Fractionating Language: Different Neural Subsystems with Different Sensitive Periods

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Theoretical considerations and psycholinguistic studies have alternately provided criticism and support for the proposal that semantic and grammatical functions are distinct subprocesses within the language domain. Neurobiological evidence concerning this hypothesis was sought by (1) comparing, in normal adults, event-related brain potentials (ERPs) elicited by words that provide primarily semantic information (open class) and grammatical information (closed class) and (2) comparing the effects of the altered early language experience of congenitally deaf subjects on ERPs to open and closed class words. In normal-hearing adults, the different word types elicited qualitatively different ERPs that were compatible with the hypothesized different roles of the word classes in language processing. In addition, whereas ERP indices of semantic processing were virtually identical in deaf and hearing subjects, those linked to grammatical processes were markedly different in deaf and hearing subjects. The results suggest that nonidentical neural systems with different developmental vulnerabilities mediate these different aspects of language. More generally, these results provide neurobiological support for the distinction between semantic and grammatical functions.

Over the past decade, neuroscientists have provided increasingly fine-grained descriptions of the biochemical, cellular, and anatomical characteristics of distinct cytoarchitectonic areas of cerebral cortex in nonhuman primates. More recently, it has also become possible to identify different cortical areas in terms of their functional characteristics (i.e., their roles in particular sensory, motor, and cognitive processes) by recording from single neurons as awake, behaving animals perform specific tasks (Wurtz et al., 1980; Desimone and Ungerleider, 1989). A complementary approach has been to assess the effects of localized lesions on particular aspects of behavior (e.g., Mishkin et al., 1983; Squire and Zola-Morgan, 1991). Functional mapping of this type has progressed very rapidly within the study of the visual system, which has been shown to be composed of multiple processing subsystems that are linked to specific cortical and subcortical areas. Moreover, the functional characteristics of the subsystems correspond to functional categories suggested by early and recent psychophysical and neuropsychological studies of the visual system in humans (von Helmholtz, 1910; Riddoch, 1917; Livingstone and Hubel, 1987). Additionally, developmental studies suggest different timetables of maturation and sensitive periods for some of these subsystems (Harwerth et al., 1986). This type of complementarity of results across behavioral, neurobiological, developmental, and clinical studies is a major goal of behavioral neuroscience, including cognitive neuroscience.

The recent (and continuing) development of noninvasive means of functionally imaging the human brain has made it feasible to take this multileveled behavioral, clinical, developmental, and neurobiological approach to the study of human language. Recent studies employing the positron emission tomography technique provide support for certain conceptions of the organization of language output systems and have helped to refine the questions about others (e.g., Posner et al., 1988; Petersen et al., 1989). The magnetic evoked response or event-related brain field technique promises to provide information about the generators that produce language-specific activity at the scalp (e.g., Yamamoto et al., 1988; Cohen et al., 1990). The event-related brain potential (ERP) technique has provided fine temporal analyses of different cognitive operations including language and has contributed information to several different conceptions of how meanings are represented in words (Rugg et al., 1986; Hillyard and Picton, 1987; Kutas and Van Petten, 1988). While these neuroimaging studies of human language have just begun, it is clear that this approach can provide evidence on the biological validity of different theoretical conceptions of the organization of language, and that it can also reveal aspects of the organization and operation of language that are not apparent from a purely behavioral perspective This type of approach, wherein information from different levels of analysis reciprocally constrain each other, can benefit several enterprises by validating, correcting, and/or refining psychologically based conceptions of language, and also by helping to identify and distinguish different brain areas on the basis of cognitive function.

Here we utilize the ERP technique to address a particular proposal concerning the structure of language that has been held by many investigators over the last two or three decades, and for which there is behavioral and clinical support, but for which there is very little neurobiological evidence from the normal brain. Theoretical considerations and considerable psycholinguistic research have been interpreted as supporting a distinction between semantic processing, that is, the processes whereby words make reference to specific objects and events, and grammatical processes, that is, the rules and processes whereby relations between objects and events are specified (Chomsky, 1965, 1981; Garrett, 1980). In English this distinction is partly captured by two lexical categories, the "content" or open class words including nouns, verbs, and adjectives that make reference to specific objects and events, and the "function" or closed class words including articles, conjunctions, and auxiliaries. It has been suggested that the small set of closed class words supports the initial syntactic parsing of sentences, that is, the determination of the phrase structure of sentences. Thus, the closed class words play a major role in grammar. Empirical studies of behavior have provided support for the idea that syntactic and semantic processes are distinct subsystems within language. For example, the ability to produce and comprehend grammatical information appears more vulnerable following lesions to anterior than posterior regions of the left hemisphere, while lesions to posterior brain regions of both hemispheres can produce deficits in semantic processing while leaving grammatical processing relatively intact (Bradley et al., 1980; Friederici and Schoenle, 1980; Grodzinsky, 1984; Rosenberg et al., 1985). Additionally, behavioral research with normal adults has documented that semantic and syntactic information—as represented in open and closed class words—participate in different types of speech errors (Garrett, 1980; Stemberger, 1982), display different patterns of asymmetries after presentation to the visual hemifields (Bradley and Garrett, 1983; Shapiro and Jensen, 1986), and have different sensitivities to context (Friederici, 1985). Studies of normal development report different developmental timetables for the acquisition of open and closed class words (Brown, 1973; Newport et al., 1977; Flores d'Arcais, 1981; Gleitman and Wanner, 1982), and studies of abnormal development suggest that the acquisition of syntax may be more dependent on the nature and timing of early language experience than is the acquisition of semantic skills (Curtiss, 1977; Yamada, 1990). Consideration of data like these, together with the different roles that open and closed class words play in language comprehension, has led many investigators to propose that processes of word recognition and/or retrieval are different for open and closed class words and further that they may be organized within nonidentical neural substrates (Garrett, 1976; Bradley, 1978; Friederici, 1986).

On the other hand, over the past five years an alternative perspective has emerged under the rubric of cognitive or functional grammar (Bates and MacWhinney, 1987; Langacker, 1987, 1991). By this view, grammatical phenomena can be accounted for on the basis of the semantic content of closed class words, which are hypothesized to be represented together with open class words within the same system. By this view, the two word types are influenced by the same general factors and any behavioral or clinical differences between them are attributed to such factors as their different frequencies of occurrence in the language (closed class more frequent), their different lengths and stress they receive (closed class words are short and unstressed), or differences in imageabilities (closed class words are low in imageability). These general processing factors, it is argued, lead to quantitative differences in the perceptibility and memorability of open and closed class words that can account for the clinical and behavioral evidence reported thus far (Martin, 1987; Carpenter and Just, 1989; Kilborn, 1991).

Biological support for a distinction between semantic and grammatical processes would be provided by evidence that these putative subsystems are organized within nonidentical systems in the normal brain. Similarly, evidence that the systems were qualitatively different, rather than varying on a continuum, would provide evidence against the proposal that different levels of similar and general functions, like those associated with the processing of frequency and length, underlie the observed behavioral results. In addition, a comparison of the effects on neural processing of frequency and length with the effects of word class would also directly address these issues.

