Separating Phonological and Semantic Processing in Auditory Sentence Processing: A High-Resolution Event-Related Brain Potential Study

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Abstract: Phonological and semantic processing was studied using high-resolution event-related brain potentials (ERPs) during a sentence-matching task to investigate the spatial distribution of the phonological mismatch negativity (PMN) and the N400 response. It was hypothesized that the two components were spatially separable and that the activity matched prior localization knowledge. Participants examined visual–auditory sentence pairs that related within a semantic hierarchy (e.g., visual: “The man is teaching in the classroom”; Auditory: “The man is in the...school/barn”). Semantic congruency was varied for the final words of the spoken sentences. Incongruent words mismatched expectation in terms of both the initial phonological features (unexpected sound) and semantic features (unexpected meaning). In addition, the category–exemplar probability of the final words was either high or low, with low probability words being more difficult to anticipate. Low probability words were predicted to selectively affect PMN activity. We found that incongruent words elicited a PMN (287 msec) and a N400 (424 msec), for both the high and low probability words. As expected, low probability congruent words elicited a small PMN but no N400. In contrast, high probability congruent words elicited neither a detectible PMN nor a N400. The primary PMN sources were in left inferior frontal and inferior parietal lobes. The primary N400 source activation occurred along the left perisylvian cortex, consistent with prior N400 source localization work. From these results, it was concluded that the PMN and N400 were localized to separate cortical language (and memory) regions and had different source activation patterns. *Hum. Brain Mapp.* 22:40–51, 2004. © 2004 Wiley-Liss, Inc.

Key words: ERP; N400; PMN; cerebral cortex; cortical current source estimation; topography; language; speech perception; word processing

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INTRODUCTION

Brain imaging studies have been providing critical information about temporal and spatial characteristics of the neural architecture that supports language. High-resolution event-related brain potentials (ERPs) and magnetoencephalography (MEG) are electromagnetic techniques that provide temporally sensitive on-line recordings of brain function along with valuable spatial information. We used ERPs to examine the phonological mismatch negativity (PMN) and the semantic N400 response during speech perception [Connolly and Phillips, 1994].

The N400 is one of the most well established ERP components linked to language. This semantic response was initially demonstrated to occur to the onset of anomalous terminal words when participants read contextually constrained sentences [Kutas and Hillyard, 1980; Kutas and Van Petten, 1994; Segalowitz and Chevalier, 1998]. It is a late negative-going waveform, which peaks at approximately 400 msec poststimulus, and has a centro-parietal scalp topography. Although the N400 was observed originally after the presentation of visual sentence stimuli [Kutas and Van Petten, 1994], variants of the component have since been obtained in a variety of language-related tasks that use different forms of stimuli, such as text, speech, and pictures [Segalowitz and Chevalier, 1998].

In the auditory modality, the N400 has been elicited to digitized speech stimuli that, similar to their visual counterparts, contained semantically incongruent terminal words [Connolly et al., 1990, 1992; Connolly and Phillips, 1994; Holcomb and Neville, 1990]. It has also been shown in cross-modal paradigms (priming designs using picture-spoken word pairs), supporting the existence of an amodal semantic-conceptual system [Connolly et al., 1995; Ganis et al., 1996; Nigam et al., 1992]. In addition, the N400 has been obtained in tasks that involve semantically related word pairs [Bentin et al., 1985; Brown and Hagoort, 1993] and has shown promise in investigations of semantic processes in diseases such as Alzheimer's disease [Schwartz et al., 1996], stroke [D'Arcy et al., 2003], and other neurologic conditions [Connolly and D'Arcy, 2000; Connolly et al., 2000].

Phonological analysis during speech processing has been linked to a component that precedes the auditory N400 [Connolly et al., 1990, 1992]. Connolly and Phillips [1994] used contextually constrained spoken sentences to determine whether the PMN could be separated from the N400. To demonstrate that the PMN was sensitive to phonological analysis and independent from the N400, the authors manipulated both the phonological and semantic features of the terminal words and recorded ERPs to the onset of these words. The results showed that the PMN could be double dissociated from the N400, i.e., the PMN occurred maximally in those conditions using words with unexpected initial phonemes regardless of the semantic appropriateness of the words, but was reduced in amplitude for expected and phonologically similar words. In contrast, the N400 was elicited only in those conditions using words that were semantically incongruent (even when the initial segment of

the anomalous word shared its initial phoneme with the anticipated congruent word). The authors concluded that the centrally distributed PMN (which peaked between 270–300 msec) was independent of the N400 and reflected phonological processing during spoken word recognition.

Results showing the PMN in speech processing studies have since been replicated [Connolly et al., 1995, 2001; Dehaene-Lambertz et al., 2000; Hagoort and Brown, 2000; Praamstra and Stegeman, 1993; van Den Brink et al., 2001]. It has also been used to evaluate and interpret language functions for patients with neurologic disease [Revonsuo et al., 1998]. Although the response is typically largest in conditions where expectations mismatch the stimulus, several experiments have also shown that it occurs in matching conditions (but with smaller amplitude). This suggests that it reflects a compulsory stage of phonological processing.

