggage— 'luck' being the expected high cloze ending). When the sentence-ending words were both phonologically and semantically unexpected, both PMN and N400 responses were elicited, and, in the opposite case, neither the PMN nor N400 responses were obtained. In agreement with this study, a PMN response, independent of the N400, has been obtained whenever a violation against the expected auditory phonemic features has been introduced [5,6,8,22,24,31].

It has been suggested that the PMN relates to the phonological processing of the speech input, possibly reflecting, in the perception of natural spoken language, the stage when lexical candidates are set up, searched or phonologically evaluated [6]. However, this process appears to be insensitive to semantic top-down effects since words not embedded in a sentence [5,6] and non-words [6] also elicit the PMN. A non-semantic paradigm in which participants were instructed to expect a word/non-word that rhymed with a presented word/non-word and began with a certain sound produced enhanced PMNs to mismatches in both word and non-word conditions [6]. Similarly, a phonological awareness task in which participants were told to judge the phonological result of deleting initial consonants of words (e.g., 'clap' without the /k/ sound) showed no differences in the PMN between incorrect word and non-word stimuli (e.g., 'cap' vs. 'ap' instead of the expected 'lap'). Further, the actual degree of mismatch between the anticipated and heard input (e.g., whether only the initial segment of the word as in 'cap' or also the subsequent segments as in 'nose' are wrong) seems not to be reflected in the PMN amplitude [22]. This suggests that the PMN is an 'all or nothing' process after a phoneme mismatch with expectations has been detected. These results are in agreement with van Petten et al. [32], who found no difference in what they described as an early N400 in sentence-ending anomalous words that rhymed with the expected word (e.g., 'scholar' instead of the expected 'dollar') and phonologically dissimilar anomalous words. These authors concluded that their effect was an early semantic N400 based on this lack of difference. The conclusion of semantic top-down influence was echoed by Hagoort and Brown [8] and van den Brink et al. [31]. However, this argument is sound only if the PMN is a process that is sensitive to matching with expectation at the whole-word level. As this does not appear to be the case, the neuronal networks underlying the PMN seem to be specialized in analyzing the acoustic and phonological aspects of speech rather than operating with lexical representations.

In addition to the acoustic-to-phonological-level PMN and the semantic-level N400, negativities peaking at similar latencies as the N400 have been reported for overall orthographic or phonological dissimilarities between word and non-word stimuli in visual rhyme judgment paradigms [25,26] and auditory lexical decision to words primed by rhyming words [23] (Experiment 1). These responses, sometimes referred to as the N450, have been interpreted by Rugg and Barrett [26] as belonging to the N400 family but to operate in the orthographic and phonological domains rather than the semantic domain.

To date, the neural generator(s) of the PMNm in relation to those of the other brain responses have not been located with confidence. Fronto-central maxima have been reported for the PMN in contrast to more centro-posterior scalp distributions found for the N400 and other N400-like responses [2–4,8,23,25,26,31]. Recent high-density EEG recordings in a visuo-auditory priming task with words and non-words suggested a left-hemispheric anterior source for the PMN, whereas an equal left- and right-hemisphere distribution with a centro-parietal maximum was observed for a later negative response peaking after 400 ms from stimulus onset and resembling the N400 [6]. The present study aimed at locating the neuronal generators of the magnetic PMN (PMNm) with whole-head magnetoencephalography (MEG) using the same stimuli and paradigm as reported by Connolly et al. [6].

2. Materials and methods

Ten native Finnish speaking, right-handed and healthy subjects (aged 2027, 6 males) with normal hearing and normal or corrected-to-normal vision participated in the experiment after giving informed consent. The study was approved by an ethical board.