Here we report data from two different approaches we have taken to these issues. First, we compare, in normal adults, the timing and the distribution of ERPs elicited by open and closed class words in sentences, to assess whether any observed differences are qualitative or quantitative and whether they can be accounted for by differences in word frequency or length, rather than to the different functions these words perform in language. At present there is very little evidence on this issue. A few studies have compared ERPs to open and closed class words, but they have not assessed the possible role of frequency or length in the observed differences, nor did they include the lateral electrode recording sites that prior studies have shown to be particularly sensitive to linguistic variables (Neville et al., 1982a; Kutas and Hillyard, 1983; Garnsey, 1985; Van Petten and Kutas, 1991). Second, we report data that permit this issue to be considered from the perspective of development. If distinct neural systems mediate different functions in language, it is likely that, as in the visual system and as suggested by behavioral data, they are characterized by different developmental timetables with different associated critical/sensitive periods. We assess this proposal by comparing ERPs to open and closed class words in normal adults to ERPs from individuals who learned English late and imperfectly because of congenital deafness. The deaf subjects learned American Sign Language (ASL) as a first language, at the normal age for language acquisition, and only later were taught English. These individuals typically acquire large vocabularies but do not fully acquire the grammar of English, rendering their reading capabilities around third grade level (Conrad, 1979). In previous studies, we have reported that both the auditory deprivation and abnormal language experience of deaf subjects have significant, albeit distinct, effects on cerebral organization (Neville and Lawson, 1987a,b). For example, when reading English words, deaf subjects do not display evidence for left hemisphere specialization, in marked contrast to normal-hearing subjects, in whom that is the typical pattern (Neville et al., 1982a,b). By contrast, deaf subjects do display asymmetries for their native language, ASL (Poizner et al., 1987; Neville, 1991). On the basis of such findings, we speculated that a critical factor in the development of cerebral asymmetries is the acquisition of grammatical processes. In the present study, we sought further evidence on this hypothesis by comparing the responses of deaf and hearing subjects to closed class words (that are hypothesized to carry grammatical information in English). Deaf and hearing subjects should display markedly different responses to such words since the deaf subjects have not fully acquired the grammar of English. By contrast, responses to open class words, which make reference to objects and events and provide semantic information, should by this hypothesis be qualitatively similar in deaf and hearing subjects. Additionally, modulations of semantic processing, as occur for example with the presentation of semantically anomalous words that elicit a large negative (N400) ERP response (Kutas and Hillyard, 1980), should also be similar in deaf and hearing subjects if semantic processing is less vulnerable to abnormal language experience. More generally, a comparison of those aspects of cerebral organization that are and are not altered under conditions of late exposure to language will provide information on the identity and separability of language-relevant neural systems and the role of different facets of language experience in their differentiation. Below, we present the results from normal-hearing adults first (Section I), followed by a comparison of these results with those from congenitally deaf adults (Section II).

I. Normal-hearing Adults

Methods

Subjects

Seventeen volunteers (eight males), between the ages of 18 and 28 years, were paid $5.00/hr to participate in this experiment. All subjects were right-handed native speakers of English with normal visual and auditory acuity.

Stimuli

Sentences rather than lists of words were chosen in an effort to activate natural language processing. A rate of one word/700 msec was chosen to gain a reasonably natural rate of word presentation while providing enough time between words to prevent overlap of ERPs to adjacent words.

The stimuli were sentences presented one word at a time on a monitor under the control of a microcomputer. Each word (200 msec duration) consisted of white letters (range, 1–12) against a dark background. Words appeared in the center of a 9.2 × 4.5 inch rectangle. The presence of the rectangle indicated that subjects were not to blink or move their eyes. The monitor was 57 inches from the subject, so words subtended a 0.3° visual angle vertically and 0.3–2.9° visual angle horizontally.

Procedure

Subjects sat comfortably in a copper-shielded, sound-attenuating room and were given instructions describing the task along with one practice session. Subjects were presented with 120 sentences in four blocks, each separated by a short break. A trial began with the onset of the rectangle in the center of the screen followed 1400–2000 msec later by the first word of the sentence. Sentences ranged in length from 6 to 13 words. The interval from the onset of one word to the onset of the next was 700 msec. Two seconds after the onset of the final word of the sentence, the rectangle was turned off and the subject was prompted to press one of two buttons to indicate whether the sentence made sense or not. Half of the final words of the sentences were highly expected given the preceding context (e.g., Each April we must pay our income *tax*.), and half were semantically anomalous (e.g., The winning candidate was preparing his acceptance *wood*.). Prior to the final words, all sentences were well formed and meaningful. The hand used to respond was counterbalanced across subjects. Each of the words in the sentences except the first and last were coded for membership in the open class (N = 446 including nouns, verbs, and adjectives) or closed class (N = 391 including articles, prepositions, conjunctions, etc.). In addition, each open class word was coded as either frequent (N = 224; defined as >90/million occurrences in Kucera and Francis, 1967) or infrequent (N = 222; defined as ≤90/million occurrences), and as either long (N = 283; defined as

≥5 letters) or short ($N = 163$; defined as <5 letters). Both groupings were based on a median split.

ERP Recordings

Scalp electrical activity was recorded with Ag/AgCl electrodes from over several sites within and between the two hemispheres and from around the eyes. The scalp sites included six locations based on the International 10-20 System: left and right frontal (F7/F8), posterior temporal (T5/T6), and occipital (O1/O2). Recordings were also taken from six other locations over left and right anterior temporal regions [50% of the distance from F7(8) to T3(4)], left and right temporal (33% of the interaural distance lateral to CZ), and left and right temporoparietal areas (33% of the interaural distance lateral to a point 13% of the nasion–inion distance posterior to CZ). These nonstandard lateral sites were selected because they overlie brain regions thought to be important in language and have shown sensitivity to experimental variables in several ERP studies of language (Neville et al., 1982a,b, 1986). Recordings from these electrodes and the vertical electrooculogram (EOG) from beneath the left eye were referenced to the linked mastoids. The horizontal EOG was recorded between electrodes placed at the outer canthus of each eye. Electrical activity was amplified with a band pass of 0.01–100 Hz.

Data Analysis

The EEG was sampled 100 msec prior to and 700 msec following each stimulus. Trials on which excessive eye movement or muscle artifact occurred were excluded from the averages (approximately 2–5% of all trials). ERPs were averaged separately for open class and closed class words at each electrode site (6) over each hemisphere (2). ERPs to open class words were also averaged according to their frequency and length. Final words that were and were not semantically anomalous were averaged separately.

Amplitudes of negative and positive values of ERP components were quantified by computer as either peak (maximal) amplitudes within a latency range or as area measures (the mean voltage within the same latency range), relative to 100 msec prestimulus baseline voltage. ERP component latencies were measured as the time of occurrence of the maximal negative or positive voltage within a given latency range. For the open and closed class words the measurement windows were 50–150 msec for the initial positivity (P100) at posterior (i.e., parietal, temporoparietal, and occipital) electrodes, 125–250 msec for the initial negativity (N170) at posterior electrodes, 50–150 msec for N100 at anterior (i.e., frontal, anterior temporal, temporal) electrodes, 100–225 msec for the initial positivity at anterior electrodes (P200), 235–400 msec for both N280 and N350 (i.e., the negativities to closed and open class words), 300–600 msec for the late positive component (LPC), and 400–700 msec for the broad negative shift. For the final words, the peak amplitude, latency, and mean area within 300–500 msec (N400) were measured on both the ERPs and the difference waves (i.e., formed by subtracting the ERP to semantically appropriate words from ERPs to semantically anomalous words). This removes ERP activity that is the same to both words and retains only the activity associated with semantic anomalies.