The PMN has been demonstrated recently in a phoneme deletion task (e.g., "clap without the /k/ sound") that had no semantic demands and produced no N400 response [Newman et al., 2003]. In this experiment, its amplitude was attenuated by expectations, producing a smaller response to "lap" than to other answers. There was no difference, however, in the PMN to answers that were phonologically similar with the expectation (e.g., cap) and answers that were totally different (e.g., nose). The PMN thus was sensitive to deviations at the single-phoneme level rather than at the whole-item level. The results suggested that the response is a stand-alone reflection of pre-lexical phonological processing of speech.

Connolly et al. [2001] used high-resolution ERPs to identify topographic characteristics of the PMN using a phonological priming paradigm. Subjects studied a visual word or non-word followed by a brief presentation of a cue letter (e.g., House, M). They were instructed to anticipate the word/non-word formed by substituting the visual word's initial letter with the cue letter. The subjects then heard an auditory target word/non-word that either matched (e.g., Mouse/H/House) or mismatched (e.g., Mouse/H/Table) their expectations. ERPs were recorded to the onset of the auditory words/non-words and the results showed that violations of phonologically based expectations elicited a significant PMN. There was no statistically reliable difference between the PMN to words and non-words, confirming that the phonological processing it reflected was independent of semantic top-down influences. In addition, the PMN was followed by a later negativity that was tentatively proposed to reflect working memory activation during ongoing phonological processing. The scalp topography of the PMN was characterized by a frontal, right asymmetrical distribution. Further analysis using spatial de-blurring techniques suggested that the distribution resulted in part from an active left anterior generator. Unfortunately, the relatively small amplitude of the PMN response in that study precluded the investigation of intracranial sources. The authors stressed the importance of future work directed at refining the spatial localization and functional role of the PMN.

The current study was designed to investigate the PMN and N400 using a visual–auditory sentence-matching paradigm. The task was designed to maximally elicit PMN and N400 using semantic hierarchies [Loftus et al., 1970]. Sentence pairs described subordinate–superordinate hierarchical relationships (e.g., classroom–school). Within each sentence pair, contextual information was established using a visual “prime” sentence (e.g., The man is teaching in the classroom). Expectation was evaluated on the basis of a second spoken “target” sentence (e.g., “The man is in the...school”). The congruence of the terminal words for the target sentences was manipulated to elicit the PMN and N400 (e.g., school/barn: phonologically and semantically expected/unexpected, respectively).

An additional manipulation concerned the category–exemplar probability, which provided a measure of expectancy. The sentence pairs were divided into high and low expectancy groups. For low probability pairs (e.g., sunken ship: ocean), it was more difficult to anticipate the terminal words because a greater number of candidates existed. For high probability pairs (e.g., shallow end: pool), there were fewer possible candidates, so the terminal word was more easily anticipated. We hypothesized that the PMN and N400 would be present¹ in incongruent conditions (both high and low), the PMN would also be present in the low-congruent condition, but neither the PMN nor the N400 would be readily detectable in the high-congruent condition.

One main objective of this experiment was to obtain more accurate spatial information about the PMN and N400. To date, the intracranial generators of the PMN have not been localized reliably. Although there has been some work examining N400 sources, most studies have localized the visual N400 [Haan et al., 2000; Helenius et al., 1998]. A recent MEG study has examined auditory N400m sources (magnetic N400), localizing them to the left perisylvian region [Helenius et al., 2002]. The authors reported, however, that it was not possible to model a PMNm in that investigation (magnetic PMN). We used high-resolution ERPs (128 channels) to clarify prior PMN scalp distribution results [Connolly et al., 2001; Connolly and Phillips, 1994] and investigate further the recent auditory N400m source findings [Helenius et al., 2002]. We hypothesized that the PMN and N400 sources would be localized to separate cortical regions, with different time courses of activation.

SUBJECTS AND METHODS

Participants

Ten English-speaking participants (six females, four males) volunteered for a study on language (and received

course credit where applicable). Their mean age was 26 ± 4.6 years and their mean level of education was 16.8 ± 2.4 years. All were given the Edinburgh Handedness Inventory and were dextral (laterality quotient range, 54.5–100) [Oldfield, 1971]. The participants had normal or corrected-to-normal vision and were screened with a self-report measure for a history of audiologic, psychiatric, or neurologic problems. Informed consent was obtained. Upon completion of the experiment, all participants were debriefed fully and any questions were answered. The study had ethical committee approval.

Experimental Paradigm

A visual–auditory sentence-matching task was designed to investigate ERP responses to the phonological (PMN) and semantic (N400) features of spoken words. For each sentence pair, the first sentence (prime sentence) was presented visually and ended in a subordinate word that primed a superordinate word. The superordinate word was anticipated as the terminal word of a second spoken sentence (target sentence). Each prime sentence contained a subject (man, woman, boy, or girl), a verb, and a prepositional phrase expressing a location. All prime sentences were constructed to establish expectancies, which were evaluated subsequently within the context of the target sentences. All auditory target sentences contained a brief, natural pause before the terminal word onset (i.e., normal prosody). Both the phonological (unexpected initial phoneme) and semantic (unexpected meaning) properties of the terminal words in the target sentences were manipulated to match or mismatch expectation (congruent or incongruent; 0.5 probability).