The words and non-words were presented in separate conditions with each experimental task consisting of 318 trials. In each trial, the first stimulus was a visual word/ non-word (e.g., 'cat') with a duration of 200 ms. A letter (e.g., 'h') of 200-ms duration followed the first stimulus after a 300-ms inter-stimulus interval (ISI). Subjects were trained to form mentally a rhyming word/non-word by replacing the first letter of the visually presented word/ non-word by the letter they had just seen and to anticipate hearing the word/non-word just formed (e.g., /hæt/). The third stimulus, an auditory word/non-word was presented after a 700-ms ISI. These auditory words/non-words either matched (/hæt/) or mismatched (e.g., /lAk/) with equal probability (p=0.5) the anticipated ones. After 300 ms, subjects saw a fixation cue of 200-ms duration marking the beginning of the next trial. The 159 matching and 159 mismatching trials occurred randomly in the word and non-word conditions.

All the words were Finnish nouns consisting of four to six letters/phonemes and beginning with a consonant. The non-words had no meaning, but obeyed the rules of Finnish orthography, in which each letter corresponds to one pronounced phoneme (and the combination 'ng' to /ŋ /). The mismatching auditory words/non-words always began with a different phoneme from the anticipated words/non-words. Further, in each trial, the mismatching word was semantically unrelated to both the first visual word and the anticipated word. The visual stimuli were created with the NeuroStim program (Neurosoft, USA) and presented on a computer screen that was placed outside the recording room and viewed through a window (the distance from the subject was approximately 1.5 m). The auditory stimuli were recorded with the same program and delivered binaurally via plastic tubes and earpieces at about 60 dB HL.

MEG was recorded in a magnetically shielded room (Euroshield, Finland) at the BioMag Laboratory of the Helsinki University Central Hospital with a 122-channel whole-head magnetometer (Neuromag, Finland). The sensor array consisted of 61 dual-sensor units, each consisting of 2 orthogonal planar gradiometers. Online averaging of the MEG epochs (sampling rate 253 Hz, bandpass filtering 0.0380 Hz) started 100 ms before and ended 800 ms after the presentation of matching and mismatching auditory words/non-words. Epochs with MEG or EOG (recorded with bipolar electrodes attached laterally to both eyes and below and above the left eye) signal amplitude exceeding 3000 fT/cm or F150 AV, respectively, were discarded from averaging, resulting in at least 80 responses averaged for the matching and mismatching words and non-words. The baseline correction always started 100 ms before stimulus presentation and ended at the point of stimulus onset. In the analysis of signal amplitudes and in source localization, the cutoff frequency for lowpass filtering of the averaged MEG signals was always 20 Hz. Low-frequency shifts were removed in the signal amplitude analysis by filtering out frequencies below 1 Hz and in source localization by using an additional baseline between 700 and 800 ms. Difference waveforms (responses to matching word/non-word subtracted from those to mismatching word/non-word) were calculated for the analysis of signal amplitudes and for source localization of the PMNm and the late negative, N400m-like responses.

In each subject, condition, and hemisphere, the presence of PMNm and/or N400m-like responses was verified by analyzing the response amplitudes. To this end, vector sum signals from each gradiometer pair were determined from the difference waveforms by first squaring the signals of the two gradiometer channels, then summing them together and finally computing a square root of the sum. The PMNm and/ or N400m-like response was considered to exist if (1) a typical response pattern for the PMN and/or N400m-like response, indicating an underlying downward current, was obtained in the time windows 200-350 and 350-600 ms, respectively, in the temporal regions; and (2) the mean amplitude of the vector sum signal in those channels showing the PMNm and/or N400m-like response exceeded for at least 50 ms (centered at the peak of the response) and was at least 1.96 times (corresponding 0.05 probability level) the mean amplitude during the prestimulus period (-100 to 0 ms).

In the cases meeting these criteria, source localization was performed using L1 minimum-norm estimation [10,16,29]. The L1 estimation results in a current distribution with the smallest integral of the absolute value of the current density that could generate the measured magnetic field and provides a minimum-norm current estimate (MCE [30]) with location and strength information for the current sources at each time point. Unlike equivalent current dipole (ECD) modeling, MCE requires no a priori information of the possible source configuration or restriction of the MEG channels included in the modeling [30]. MCE provides a similar result as dipole modeling; however source strengths tend to be smaller and the sources more superficial in MCE than in dipole modeling [28].