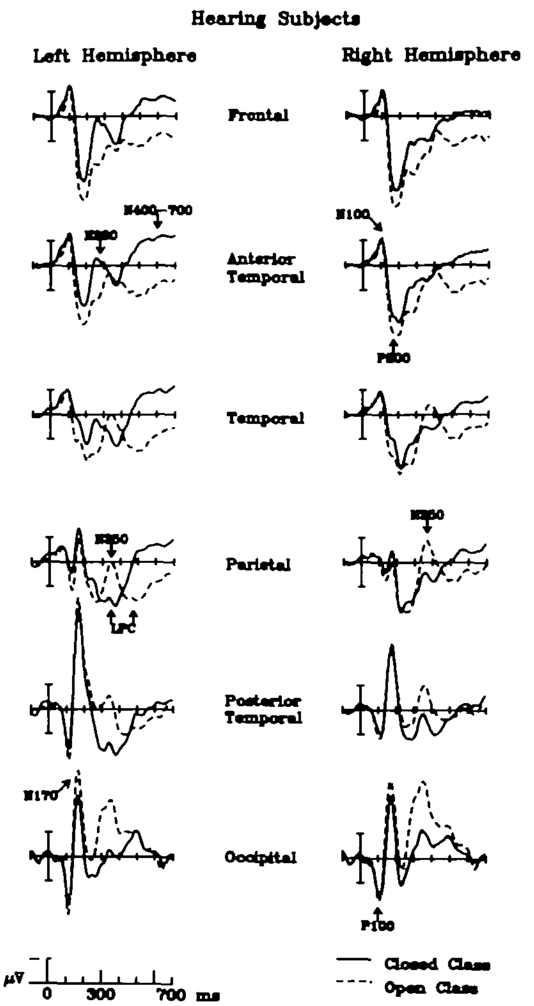

Figure 1. ERPs averaged across 17 normal-hearing adults, elicited by closed and open class words in the middle of visually presented, English sentences. Recordings from several sites over the left and right hemispheres. Closed class words elicited an N280 response over anterior regions of the left hemisphere. Open class words elicited an N350 response over posterior regions of both hemispheres.

ERP measures were subjected to a three-way analysis of variance (ANOVA) with repeated measures on two levels of word type, two levels of hemisphere, and six levels of electrode. Subanalyses of variance were performed to clarify significant interactions further. The Geisser–Greenhouse correction (Geisser and Greenhouse, 1959) was applied to all repeated measures with greater than one degree of freedom.

Results

Behavior

Hearing subjects were virtually perfect (98–100%) in judging whether the sentences did or did not make sense.

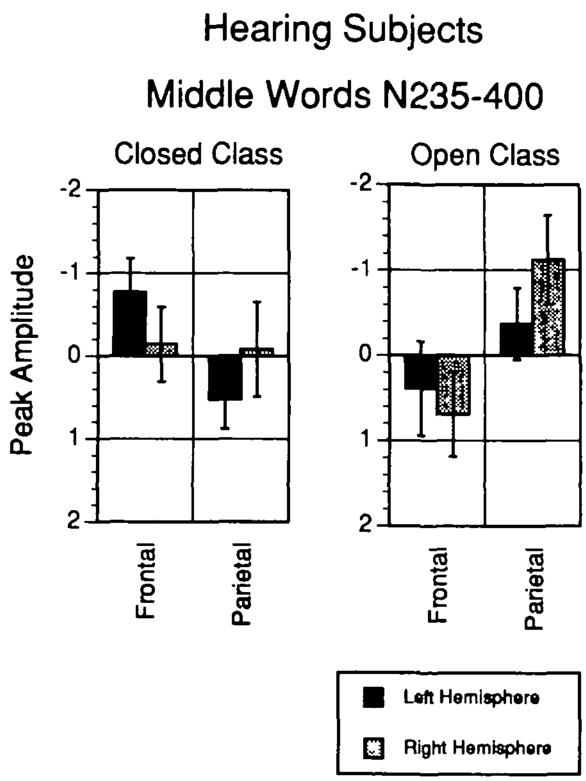

Figure 2. Amplitude of the peak negativity ($\mu V \pm SE$) within the 235–400 msec window. ERPs to closed class words were most negative over anterior sites of the left hemisphere, while ERPs to open class words were most negative over parietal sites of the right hemisphere.

ERP Components: Morphology and Distribution

Early Components: 0–200 msec. As seen in Figure 1, the words elicited a series of positive and negative deflections that differed in latency and amplitude as a function of electrode location and word type. Prominent over posterior regions was a positivity at 100 msec (P100). This was followed by a negativity at 170 msec (N170) that was larger from the left than the right hemispheres for all words [hemisphere, $F(1,16) = 6.29$, $p \leq 0.02$]. Over anterior sites an initial negativity occurred around 100 msec (N100) followed by a positivity at 200 msec (P200) that was also asymmetric as in previous studies [left hemisphere more negative hemisphere, $F(1,16) = 8.8$, $p \leq 0.009$].

Later Components: >200 msec. Following these early events, the morphology of the waveforms differed for open and closed words. Closed class words, but not open class words, elicited a negative component, of maximal amplitude at 280 msec (N280) that was only apparent in recordings from frontal, anterior temporal, and temporal sites of the left hemisphere (marked N280 in Fig. 1). Also apparent in Figure 1, open class words elicited a negative component at 350 msec (N350) that was apparent over temporal and posterior sites of both hemispheres. The N280 was followed by an LPC, largest from parietal sites, that peaked around 350 msec. The N350 was followed by an LPC that peaked around 450 msec. A slow negative shift from 400 to 700 msec (N400–700) was present over anterior sites in response to closed class words only.

Effects of Word Class

Early Components Over anterior sites, the two word types were significantly different by 150 msec after word onset. ERPs to closed class words were more negative than were ERPs to open class words [P2 peak amplitude, word type effect, $F(1,16) = 13.0$, $p \leq 0.002$]. Over posterior temporal and occipital sites, the N170 was significantly larger in response to open than to closed class words [word class × electrode, $F(2,32) = 38.1$, $p \leq 0.0001$]. This effect was larger over the left hemisphere [word class × electrode × hemisphere, $F(2,32) = 8.3$, $p \leq 0.001$].

N280 and N350. Major distinctions between the word classes occurred in the latency, distribution, and hemispheric asymmetry of negative components occurring between 235 and 400 msec.

Latency: The peak negativity in this window was significantly earlier for closed than open class words [mean, 280 vs 350 msec; word class, $F(1,16) = 22.6$, $p \leq 0.0001$]. As seen in Figure 1, this effect is clearest over anterior temporal and temporal sites where both the early (N280) response to closed class words and the later (N350) response to open class words are evident [word type × electrode, $F(5,80) = 2.83$, $p \leq 0.03$].

Amplitude: As seen in Figures 1 and 2, whereas the N280, elicited in response to closed class words, was largest from frontal and anterior temporal regions of the left hemisphere, the N350, largest in response to open class words, was large from over posterior sites of both hemispheres [word type × electrode: peak amplitude, $F(5, 80) = 25.0$, $p \leq 0.0001$; mean area, $F(5,80) = 34.8$, $p \leq 0.0001$; word type × electrode × hemisphere: mean area, $F(5,80) = 5.1$, $p \leq 0.01$]. Subanalyses confirmed that the N280 to closed class words was significantly larger from left than right frontal and anterior temporal sites [$F(1,16) = 5.5$, $p \leq 0.03$; $F(1,16) = 5.7$, $p \leq 0.03$]. The N350 to open class words was largest from posterior electrode sites and tended to be larger from the right hemisphere [electrode, $F(2,32) = 21.9$, $p \leq 0.0001$; hemisphere (parietal sites), $F(1,16) = 4.0$, $p \leq 0.06$] (see Fig. 2).

LPC Latency: Between 300 and 600 msec a positive component (LPC) was evident in ERPs to both word types (labeled LPC in Fig. 1). The latency of the LPC peak was 50–100 msec earlier for closed than for open class words [word type, $F(1,16) = 15.4$, $p \leq 0.001$]. As seen in Figure 3, this effect was only significant within the left hemisphere [word type × hemisphere, $F(1,16) = 9.9$, $p \leq 0.006$].

Amplitude: For closed class words, LPC was larger from parietal and posterior temporal regions, while for open class words it was larger anteriorly [electrode × word type: peak amplitude, $F(5,80) = 15.2$, $p \leq 0.0001$; mean area, $F(5,80) = 20.7$, $p \leq 0.0001$]. As seen in Figure 1, the amplitude of the LPC was larger from the left than the right temporal, parietal, and posterior-temporal regions for both word classes [electrode × hemisphere, mean area, $F(5,80) = 5.5$, $p \leq 0.004$].