Sentence pairs (100) were constructed and given as a normative sentence completion survey to 58 individuals. All individuals (43 females and 15 males) were fluent in English, the mean age was 26.1 ± 8.5 years, and the mean level of education was 16.7 ± 3.1 years. The exemplar–subordinate probability for congruent words in each sentence pair was calculated [Bloom and Fischler, 1980]. The probability estimates were calculated based on the most frequent terminal words used to complete the target sentences. Only sensible answers were considered, with four sentence pairs being rejected because of unacceptably high proportions of inappropriate responses (>33%). A median split of exemplar–subordinate probabilities was used to divide the remaining 96 sentence pairs into two groups (high and low). Sentence pairs with probability above/below a 0.655 cutoff were labeled as high and low, respectively. The high group (48 sentences) had a mean probability of 0.869 ± 0.099 and the low group (48 sentences) had a mean probability of 0.546 ± 0.133 . The high and low sentence pairs were assigned randomly to the congruent and incongruent conditions. For the incongruent condition, semantically anomalous terminal words with initial phonemes that did not match any of the normative responses were selected from the normative data to replace the original words. The use of normative data controlled for word frequency effects. The mean word

¹It should be noted that the PMN and to a lesser degree the N400 are observed in most conditions but are of increased amplitude in conditions involving the violation of phonological and semantic expectations, respectively. References to the absence of the PMN in some conditions might be better understood as a relative rather than an absolute absence, insofar as some sign of the PMN may be observable in any condition requiring phonological processing.

lengths were 5.96 ± 1.99 for high-congruent, 6.12 ± 2.13 for high-incongruent, 5.79 ± 2.47 for low-congruent, and 6.13 ± 1.83 for low-incongruent items. The exemplar-superordinate probabilities and word lengths (in number of letters) were evaluated for congruent and incongruent conditions but no statistical difference was found.

There were four experimental conditions: (1) the high-congruent condition (e.g., The boy is swimming in the shallow end. "The boy is in the...pool."); (2) the low-congruent condition (e.g., The woman is swimming in the sunken ship. "The woman is in the...ocean."); (3) the high-incongruent condition (e.g., The girl is singing in the recording booth. "The girl is in the...wagon."); and (4) the low-incongruent condition (e.g., The man is entering through the swinging doors. "The man is in the...marsh."). Each of the conditions contained 24 sentence pairs. The number of sentence pairs/condition was restricted by the upper limit of available sentence pairs in the experiment.

The prime sentences were presented visually on a 35.5 cm computer monitor positioned 1 m away. The text stimuli were presented in yellow letters on a black background (36-point font size). The mean width of the sentence stimuli was 20.15 ± 1.87 cm and the mean height was 3.08 ± 0.51 cm. The visual stimuli subtended a visual angle of approximately 1.76 degrees. The target sentences were presented in the auditory modality and were digitized from natural speech by a female voice with the NeuroScan Inc. stimulus software package. The sentences were recorded at 100 dB within a fixed 3-sec sample duration. The speech was sampled at 20,000 Hz with the low pass filter at 10,000 Hz (low pass slope = 24 dB/octave). The stimulus onset was defined as the beginning of the terminal words in the target sentences and was marked by a stimulus trigger that was positioned manually at the onset of the sound spectrum for each word.

Experimental Procedures

The experiment began with a practice phase in which participants were given a description of the sentence pairs and instructed to anticipate the superordinate word for each target sentence (using three sample trials). The task began after successful completion of the practice phase. For a single trial, the prime sentence was presented on the computer screen (for 10 sec) and was immediately followed by the target sentence, presented binaurally using audiometric-quality insert earphones. Participants were instructed to fixate on a crosshatch positioned in the center of the computer screen while listening to the target sentences. The target sentence interval was 6 sec (sentence onset to next trial), providing approximately a 3-sec response window. Participants were instructed to indicate, with a button press, whether or not the terminal word matched the expected superordinate word. They were told to respond as accurately as possible and that the speed of their response was not important. Their response hand (left or right) was counterbalanced. The sentence pairs were presented in a fixed

pseudo-random order (with no more than three repetitions of the same condition).