For source localization of the PMNm and N400m-like responses, MCEs were calculated between 150 ms and 700 ms from the difference waveforms [9] that, based on the experimental design, were used to disentangle the neuronal activity underlying these responses from that related to other ongoing language processes. A spherical model of the head was employed in the estimation. Activity in a time window of about 25 ms centered at the peak of each response was integrated for identification of reliable sources within the temporal areas. Within this time window, the strongest, downward-oriented current source in the left and right temporal regions was selected for the word and non-word PMNm and N400m-like responses, respectively. The N1m (the magnetic counterpart of the N1 [12], a response peaking at around 100 ms indexing acoustic analysis [21]) current sources for matching and mismatching words/non-words were determined from the corresponding MCEs within the time window of 80-180 ms with the same procedure.

In the statistical analysis, the source locations and strengths of the N1m to the matching and mismatching words/non-words were analyzed in three-way repeated measures ANOVAs with the factors lexicality (word/non-word), congruence (match/mismatch), and hemisphere (left/right). Finally, the source locations and strengths of the left hemisphere N1m, PMNm, and N400m-like responses were compared in one-way repeated measures ANOVAs performed separately for words and non-words.

3. Results

Following the N1m response to both types of stimuli, the response to the mismatching words/non-words diverged from that to the matching words/non-words. The first systematic difference was typically obtained between 200 and 350 ms and was identified as the PMNm. In addition, a negative sustained response was observed between 350 and 600 ms. Fig. 1a shows MEG responses in one representative subject to the matching and mismatching stimuli and the corresponding difference waveforms. In this subject, the PMNm response for words peaked at around 270 ms and the late N400m-like response at around 360 ms. For non-words, the PMNm peaked at about 320 ms and the N400m-like response at about 480 ms.

We first tested in each subject, condition, and hemisphere the presence of PMNm and N400m-like responses (see Fig. 1b) by analyzing the vector-summed signal amplitudes calculated from the difference waveforms between the mismatching and matching stimuli. In the word condition, a statistically significant PMNm was obtained in 7 subjects out of 10 and a N400m-like response in 8 subjects in the left hemisphere, with 6 subjects showing both the left-hemisphere PMNm and N400m-like responses. In the non-word condition, left-hemisphere PMNm and N400m-like responses were obtained in 7 and 6 subjects, respectively, with 6 subjects (not identical to those in the word condition) showing both responses. In the right hemisphere, only a few subjects showed prominent PMNm and N400m-like responses (for words, a PMNm occurred in 4 and a N400m-like response in 3 subjects; for non-words, a PMNm in 5 and a N400m-like response in 4 subjects).

Source localization using MCE was performed only for the statistically significant PMNm and N400m-like responses. In Fig. 1a, the mean MCEs in a time window of approximately 25 ms centered at the peak of the response are shown for the PMNm and N400m-like responses of the subject S1. In addition to the sources for the PMNm and N400m-like responses, the N1m source was determined for the matching and mismatching words and non-words to provide a landmark of the auditory cortex. The N1m source locations for the words and non-words differed in the lateral-medial direction so that the N1m was more medial for non-words than for words (three-way ANOVA with factors lexicality, congruence, and hemisphere; main effect of lexicality, F(1,8)=7.20, Pb0.05). Since no interactions involving the congruence, factor were found, the mean values of the source locations and strengths for the word and non-word match and mismatch N1m responses were used in the subsequent analysis.

The mean latencies, locations, and strengths for the N1m, PMNm and N400m-like response ('N400m') are shown for the words in Table 1 and for the non-words in Table 2.