N400–700. From 400 to 700 msec, the closed class words elicited a slow negative potential that was ab-

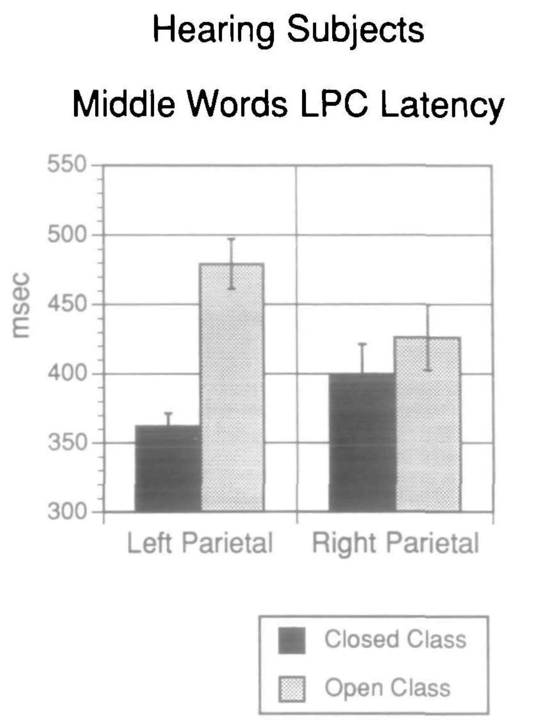

Figure 3. The latency of the LPC (mean msec ± SE) was significantly earlier for closed than for open class words in ERPs from the left hemisphere.

sent in the ERPs to the open class words [word type, mean area, $F(1,16) = 11.3$, $p \leq 0.004$; see Figs. 1, 4]. This negativity to closed class words was largest from anterior sites of the left hemisphere. During the same time period, the responses to open class words displayed a slow positivity that, over posterior regions, was larger from the left than right hemisphere [word type × electrode, $F(5,80) = 15.3$, $p \leq 0.0002$; word type × hemisphere × electrode, $F(5,80) = 5.8$, $p \leq 0.002$; see Fig. 1].

These data show marked differences in ERPs to words as a function of their membership in lexical categories. In order to interpret such effects, however, it is necessary to assess the role that word frequency and length may play in these differences.

Effects of Word Frequency and Word Length

Frequency Open class words that were less frequent elicited larger-amplitude N170 responses over posterior locations than did more frequent open class words [frequency, $F(1,16) = 4.9$, $p \leq 0.04$; see Fig. 5, top]. In addition, over posterior regions, the amplitude of the N350 response was larger to infrequent than to frequent words [frequency N350 peak amplitude, $F(1,16) = 22.6$, $p \leq 0.0002$; mean area, $F(1,16) = 22.8$, $p \leq 0.0002$; frequency × electrode, $F(5,80) = 8.1$, $p \leq 0.004$; see Fig. 5]. Over anterior regions, word frequency did not affect the morphology, latency, or amplitude of any ERP components.

Length. Over occipital sites, longer open class words elicited larger-amplitude N170 responses than did shorter words [length × electrode, $F(2,32) = 6.8$, $p \leq 0.01$]. A major effect of word length was that over frontal regions longer words elicited ERPs that were more positive than shorter words (see Fig. 5, bottom). This positivity began around 200 msec and lasted the duration of the epoch. Thus, all three area measures reflected this effect [length × electrode: area 235–400, $F(5,80) = 14.8$, $p \leq 0.0001$; area 300–600, $F(5,80)$

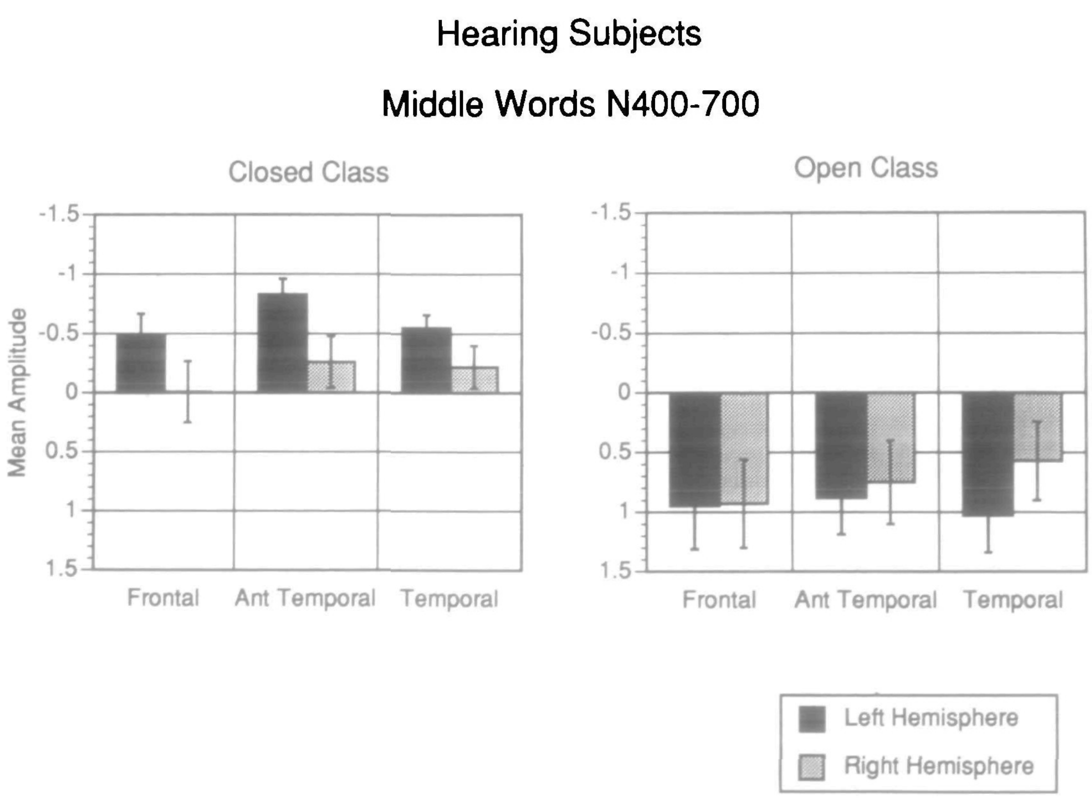

Figure 4. The negative-shift N400–700 (mean area ± SE) was elicited by closed class words only. It was larger from the left hemisphere.

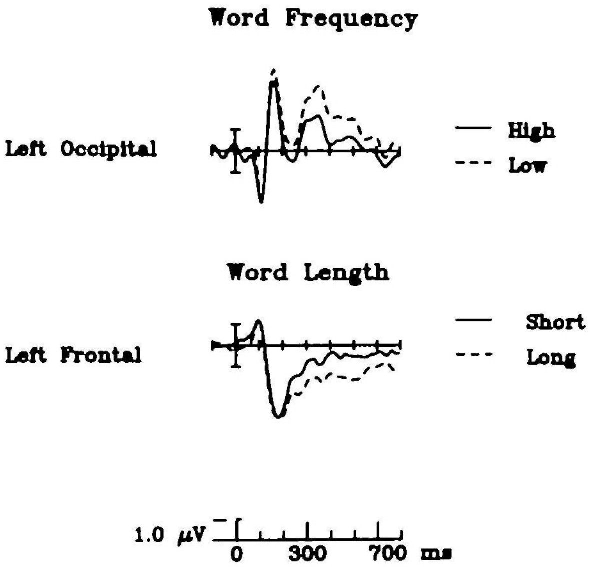

Figure 5. *Top*, ERPs elicited by low-frequency words elicited larger N170 and N350 responses over posterior regions than did high-frequency words. *Bottom*, Longer words elicited ERPs that were more positive over frontal regions than did shorter words.