Electrophysiologic Recordings

Electroencephalograph (EEG) activity was recorded using a 128-channel NeuroScan Synamps system with all electrodes referenced to an electrode on the nose (with a common reference derived off-line for spatial analyses). The electrodes were fitted within a NeuroScan Quik-Cap using an extension [American Electroencephalographic Society, 1991] of the International 10/20 System [Jasper, 1958]. An electrooculogram (EOG) recorded vertical and horizontal eye movements, as well as blinks. EOG activity was recorded by electrodes placed above, below, and on the outer canthi of both eyes. The ground electrode was at the AFz site. All electrodes were Ag/AgCl and impedances were maintained at or below 10 K Ω . The continuous EEG recordings were obtained using a bandpass of 0.05–30 Hz (digitally sampled at 500 Hz). Continuous recordings were then epoched off-line beginning 100 msec before the stimulus onset and ending 1,000 msec after the stimulus onset (550 data points). Trials contaminated with EOG activity greater than $\pm 75 \mu\text{V}$ (–100–750 msec) were excluded from the analysis. The mean percentage of total trials rejected from the analysis was $8.0 \pm 8.5\%$. The remaining trials were averaged by experimental condition, taking behavioral performance into account. The mean percentage of correct responses was $98.9 \pm 0.88\%$, indicating that the subjects' performance was near perfect. Grand average waveforms over subjects were derived from averaging the individual waveforms for the experimental conditions.

Statistical Analyses

In all, ERP data were derived from 90 representative sites (Fig. 1). To reduce the number of statistical comparisons across electrode sites, a linear derivation was used to compute waveforms for nine scalp regions. The regions were divided into left (L), midline (M), and right (R) sectors as well as frontal (F), central (C), and posterior (P) sectors (LF, MF, RF, LC, MC, RC, LP, MP, and RP). The waveform for each region was derived from 10 electrode sites in the specified sector and electrode selection for each region was uniform across all participants.

Two statistical analyses were conducted using the average amplitude method: one on the standard waveforms and the other on the difference waveforms. Standard waveform analysis was conducted to determine whether differences in the waveforms corresponded to the PMN and N400. The PMN was defined as the peak occurring in the 250–350-msec poststimulus interval. The N400 was defined as the peak occurring in the 350–550-msec poststimulus interval. Within the PMN time interval, average amplitudes were calculated for successive 50-msec epochs. Within the N400 time interval, average amplitudes were calculated for successive 100-msec epochs. The intervals for the N400 were larger because this component was characterized by broader peak morphology. Difference waveforms were computed to isolate

Figure 1.

Nine regions, comprising ten electrodes per region, were selected from the 128-channel montage. Electrodes in each region are identified using solid, dashed, dotted, and dashed-dotted lines (LF, MF, RF, LC, MC, RC, LP, MP, RP; see methods).

the two components and examine region effects in further detail. Both analyses were done using a repeated measures analysis of variance (ANOVA) with conservative degrees of freedom [Greenhouse and Geisser, 1959]. The ANOVA included condition (four levels), time (four levels), and region (nine levels) as factors. Significant main effects and interactions were submitted to additional post-hoc analyses using the Tukey Honestly Significant Difference (HSD) test. An α level of $P < 0.05$ was required for statistical significance.

Spatial Analyses

Spatial analyses were done using Brain Electromagnetic Source Analysis (BESA, MEGIS v. 3.0) [Scherg and Picton, 1991]. PMN and N400 spatial analyses used source analysis as well as spherical spline and current source density (CSD) maps. The data were preprocessed to minimize the effects of waveform variance on the spatial estimates. A more conservative EOG artifact rejection procedure (-100 – $1,000$ msec) was used, which increased the mean percentage of total trials rejected ($16.4 \pm 16.1\%$). Artifact channels and contaminated electrodes (e.g., sites over the ears) were excluded from the analysis. The averaged data were also re-filtered using a 10-Hz low-pass filter. The analysis was conducted using a four-shell spherical head model with conductivities

estimated for the cerebrospinal fluid (1.0), skull (0.0042), and scalp (0.33). Data from all 10 subjects contained clear PMN and N400 components. Grand average difference waveforms were selected to provide an overall estimate of the PMN and N400 active regions across subjects. This procedure limited the number of dipoles in the analysis and allowed for a global model in which to test the experimental hypothesis. Individual variance and differences in source locations between standard and difference waveforms were also evaluated [Démonet and Thierry, 2001; Haan et al., 2000]. To ensure that the global results were representative, additional modeling and an individual reliability assessment were done for validation.

A brief description of the modeling procedure is provided below. The number of sources was estimated using principal component analysis (PCA). PCA revealed that four to six sources (bilateral, 8–12) accounted for 98–99% of the variance. A regional source strategy was used to determine whether the PMN and N400 could be represented by different sources and activation time courses (or source waveforms) [Picton et al., 1995]. The modeling procedure comprised two steps: (1) formation of the initial model to identify the general areas of activity; and (2) development of the advanced model to fit the location and orientation of

Figure 2.

Grand average ERPs ($n = 10$) to the terminal words in all four experimental conditions for all nine regions. The PMN (diamond) and N400 (asterisk) were elicited in the high- and low- incongruent conditions as well as the low-incongruent condition. Time (msec) is on the x-axis and voltage (μV) is on the y-axis (negative is up). EOG sites were artifact free (data not shown).

individual dipoles. Location and source waveforms were the primary parameters of interest. The orientation parameter was used along with a photographic atlas [DeArmond et al., 1989] to obtain neuroanatomic estimates. Brodmann's areas (BAs) are reported in combination with anatomic descriptions. The quality of the model was evaluated based on the goodness-of-fit/residual variance (RV) between the projected waveforms and the actual data.