Statistical analysis was restricted to the left-hemisphere source locations and strengths that were compared separately for words and non-words, as the number of subjects (N=4) showing both word and non-word PMNm and N400m-like responses was not sufficient for statistical comparisons between responses to words and non-words. Both in the words and non-words, the source locations of the N1m, PMNm and N400m-like responses differed in the anterior-posterior direction (words: F(2,10)=7.10, P<0.05; non-words: F(2,10)=7.19, P<0.05; Fig. 2). Post-hoc analysis revealed that the current source of the word PMNm was located significantly anterior to that of the word N400m-like response (P<0.01). For the non-words, the PMNm source was located significantly anterior to both the sources of the N1m (P<0.04) and the N400m-like (P<0.01) responses. The mean distance from the PMNm source to the sources of the N1m and N400m-like responses was 10 and 20 mm for words, respectively, and 14 and 25 mm for non-words, respectively. The source of the N400m-like response was located, on average, 10 mm posterior to the N1m source for both words and non-words, but these differences did not reach statistical significance. The left-hemisphere source strengths and locations in the lateral-medial and inferior-superior directions did not differ statistically significantly for the N1m, PMNm and N400m-like responses.

4. Discussion

The present study examined cortical activation related to the processing of aurally presented words, concentrating particularly on the phonological analysis stage. In a visuo-auditory priming task with words or non-words, an expectation of specific speech input was created and then violated 50% of the time by presenting an auditory word/non-word that did not match with the expectation. Importantly, the mismatching stimuli always began with an unexpected phoneme, introducing with the words and non-words a clear phonological violation that could be time-locked with the word/non-word onset. Magnetic responses to the matching and mismatching words and non-words were recorded and analyzed. In general, the words and non-words elicited three consecutive and prominent components with systematic differences between the responses to the matching and mismatching words/non-words observed dominantly in the left temporal regions starting at approximately 200 ms from the stimulus onset.

Both the matching and mismatching stimuli elicited a distinct bilateral N1m response that peaked around 135 ms. Based on the MCE analysis [28,30], anticipation of the incoming verbal stimulus did not seem to affect these early processing stages before 200 ms. The N1m source strengths, locations, and latencies at the peak of the source strength did not differ statistically significantly between the matching and mismatching stimuli. This suggests that the initial (acoustic-phonetic) analysis took place in the same or overlapping neuronal networks of the auditory cortices [15].

After the N1m, stimuli mismatching with the anticipation elicited a PMNm response peaking at about 280 ms for the words and at about 300 ms for the non-words in the left hemisphere. The non-significant difference in latencies is almost certainly artifactual as responses from somewhat different participant populations were localized in the two conditions (despite identical Ns of 7), and a parallel difference could not be detected in the earlier reported EEG data from the same experiment. As in our earlier analysis of EEG data from the same task [6], a later magnetic response corresponding to the reported electrical one was obtained, presumably reflecting whole-item processing. N400-like late negativities have also been observed for sentence-beginning or -middle words that, as a consequence of their position in the sentence, have not been strongly primed by a preceding sentence-based context [8,15]. For both words and non-words, the late, negative, N400m-like response peaked at about 450 ms and reflected perhaps mainly form-based analysis given the lack of semantic context or semantic strategy requirements. This interpretation would be consistent with its relatively small amplitude. The PMNm and N400m-like responses were large enough to permit source localization with MCE in the left hemisphere for the words in 7 and 8 subjects, respectively, and for the non-words in 7 and 6 subjects, respectively (Tables 1 and 2). In the right hemisphere, considerably less activation related to the mismatching stimuli was observed and a similar response pattern was obtained only in a few subjects. Therefore, the focus of the analysis was on the left-hemisphere temporal areas.