= 14.0, $p \leq 0.0001$; area 400–700, $F(5,80) = 8.1$, $p \leq$ 0 001]. Nonetheless, this effect of length in open class words did not yield an N400–700 response like that elicited by closed class words. Moreover, open class words that were both short and highly frequent did not elicit the left-lateralized N400–700 response. This is shown in Figure 6, which displays current source density (CSD) maps of the mean activity from 400 to 700 msec in response to the closed class words, all open class words, and short, frequent open class words. The CSD is calculated as the second spatial derivative of the voltage across the scalp. It provides a reference-free estimate of the electrical currents flowing from the brain perpendicular to the scalp (Nunez and Katznelson, 1981). The CSD maps in Figure 6 were calculated using the spherical-spline interpolation algorithm developed by Perrin et al. (1989). The maps show that whereas the closed class words elicited a focal sink over anterior temporal region of the left hemisphere, this pattern is absent in response to open class words, regardless of their frequency or length.

Discussion

These results demonstrate that while open and closed class words elicited early sensory responses that were similar, after 150 msec they activated nonidentical patterns of neural activity in normal young adults. ERPs to closed class words were characterized by an asymmetrical negative peak at 280 msec that was largest over frontal and anterior temporal regions of the left hemisphere. By contrast, ERPs to open class words were characterized by a symmetrical negative peak at 350 msec, largest over posterior cortex. Both N280 and N350 were followed by a positive component

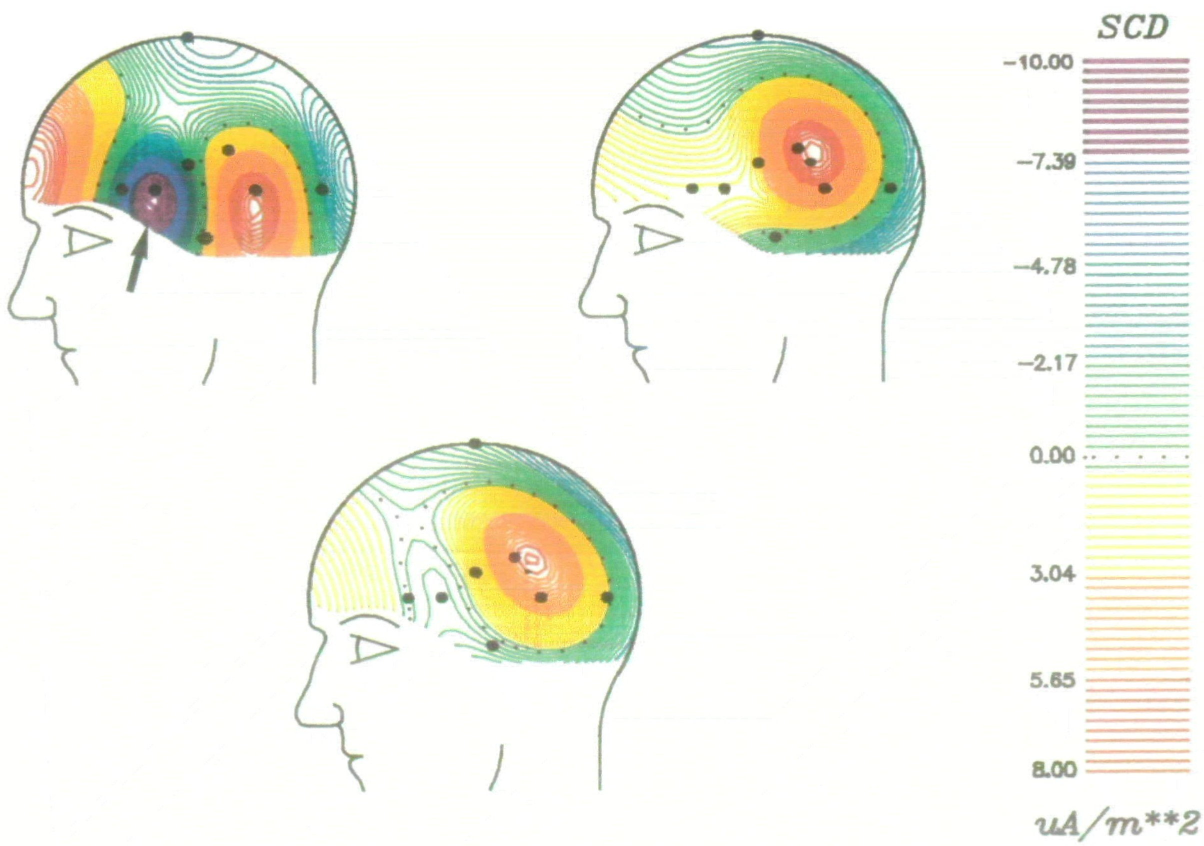

Figure 6. Topography of scalp current densities (*SCD*) calculated for the N400–700 (mean area from 400 to 700 msec) in response to closed class words (*top left*), all open class words (*top right*), and short, frequent open class words (*bottom*). Maps are averages across 17 hearing subjects. The *longer wavelengths* represent current sources (current flowing out of the head); the *shorter wavelengths* represent current sinks. Each map utilizes the same scale. The map for closed class words displays a prominent sink over anterior temporal regions. Neither of the maps for open class words displays this pattern.

(LPC) that was largest over temporal and parietal regions of the left hemisphere. However, this LPC occurred 50–100 msec earlier in response to closed than open class words. Following LPC, ERPs to open class words remained positive while ERPs to closed class words displayed an asymmetric negative shift (N400–700) that was largest from left anterior sites.

Frequency and Length Effects

Before considering interpretations of these effects in terms of different language processes, we will consider which of the observed ERP differences elicited by these different word classes can be accounted for by their different frequencies or lengths. The amplitude of posterior N170 was larger to open than closed class words. However, it was also larger to infrequent than frequent words and to longer than shorter words. Thus, since open class words are less frequent and longer than closed class words, the word type effect on this component may not be indexing a difference fundamental to the open/closed distinction, but may be due in part to frequency and length.

A major difference between word types was the presence, in ERPs to closed class words, of an N280 response localized to anterior regions of the left hemisphere. This component was not elicited by open class words of high or low frequency, or words that were short or long in length. Thus, this effect appears to be a word class effect that is not due to frequency or length.

Another salient difference between open and closed class words was the presence of a large N350 response to open class words. This response was small in ERPs to closed class words. Word frequency also significantly determined N350 amplitude (as has been reported previously; see Rugg, 1990; Van Petten and Kutas, 1991): more frequent open class words elicited smaller posterior N350 responses than did less frequent words. Since closed class words are more frequent than open class words, it is conceivable that the small N350 elicited by them is due in part to a word frequency effect. However, since there are very few open class words as frequent as closed class words, this point must remain moot. In any event, the effect of reducing the N350 may have important functional consequences by increasing the speed and automaticity of processing of closed class words. Consistent with this idea are studies that have linked N350-like responses (i.e., the N400) to conscious, controlled processes that depend on conscious awareness (Brown et al., 1989; Neville et al., 1989).

The latency of the LPC was earlier for closed than open class words. Since LPC latency was unaffected by word frequency or length, this effect appears to be due to word class. The amplitude of the LPC displayed a more anterior distribution for open than closed class words. Since a major effect of length was to add a symmetrical frontal positivity to the ERPs from 200 msec to the end of the epoch, and since open class words are longer than closed class words, the difference in LPC distribution may be due to length rather than word class.

The N400–700 response, largest to closed class words over frontal regions of the left hemisphere, also differentiated the two word types in a way that was not accounted for by word frequency or length.

In a separate study (H. J. Neville, S. A. Coffey, and P. J. Holcomb, unpublished observations) employing different sentences, we have observed these same effects of frequency and length on each of these ERP components. Additionally, in that study we assessed the effects of word imageability on the open/closed class distinction. Neither imageability alone nor in combination with frequency and length (e.g., low-imageable, high-frequency, shorter words vs high-imageable, low-frequency, longer words) reproduced the pattern of observed differences between open and closed class words.

In summary, the ERP effects that were attributable to frequency and length were quantitative and consisted primarily of modulations of the amplitudes of different ERP components. By contrast, effects of word class were qualitative and included the addition of ERP components to one word class that were not apparent in ERPs to the other word class.