RESULTS

Analysis of Standard Waveforms

Figure 2 shows grand average waveforms for all four experimental conditions at nine regions. A repeated measures ANOVA was conducted with condition (high-congruent, low-congruent, high-incongruent, and low-incongruent), time (250–300 msec, 300–350 msec, 350–450 msec, and 450–550 msec), and region (LF, MF, RF, LC, MC, RC, LP, MP, and RP) as factors. Although main effects for condition ($F[3,27] = 36.38$, $P < 0.0001$, $\epsilon = 0.74$) and time ($F[3,27] =$

6.31, $P < 0.05$, $\epsilon = 0.37$) were found, the data were best interpreted within the significant two-way condition $\times$ time interaction, $F(9,81) = 4.86$, $P < 0.005$, $\epsilon = 0.57$. Post-hoc analyses of this interaction demonstrated that the negative amplitudes in both incongruent conditions were similarly enhanced across times 1 to 3 (250–450 msec), relative to amplitudes in the high-congruent condition (PMN and N400). The amplitudes in the low-congruent differed from those in the high-congruent condition, with a prominent negative-going peak at times 1 and 2 (PMN: 250–350 msec) followed by response attenuation at times 3 and 4 (350–550 msec). Although the PMN peak was smaller than were those in the incongruent conditions, the results confirmed its existence in the low-congruent condition (without a N400). The amplitudes in the high-congruent condition remained stable across times 1 to 3 (250–450 msec) and became more positive at time 4 (450–550 msec). There was no meaningful interaction involving the condition and region factors. The nonsignificant region main effect was $P = 0.054$. Individual variance in component timing, however, may have hampered the region analysis. For this reason, it was decided to pursue this effect further using difference waveforms along with a peak-fitting procedure in an effort to minimize effects of individual variance.

Analysis of Difference Waveforms

Given the comparability of the PMN and N400 results in both incongruent conditions in the standard waveform analysis, these two conditions were averaged together and the high-congruent condition was subtracted (i.e., incongruent minus high-congruent). The low-congruent condition was excluded from this difference analysis because it contained a PMN (and was analyzed separately). Peaks for the PMN (200–350 msec) and the N400 (350–600 msec) were identified in the individual waveforms. The size of both windows was increased to accommodate for individual variance in peak timing. The amplitude interval for both components (50 msec, centered at the peak) was calculated for the individual waveforms. The purpose of this latency-fitting procedure was to focus the analysis specifically on the PMN and N400 peaks. The average amplitude values thus were adjusted for individual variation in PMN and N400 peak latencies. The average peak latency was 287 ± 17.8 msec for the PMN and 424 ± 61.5 msec for the N400.

The objective of the difference waveform analysis was to determine whether a significant region effect was present after compensation for individual differences in component latency. Figure 3 depicts the grand average difference waveforms for the nine regions. A repeated measures ANOVA was conducted with time (PMN and N400) and region (LF, MF, RF, LC, MC, RC, LP, MP, and RP) as factors. The main effect of time was not significant ($F < 1.0$); however, there was a significant main effect of region ($F[8,72] = 2.92$, $P < 0.05$, $\epsilon = 0.4$) and post hoc analyses revealed that, although broadly distributed, the PMN and N400 were both largest at the MC and RC regions. The two-way time $\times$ region interaction was not significant.

Figure 3.

Grand average difference waveforms derived by subtracting the high-congruent from the incongruent condition (high- and low-combined). Nine regions show the broad central, right asymmetrical peak distribution. The PMN (diamond) peaked at approximately 287 msec and the N400 (asterisk) peaked at approximately 424 msec. All other details as for Figure 2.

Spatial Analyses

Examination of the spline maps for the PMN and N400 showed that both components were characterized by a broadly distributed central topography, corroborating the previous statistical analyses. There were, however, some differences between the two components. The PMN had a central peak distribution, whereas the N400 was characterized by a centro-parietal distribution (Fig. 4a).

Figure 4 depicts the results of BESA source analyses [Picton et al., 1995; Scherg and Picton, 1991]. The analysis began by using a PCA (0–1,000 msec) to estimate that between 8–16 sources accounted for over 99% of the variance. A regional source strategy was used. Active regions were identified using regional sources in an initial model. A regional source is comprised of three dipoles in the same location, but oriented in orthogonal planes (i.e., orientation-independent). To localize the sources, the simplest possible assumptions were made, with levels of complexity being added only when necessary [Berg et al., 1999]. As one of the recommended procedures in BESA, a single source was localized to the midline region at the eyes to account for residual ocular activity. Symmetry constraints were used for bilateral

sources and solutions in which the dipoles interacted were avoided. In the advanced model, the regional source constraints were released and location and orientation parameters were fitted separately and together until stability was achieved.