Source localization with MCE revealed that the current source of the PMNm was significantly more anterior to that of the N400m-like response for the words and both the N400m-like response and the N1m for the non-words in the left hemisphere. The source location of the N400m-like response being slightly posterior to the N1m source agrees with recent MEG results of the N400m in sentence contexts originating in the left posterior-temporal regions [9,13,14,27] in the vicinity of the N1m source [15]. Further, the PMNm source location anterior to the N400m-like response and the N1m implies that the PMNm originates, at least in the left hemisphere, from the anterior parts of the temporal cortex. This finding adds to the earlier EEG findings [2–4,8,31] showing frontal or fronto-central, rather than posterior topographies for the PMN. Though the present MEG results are compatible with the EEG findings, it should be noted as always when EEG and MEG data are being compared, that radial sources are not well captured in MEG recordings whereas all sources contribute to the EEG signal [11].

The present study provides the first indication that the PMN may be recorded with MEG and, further, that its source may be identified relative to the sources of other dominant responses. Earlier MEG studies have not succeeded in directly isolating and localizing the cortical generator(s) of the PMN response. For instance, Helenius et al. [15] employed whole-head MEG and varied the sentence-ending words in their semantic and phonological appropriateness. They found no separate PMNm for the phonologically unexpected sentence-ending words that occurred in two of their conditions; one in which a low cloze probability word replaced the highest cloze word (The pigs wallowed in the pen-'mud' being the highest cloze word) and another in which the incongruent terminal word shared its initial phoneme with the highest cloze word (The gambler had a streak of bad luggage—'luck' being the highest cloze word). The lack of a clearly distinct PMNm in their data might, at least partly, be explained by their use of fixed N1m or N400m source locations for examining the strength and time behavior of the current sources, though, according to the present results, the PMNm is presumably generated slightly anterior to the N1m and N400m. The auditory MEG response to incongruence in Helenius et al.'s study [15] appeared more anterior than in the present study, and may therefore have incorporated activity from both PMN and N400 processes. In any case, the present task evoked a distinct PMNm and a minimal late negativity, and was thus optimal for the identification of the PMNm source.

It is also highly likely that the N400m-like response seen in the present experiment is not a true semantic N400 as described in the literature. For example, the rather wide distribution of source locations of the N400m-like response seen in this study contrasts with the tighter distribution seen for the sources of the 'classic' N400m (e.g., Ref. [15]). On the other hand, in the EEG data from the present task [6], the late, N400-like negativity had a symmetric centro-parietal topography similar to that observed for N400 with more classical paradigms. In agreement with this, all sources of the N400m-like response are parallel or posterior to the N1m source in the present MEG data. Further, it is noteworthy that, in the EEG data [6], no differences in the late response were observed between word and non-word stimuli and that in the present data, the left-hemisphere pattern of source loci for the non-words resembled that for the words (Figs. 1 and 2). These observations speak for the fact that both words and (rather word-like) non-words evoke some amount of activation in the posterior-temporal areas though in the present visuo-auditory task semantic evaluation of the stimuli is not required at all. This suggests that the N400-like response seen in this experiment was form-based, similar to the N450 observed by Rugg [25] and Rugg and Barrett [25,26] and the N400-like response in auditory lexical decision experiments [23] (Experiment 1).

Taken together, even though our understanding of the PMN as a marker of phonological processing is still in progress [22], the present results highlight the consecutive stages (acoustic-phonetic, sub-lexical phonological and whole-word level) in the analysis of the speech signal. Further, these findings suggest that at least partly distinct temporal regions in the left hemisphere, which is known to possess a large variety of areas specialized in language processing [1,20], appear to underlie these steps in auditory word recognition.