The major open/closed class distinctions that *cannot* be accounted for by frequency or length are (1) the presence, in ERPs to closed but not open class words, of the N280 localized to anterior regions of the left hemisphere; (2) the latency difference in the LPC, which was 50–100 msec earlier to closed than open class words; and (3) the asymmetric N400–700 over anterior regions of left hemisphere, also elicited to closed class words.

It is reasonable to speculate that these differences in the morphology, timing, and distribution of ERPs elicited by open and closed class words are generated by the activation of different neural systems that are organized to process the different kinds of linguistic information that these word classes provide. The early onset of the N280 to closed class words only is compatible with the results of behavioral studies showing that closed class words are accessed quickly and automatically. The distribution over left anterior areas is compatible with a large clinical literature documenting deficits in the comprehension and production of grammar following damage to these regions. This response may index the activation of processes important in the look up and/or identification of these words within a system that only includes representations of closed class words (hence the absence of this response to open class words). We recently reported that the amplitude of an ERP component with a similar distribution is increased in response to violations of phrase structure in sentences (Neville et al., 1991). Hence, this component may also index processes concerned with parsing sentence structure.

Open class words elicited a distinctive response that peaked around 350 msec (N350). The N350 was present bilaterally, but it tended to be larger over the right hemisphere, over central and posterior regions. The latency and distribution of N350 suggest that it is a member of the group of responses referred to as the N400, a response that is sensitive to semantic context and expectancy (Holcomb and Neville, 1990; Fischler and Raney, 1991; Van Petten and Kutas, 1991). Thus, this response may index the identification and/or contextual integration of words. Closed class words elicited a small N350 response consistent with the idea that they may be organized within two lexical systems and/or participate in both functions.

Both N280 and N350 were followed by a positive shift, LPC, that was largest from temporal and parietal sites of the left hemisphere. The latency and distribution of the LPC make it likely that it is a member of the P300 group of events (Pritchard, 1981; Donchin and Coles, 1988; Fabiani et al., 1990). In this paradigm, the LPC may have been indexing the updating of language-relevant memory systems within the left hemisphere (Karis et al., 1984; Neville et al., 1986; Paller, 1990). This process appeared to be similar for the two word classes, but it occurred earlier for closed than for open class words. This result is also compatible with the evidence that suggests there is faster and more automatic access of closed class words. Additionally, the duration of the LPC differed for the two word classes. For open class words, the LPC continued until the presentation of the next word. By contrast, for closed class words it was abruptly (i.e., within 150 msec) replaced by a negative shift (N400–700) that was large over anterior regions of the left hemisphere. This asymmetrical negative shift continued until the presentation of the next word. The restriction of this component to closed class words, and its focal distribution similar to that of the N280 suggest that it may arise in conjunction with parsing based on the syntactic information provided by the closed class words. The similarity of the CSDs for the N280 (Fig. 9) and the N400–700 (Fig. 6) is consistent with the hypothesis that similar systems generate these events.

The precise functional significance of these ERP components will be clarified in future research along several lines, including studies within the auditory modality and of other languages, and in research with children in order to chart those aspects of cerebral organization that can be linked to specific changes in language abilities (Holcomb et al., in press; Mills et al., in press). The data currently in hand, however, provide evidence in support of the hypothesis that, from a neurobiological point of view, it is meaningful to distinguish, within the language domain, different systems strongly linked to the open and closed word classes, that process primarily semantic and grammatical information. Important support for this distinction also has come from recent reports of patients with focal lesions who have defects in accessing open class words, but in whom access to closed class words is intact (Damasio and Damasio, 1990; Damasio et al., 1991).

In the next study, we sought further evidence on this hypothesis, employing a developmental approach. We asked whether these subsystems that appear to be distinct in the adult have different sensitivities in development, that is, whether altered language experience differentially impacts the development of these neural systems.

II. Congenitally Deaf Adults

Methods

Subjects

Ten volunteers (five males; age range, 24–32 years) were paid to participate. Each subject was profoundly deaf (≥90 dB loss bilaterally) and had been so since birth due to a genetic etiology in which the CNS is not directly affected. All subjects were neurologically normal except for their deafness, were right-handed, and had normal visual acuity. All were born to deaf parents and learned a visual-manual language, American Sign Language (ASL), from their parents, at the normal age for language acquisition. These subjects were exposed to English later than normal, at residential schools for the deaf, and their scores on tests of fluency in reading and knowledge of English grammar were significantly below those of the hearing subjects [reading time, $F(1,17) = 8.7$, $p = 0.008$; Saffran and Schwartz Grammaticality Judgment Test, $F(1,18) = 4.7$, $p \leq 0.04$].

Other aspects of the methods were as described for the hearing subjects (Section I above).

Results

Behavior

The deaf subjects were virtually perfect in judging anomalous sentences (99%) but were less accurate than the hearing subjects in evaluating the appropriateness of nonanomalous, "best completion" sentences (93% vs 98%; $F(1,25) = 16.6$, $p \leq 0.0004$).

ERPs

Open Class Words. As seen in Figure 7, the overall morphology of ERPs elicited by open class words was similar in deaf and hearing subjects. Over occipital sites, ERPs in both groups were characterized by P100 followed by an N170 and an N350. There were no group differences in the latency, amplitude, or distribution of these components. The LPC component also displayed a similar latency and distribution in the two groups. Over anterior regions, ERPs from the two groups also displayed similar components, including the N100 and P200 peaks. The latency of the N100 component was earlier (by approximately 30 msec) in deaf than in hearing subjects, especially over right temporal regions [peak amplitude, group × electrode × hemisphere, $F(2,50) = 4.7$, $p \leq 0.02$]. Additionally, over anterior sites, beginning around 250 msec, ERPs from deaf subjects tended to be more positive than those from hearing subjects [mean area 300–600, $F(1,25) = 3.4$, $p \leq 0.07$; peak amplitude 300–600, $F(1,25) = 5.0$, $p \leq 0.03$; mean area 400–700, $F(1,25) = 5.7$, $p \leq 0.02$].

Closed Class Words. As seen in Figure 8, over occipital regions closed class words elicited ERPs from deaf and hearing subjects that were of similar morphology and timing (nonsignificant differences for latency or amplitude of P100, N170, or LPC). However, at anterior temporal and frontal sites, ERPs to

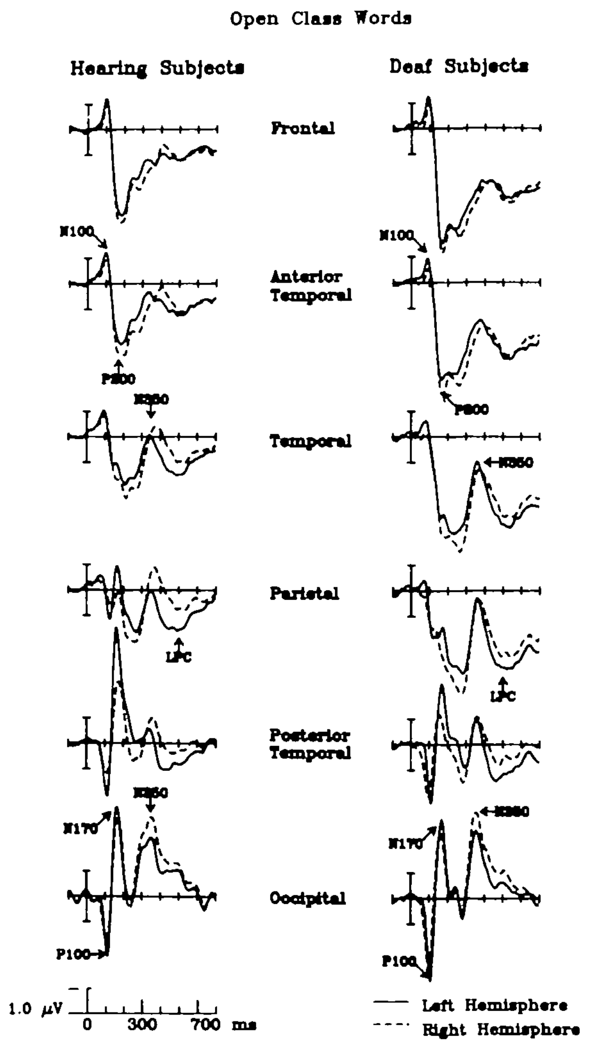

Figure 7. ERPs elicited by open class words averaged across 17 hearing and 10 congenitally deaf subjects. Recordings from several positions over homologous regions of the left and right hemispheres are superimposed. Deaf and hearing subjects display similar responses.