Initial model

The initial model showed that neuroanatomic regions with known involvement in speech processing were localized successfully using 10 regional sources. Source fitting revealed bilateral PMN and N400 activation in the inferior frontal and posterior superior temporal regions (bordering the parietal lobes). The activation was most pronounced in the left hemisphere. In addition to the PMN and N400, activation related to the task requirements could also be modeled. In particular, sources were detected in the central sulcus region, consistent with the physiologic demands of button pressing. The preliminary results revealed that the modeled spline maps matched the data spline maps. The goodness-of-fit for the initial model was above 90% (RV = 9.59%; 253–475 msec).

Advanced model

The primary focus of the advanced model was on the PMN and N400. Releasing the regional source constraints and fitting the location and orientation parameters of individual dipoles derived the advanced model. The dipoles were fitted using the peak activation in the source waveforms. Sources with symmetrical constraints were fitted initially with the constraints maintained and then readjusted with the constraints released. In addition, the response dipoles were maintained in the model, with four separate dipoles being modeled in the bilateral pre- and postcentral gyri (BAs 3/4). The modeling process was complete when stability was achieved (i.e., dipole parameters remained constant during fitting).

PMN and N400 source locations and source waveforms were the major parameters of interest (Fig. 4b and 4c, respectively). The two bilateral anterior sources remained in the inferior frontal regions. Examination of the source waveforms revealed that these were likely related to the PMN due to the peak latency. An earlier negativity was clearly present in the source waveform for the left dipole localized to Broca's area (PMN_{S1}: BAs 44/45), with the peak occurring at 283 msec. A second PMN dipole was localized in the left inferior parietal lobe (PMN_{S2}: BAs 39/40). The source waveform for PMN_{S2} matched that observed in PMN_{S1}, with the peak at 283 msec. The additional PMN_{S2} dipole reduced the residual variance further, supporting the contribution of the left inferior parietal lobe. The peaks in the PMN source waveforms corresponded with those recorded on the scalp. Moreover, the PMN sources remained active for the remainder of the epoch, suggesting that phonological processing (or a closely related process) continued well after peak activation.

Two bilateral N400 sources remained localized to the posterior superior temporal gyrus (pSTG), with greater activation in the left hemisphere (Wernicke's area). The left N400

Figure 4.

The PMN and N400 were modeled using BESA. **A:** Data spline maps (left) and model spline maps (right) show comparable distributions for both components. **B:** Left sagittal, axial, and right sagittal views depicting the location of the PMN, N400, and response sources. The primary sources, labeled in the left hemisphere, were the PMN_{s1} (Broca's area; BA 44/45), PMN_{s2} (inferior parietal lobe; BA 39/40), N400_{s1} (Wernicke's area; BA 22),

N400_{s2} (supratemporal plane; BA 22), and N400_{s3} (polymodal temporal-parietal-occipital region; BA 39). **C:** Source waveforms showing the contributions of the PMN and N400 dipoles to the scalp recorded activity. Note the differences in peak onset and morphology between the two components (PMN, 283 msec; N400, 404 msec). The residual variance was 7.82% (253–475 msec).

source waveform (N400_{s1}; BA 22) was similar to the scalp-recorded N400, peaking at 404 msec. A second N400 dipole (N400_{s2}; BA 22) was localized to the left supratemporal plane (STP) of the superior temporal gyrus, anterior to N400_{s1}. The N400_{s2} source waveform matched closely the N400_{s1} source waveform, and also peaked at 404 msec. A third N400 dipole (N400_{s3}; BA 37) was localized to the left polymodal (temporal-parietal-occipital) region. The N400_{s3} peak latency matched those of the other sources, but the response was reduced in amplitude and may have been a secondary generator.

Source analysis successfully disentangled the PMN and N400 components. For the advanced model, the goodness-of-fit was above 92% (RV = 7.82%; 253–475 msec). Adding another test dipole to evaluate the model did not appreciably reduce the RV. The PMN results implicated phonologi-

cal analysis as well as possible verbal WM involvement. The PMN "rode" on top of the N400 component, however, and as such was smaller in terms of relative amplitude. We therefore evaluated whether similar results could be obtained for an isolated PMN.

PMN-only model

To verify that the PMN sources were reliable, difference waveforms were also obtained for the low-congruent condition (low-congruent minus high-congruent). The low-congruent waveforms contained only a PMN component, with no (or little) N400 activation. If N400 activity were effectively absent, then it should be possible to model the PMN sources in isolation. The PMN source models in this condition addressed two critical issues: (1) whether or not the

Figure 5.

BESA results for the PMN-only in the low-congruent condition showing the replication. Bilateral probe N400 dipoles could not be modeled. Instead, the fitting procedure revealed novel activation in dorsolateral prefrontal areas (DLPFC). **A:** Scalp maps (data, model, CSD). Note that the spline maps provide a good estimate of the PMN's topography (in the absence of the N400). **B:** Left and

right sagittal views with PMN and DLPFC sources (labeled in the left hemisphere) along with the fronto-central scalp recorded activity (center). **C:** Source waveforms showing the contributions of the PMN and DLPFC dipoles to scalp recorded activity. All PMN (diamond) sources showed sustained activation peaking around 283 msec. The residual variance was 10% (253–354 msec).