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Table 1
The mean latencies, source locations, and strengths of N1m, PMNm, and N400m-like response for the words (S.E.M. in brackets)

Response	Hemisphere	*N*	Latency (ms)	Source location (mm)			Source strength (nAm)
				x	Y	Z	
N1m	Left	10	137 (4)	−54.0 (2.6)	−1.5 (3.6)	49.0 (2.8)	10 (1.5)
	Left[a]	6	133 (6)	−56.7 (2.1)	0.0 (3.4)	50.8 (3.7)	10.6 (1.8)
	Right	10	140 (5)	53.5 (2.2)	1.5 (3.2)	51.0 (2.6)	10.5 (2.0)
PMNm	Left	7	278 (10)	−50.0 (3.8)	8.6 (6.7)	48.6 (5.5)	5.8 (1.4)
	Left[a]	6	281 (11)	−50.0 (4.5)	13.3 (5.6)	46.7 (6.1)	6.2 (1.6)
	Right	4	279 (18)	60.0 (0)	7.5 (8.5)	47.5 (11.1)	3.9 (1.1)
“N400m”	Left	8	452 (24)	−48.8 (4.4)	−11.3 (3.0)	46.3 (4.6)	10.1 (3.7)
	Left[a]	6	442 (27)	−46.7 (5.6)	−11.7 (4.0)	40.0 (2.6)	11.5 (4.9)
	Right	3	500 (56)	56.7 (3.3)	16.7 (13.3)	33.3 (6.7)	4.9 (2.7)

In the source locations, x refers to the lateral–medial, y the anterior–posterior and z inferior–superior direction, with the origin located at the cross-point of the line between the preauricular points and the nasion. Note that these values are not Talairach coordinates.

[a] Mean values of the six subjects with both PMNm and N400m-like responses in the left hemisphere.

Table 2
The mean latencies, source locations, and strengths of N1m, PMNm, and N400m-like response for the non-words (S.E.M. in brackets)

Response	Hemisphere (ms)	*N*	Latency (ms)	Source location (mm)			Source strength (nAm)
				x	y	z	
N1m	Left	10	135 (3)	−51.5 (1.8)	−1.5 (3.0)	50.5 (2.5)	10.5 (1.8)
	Left[a]	6	137 (4)	−50.8 (1.5)	−1.7 (4.8)	50.0 (3.4)	11.6 (2.6)
	Right	10	142 (4)	50.5 (3.5)	1.0 (2.9)	53.0 (2.1)	12.9 (1.9)
PMNm	Left	7	305 (5)	−60.0 (0)	12.9 (5.7)	55.7 (5.7)	4.0 (0.8)
	Left[a]	6	308 (5)	−60.0 (0)	16.7 (4.9)	58.3 (6.0)	4.4 (0.8)
	Right	5	300 (13)	60.0 (0)	12.0 (6.6)	44.0 (9.3)	4.0 (0.9)

	Left	6	450 (35)	−51.7 (5.4)	−11.7 (4.8)	46.7 (7.1)	8.1 (2.6)
	Left[a]	6	450 (35)	−51.7 (5.4)	−11.7 (4.8)	46.7 (7.1)	8.1 (2.6)
“N400m”	Right	4	401 (13)	60.0 (0)	5.0 (6.5)	65.0 (8.7)	3.9 (1.4)

In the source locations, *x* refers to the lateral−medial, *y* the anterior−posterior and *z* inferior−superior direction, with the origin locating at the cross-point of the line between the preauricular points and the nasion.

[a] Mean values of the six subjects with both PMNm and N400m-like responses in the left hemisphere.