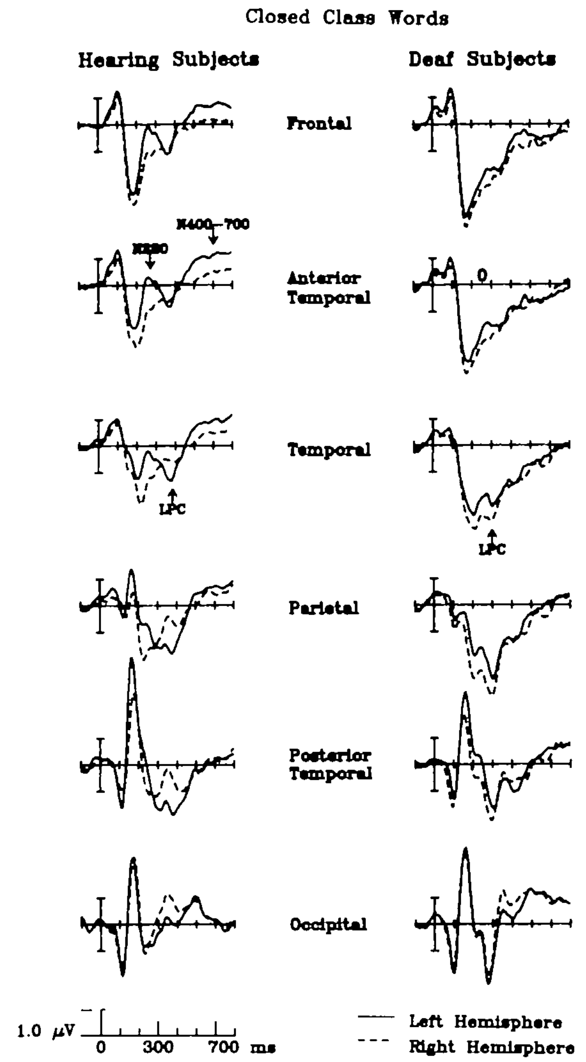

Figure 8. ERPs elicited by closed class words averaged across 17 hearing and 10 congenitally deaf subjects. ERPs from hearing subjects were asymmetrical and displayed prominent N280 and N400–700 responses from anterior regions of the left hemisphere. ERPs from deaf subjects were symmetrical and lacked the N280 and N400–700 responses.

closed class words were asymmetrical in the hearing subjects but were symmetrical in the deaf subjects ERPs from hearing subjects displayed the N280 response in recordings from over the anterior regions of the left hemisphere, but ERPs from deaf subjects did not display this component [absence marked 0 in Fig. 8; peak amplitude, N235–400 group, $F(1,25) = 6.3, p \leq 0.01$]. This group difference was only significant in the left hemisphere [$F(1,25) = 8.3, p \leq 0.008$].

In Figure 9, CSD maps of the peak activity elicited by closed class words between 235 and 400 msec are compared from hearing (top) and deaf (bottom) subjects. The CSD maps show that current source and sink activity within the right hemisphere is similar for the two groups. However, over the left anterior temporal region, the hearing subjects display a sharply focused sink while the deaf subjects do not.

As seen in Figures 8 and 10, the negative shift (N400–700), prominent from left anterior temporal regions in hearing subjects, was reduced or absent in the deaf subjects, and activity in this window was symmetrical in deaf subjects [group × electrode, $F(5,125) = 5.8, p \leq 0.005$; group × electrode × hemisphere, $F(5,125) = 2.2, p \leq 0.09$].

Semantic Anomalies. Further evidence for the hypothesis that semantic processes were similar in the two groups was sought by comparing ERPs to semantically anomalous information. The sentence final words that were semantically anomalous elicited a large negative component around 400 msec (N400), while final words that were semantically appropriate did not. This effect was observed in both hearing and deaf subjects (see Fig. 11). As in past research, the N400 was slightly larger from right parietal areas [final word type × electrode × hemisphere, $F(5,125) = 3.8, p \leq 0.02$]. The effects of semantic anomalies are captured in the difference ERPs, formed by subtracting ERPs to "best completion" words from ERPs to "anomalous completions" (see Fig. 12). These effects

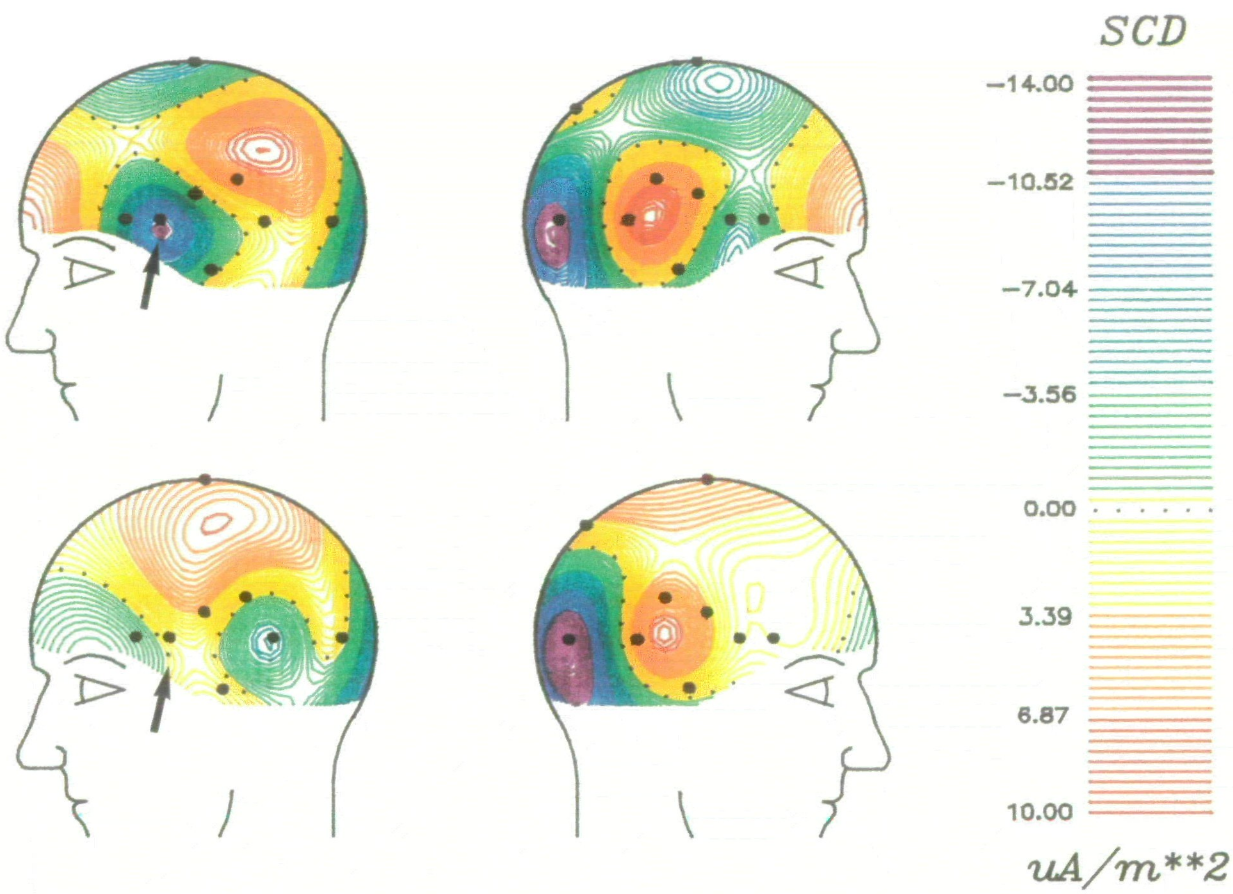

Figure 9. Scalp topography of CSDs calculated for the N280 (most negative peak in the window of 235–400 msec) in response to closed class words. Maps in the *top row* are averages across 17 hearing subjects; *below* are maps from 10 congenitally deaf subjects. The *longer wavelengths* represent current sources (current flowing out of the head); the *shorter wavelengths* represent current sinks. Each map utilizes the same scale. The maps of the hearing and deaf subjects were similar over the right hemisphere. Over the left hemisphere, the maps of hearing subjects display a prominent sink over the anterior temporal region that is absent in the maps from the deaf subjects (marked by the *arrows*)