PMN dipole locations could be replicated; and (2) whether or not N400 dipoles could be modeled to verify the apparent absence of the N400.

Figure 5 presents the PMN data. The peak had a central (slightly right asymmetrical) distribution, and current source density (CSD) maps revealed left anterior activation similar to that reported by Connolly et al. [2001]. The PMN-only spline maps provided a good estimate of the component's isolated scalp topography, in the absence of the N400. Source analysis showed that the locations of the PMN dipoles matched those obtained when it was modeled simultaneously with the N400 (Fig. 5b). Specifically, there were two bilateral sources in the inferior frontal regions, with the source activation showing a left activation asymmetry (Fig. 5c). The PMN_{s1} was again localized to Broca's area (BAs 44/45). There was also a left hemisphere source in the inferior parietal lobe (PMN_{s2}; BAs 39/40). It was not possible to model a N400 dipole (regardless of interval size). Indeed, when bilateral probe dipoles were placed in the N400 re-

gions and fitting procedures were conducted, these sources were localized to the dorsolateral prefrontal regions (DLPFC; BAs 8/9). For the PMN-only model (advanced solution), the goodness-of-fit was 90% (RV = 10%; 253–354 msec).

Individual reliability

To determine whether the overall source location estimates were representative across individuals, the initial PMN-N400 model was subsequently applied to the individual data. Regional sources were used to test the reliability of active areas across individuals. Difference waveforms for all 10 participants were imported into BESA. The fit for each data set was then recorded to evaluate the model's reliability. The mean goodness-of-fit was greater than 85% (RV = 13.35 ± 3.61 , range = 8.9–18.3%; 253–475 msec), demonstrating that the grand average model was representative.

DISCUSSION

The PMN and N400 in Speech Perception

Prior work has linked the PMN to phonological processing and the N400 to semantic analysis during speech perception [Connolly and Phillips, 1994]. The current results show that these responses can be elicited by naturalistic spoken sentences that are by themselves completely sensible, but violate expectations formed by reading preceding sentences [Fischler et al., 1985]. The ERP findings supported the first hypothesis that the PMN and N400 would be elicited maximally to unexpected phonological and semantic features (respectively), and that the PMN alone would be sensitive to low probability semantically congruent endings (Fig. 2).

The PMN (287 msec) and N400 (424 msec) components were present in the high and low incongruent conditions, validating the experimental task. Both components were characterized by relatively large amplitudes (PMN $\sim 4 \mu\text{V}$; N400 $\sim 8 \mu\text{V}$), which facilitated the spatial analyses. The presence of only the PMN component in the low-congruent condition was a key finding in this study. The high-congruent condition differed from the low-congruent condition as a function of the possible number of acceptable candidates, with the latter being characterized by a greater number of alternatives. The sensitivity of the PMN to the number of active word candidates provides strong evidence for a functional interpretation that involves the size of the phonological search set maintained in WM.

Examination of the PMN and N400 scalp distribution suggested a central-parietal topography overall (Fig. 3). The spline maps showed that the PMN peaked in the central region [Connolly and Phillips, 1994], whereas the N400 peaked in the centro-parietal region [Kutas and Van Petten, 1994] (Fig. 4a). CSD maps depicted a number of active areas, including the left anterior region during the PMN time range (Fig. 5a). These results replicated the Connolly et al. [2001] study and confirmed the central PMN distribution. Source analysis revealed bilateral PMN and N400 dipoles (Fig. 4 and 5), with greater activation in the left hemisphere. Source analysis, however, is necessarily an approximation and the location of these dipoles provided only a global estimate. The main objective of the dipole modeling procedure in this study was to test a hypothesis about the spatial dissociability of the PMN and the N400 sources (with less emphasis on spatial resolution). We predicted that the PMN and N400 originate in separate neuroanatomic areas and have different activation time courses. Because sources for these components were reliably localized to language regions and the source waveforms represented different processes in time, the second hypothesis was supported also.

PMN sources were localized to the left inferior frontal region (PMN_{S1}; in Broca's area) and the left inferior parietal lobe (PMN_{S2}). Some activation was also observed in the homologous inferior frontal area of the right hemisphere. The source waveforms for PMN dipoles revealed similar time courses with a pronounced peak in the range of 280–

290 msec, fitting well with the scalp-recorded PMN. Of particular interest was the finding that dipoles in the PMN-only model were localized to the same regions as those in the difference waveforms, but no active regions for the N400 could be identified (Fig. 5). The location of PMN_{S2}, the sustained source activation profile, and the novel DLPFC activation provided additional insight into the importance of verbal WM in phonological tasks that involve matching to anticipated templates [Connolly et al., 2001; D'Arcy et al., 2000]. Incongruent words (low and high probabilities) did not elicit DLPFC activation because there was a minimal search requirement for a mismatching word.