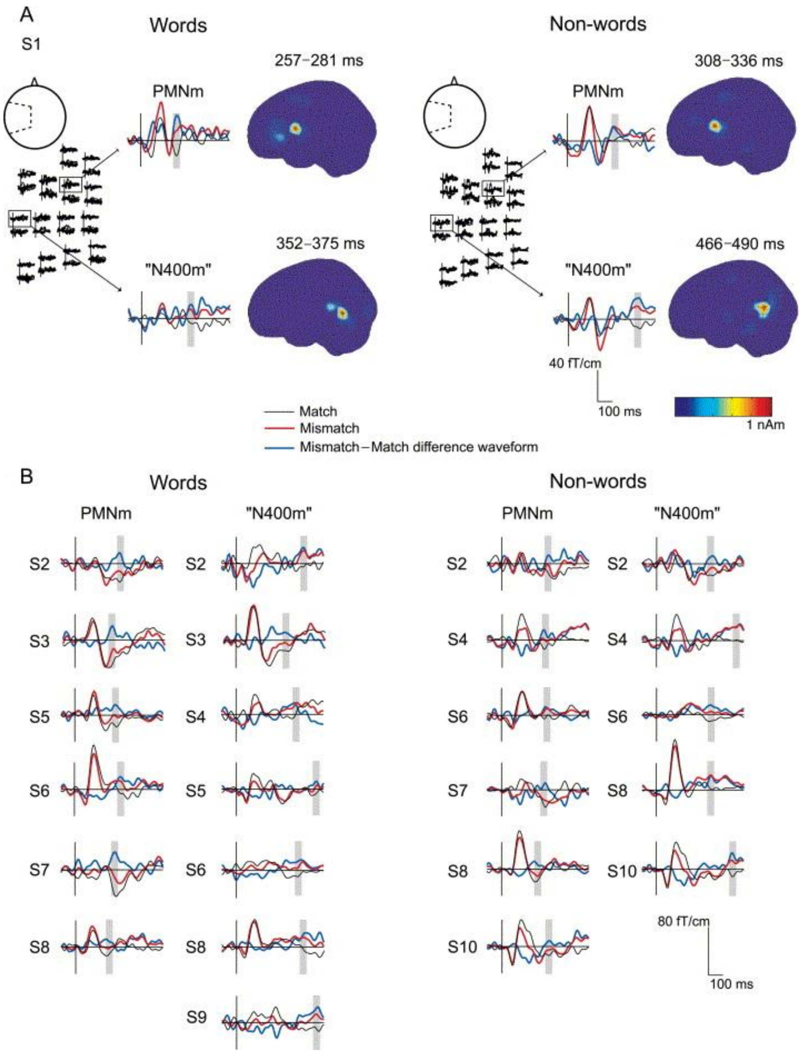

Fig. 1. (A) MEG responses to words (left) and non-words (right) in subject S1 in those left-hemisphere channels with the maximum amplitude for the PMNm and the N400m-like response and the corresponding L1 minimum-norm estimates (MCEs) over a 25-ms time window centered at the peak of the response. The gray vertical bars indicate the 50-ms time periods with significant PMNm and N400m-like responses. The MCEs are shown only in the regions of interest (ROIs), with the centers of the ROIs placed at the loci with the strongest current (the radius of the ROIs was always 1 cm). (B) MEG responses to words (left) and non-words (right) in all those subjects with PMNm and N400m-like responses at the left-hemisphere channels with maximum response amplitude. Again, the gray vertical bars indicate the 50-ms time periods with significant PMNm and N400m-like responses.

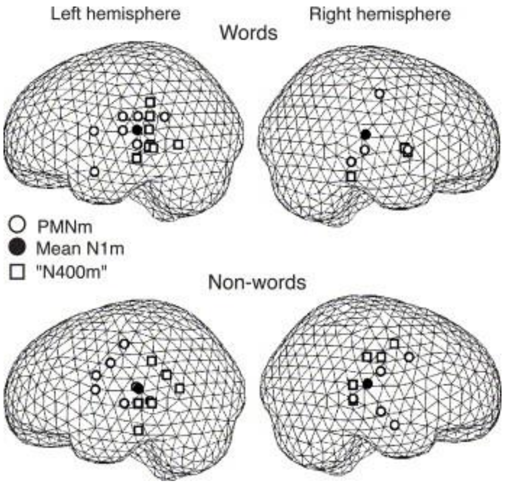

Fig. 2. A schematic illustration of the left- and right-hemisphere source locations for the PMNm (circle) and N400m-like response (square) in words (above) and non-words (below) in each subject as superimposed on a triangle net representing the cortical surface. The mean location for N1m is marked with a black circle.