With respect to the N400, there was a dipole in the left pSTG (N400_{S1}; Wernicke's area), with similar but reduced activation in the homologous area of the right hemisphere. A second N400 dipole (N400_{S2}) was localized, anterior to N400_{S1}, to the left supratemporal plane (STP). A third (N400_{S3}) was localized to the left polymodal (temporal-parietal-occipital) region. The source waveforms for all three dipoles were comparable with major peaks being centered in the N400 time range. The N400_{S1} and N400_{S2} were characterized by similar activation patterns with an overall morphology that resembled closely the scalp recorded N400. The activation pattern for N400_{S3} was reduced relative to the others, and thus may be of less significance. The current N400 dipole results replicated MEG findings that highlight the left perisylvian region as a source for N400 activity [Helenius et al., 1998, 2002].

The Evolution of a Speech Perception Network

The neuroanatomic regions identified fit well with a proposed network for speech perception in which the posterior-superior temporal lobe (bilaterally) is the primary substrate for constructing sound-based speech representations [Hickock and Poeppel, 2000]. The model suggests that although both hemispheres contribute to speech perception, there is a left hemisphere asymmetry. Two functional neuroanatomic pathways are thought to diverge from the left posterior-superior temporal lobe. The first pathway involves sound-based representations of speech, assembled in the bilateral posterior STP and posterior STG, which interface with amodal semantic-conceptual representations of the mental lexicon in the left temporal-parietal junction. The second pathway involves accessing sub-lexical speech segments and possibly verbal working memory. In this pathway, the left inferior frontal region and the left inferior parietal lobe may support an auditory-motor interaction during the process of subvocal articulation. Subvocal articulation is assumed to provide a temporary storage system for acoustic or speech-based information, which fades away within seconds unless otherwise maintained by rehearsal [Baddeley, 1996].

The current results implicate all of the above regions during spoken sentence processing. In addition, the experimental independence of the PMN and N400 provide clarification about aspects of the speech stimulus that may be responsible for producing activation in a particular region, corroborating the results of less temporally resolved func-

tional imaging studies [Démonet et al., 1992, 1994]. In light of the convergence across imaging modalities, we tentatively propose that the interaction between these two pathways enables construction of speech representations using phonological input. In this architecture, compulsory PMN activity can be attenuated when the processing of sound-based speech representations are compatible with sub-lexical speech segments, already represented in working memory. The increased PMN activity in the low-congruent condition, in which there is a lower probability that the contents of working memory match the input, supports this interpretation.

The functional role of the N400 sources in left perisylvian regions needs to be refined. Most functional interpretations of the N400 stress the evaluation of a word's semantic content as it relates to the sentential context and semantic memory structure [Federmeier and Kutas, 1999; Kutas and Van Petten, 1994]. Given that similar temporal regions have been identified for visual N400 dipoles using ERPs and MEG [Helenius et al., 1998; Simos et al., 1997], the convergence lends further support to the notion that the left perisylvian region is involved in some form of amodal semantic-conceptual processing. In addition, the electromagnetic source findings concur with results from positron emission tomography (PET) and fMRI studies [Cabeza and Nyberg, 2000; Kiehl et al., 2002; Newman et al., 2001; Price, 2000]. The functional role of the superior (and middle) temporal cortex may include the evaluation of the semantic content, independent of sensory modality. The constellation of functions subsumed by the left perisylvian region, however, remains to be fully understood and it is clear that several other regions contribute to N400 activity (e.g., anterior medial temporal sources) [McCarthy et al., 1995; Nobre and McCarthy, 1995].

The Role of Working Memory in Speech Perception

Functional imaging evidence of working memory involvement in speech perception, particularly phonological template matching, is mounting. D'Arcy et al. [2000] reported a N2b component elicited by phonological deviations from a cognitive template maintained in working memory. Thierry et al. [1999] investigated phonological processing in a fMRI study and reported evidence of working memory involvement. They found activation consistent with the contribution of Broca's and Wernicke's areas, and in particular, activation in the left supramarginal region. Temporal analysis of the hemodynamic responses revealed a decoupling between sensory and association speech regions during phoneme monitoring, but not during fast repetition. The decoupling was hypothesized to reflect sustained, delayed processing consistent with the functional model of the phonological loop [Baddeley, 1996]. In the Connolly et al. [2001] rhyme anticipation study, a later negativity was observed after the PMN. We speculated that the later negativity reflected sustained activation associated with continued phonological processing and the influences of working memory. The findings in the current experiment substantiate the view that

active processing in fact continues well beyond the early peak activation of the PMN. The sustained activation in Broca's area and the left inferior parietal region is consistent with other neuroimaging results supporting the conceptualization of a phonological loop [Démonet et al., 1992, 1994; Paulesu et al., 1993; Thierry et al., 1999]. Given these results, it will be critical to consider the potential influence of underlying WM activity in ERP language components.

CONCLUSIONS

The present experiment provided a framework in which to study the spatial characteristics of the PMN and N400. PMN activation arose mainly from the left inferior frontal and left inferior parietal regions. Activation in these regions was thought to reflect phonological analysis and working memory during speech perception. Active regions involved in generating the auditory N400 included but were not limited to areas in the left perisylvian vicinity. Further work is needed to spatially resolve the sources and refine their functional significance.

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