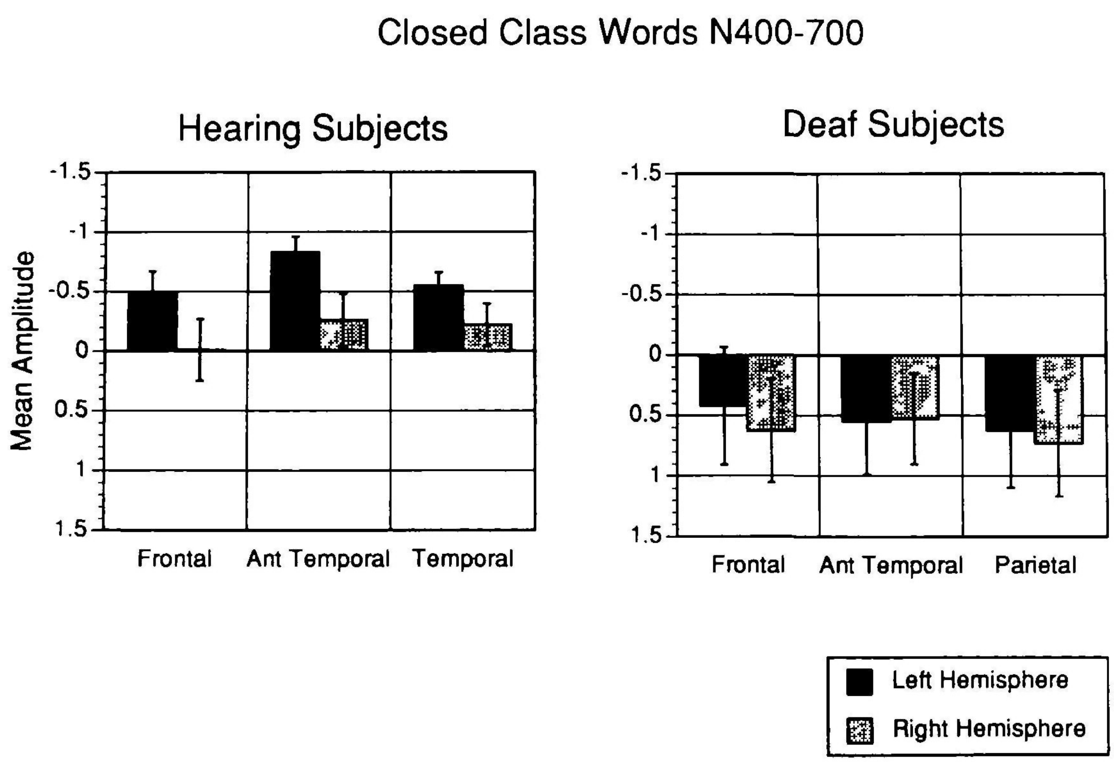

Figure 10. Mean amplitude of N400–700 (±SE) to closed class words from over anterior sites of hearing and deaf subjects. This area is negative from hearing subjects, and it is asymmetrical (left more negative). By contrast, in deaf subjects closed class words elicit a symmetrical positivity

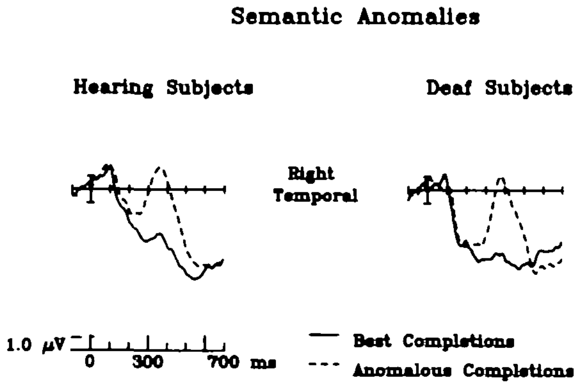

Figure 11. ERPs elicited by semantically appropriate (best completions) and anomalous words at the ends of sentences: grand averages across 17 hearing and 10 deaf subjects. Both groups displayed large negative peaks to semantically anomalous words.

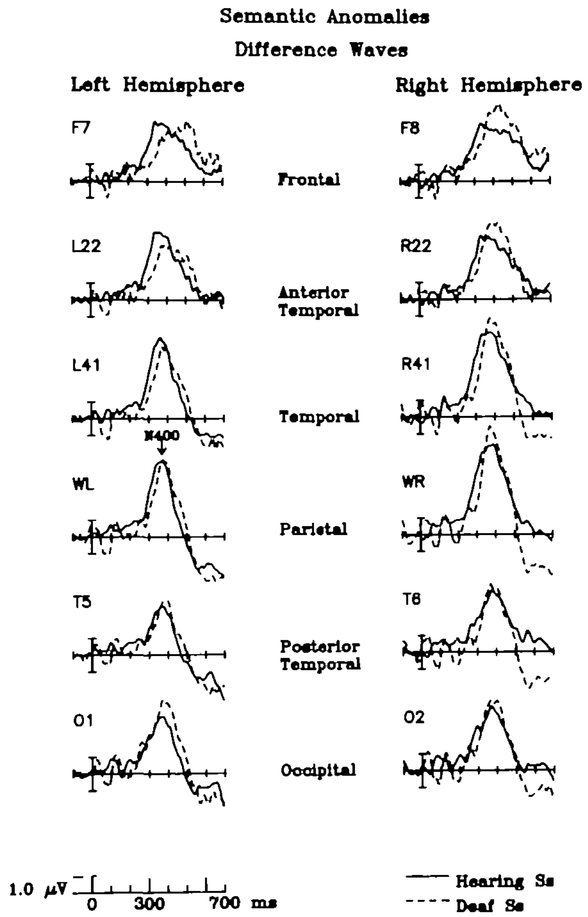

Figure 12. Difference ERPs, formed by subtracting ERPs to semantically appropriate words from ERPs to semantically anomalous words, isolate the effects of semantic anomalies (the N400). Grand averages across 17 hearing and 10 deaf subjects are superimposed. The two groups display similar effects of semantic anomalies.

were similar in amplitude, morphology, and distribution in deaf and hearing subjects (peak amplitude and mean area, NS; see Figs. 12, 13). For both deaf and hearing subjects, the amplitude of N400 was largest from parietal regions and from the right hemisphere [hemisphere, $F(1,25) = 9.5$, $p \leq 0.004$; electrode, $F(1,125) = 4.5$, $p \leq 0.02$; hemisphere × electrode, $F(1,125) = 3.0$, $p \leq 0.05$]. The latency of N400 was slightly later in the deaf subjects [group, $F(1,25) = 4.6$, $p = 0.04$; mean: hearing, 383 msec; deaf, 407 msec].

Discussion

Congenitally deaf subjects who learned English late and through the visual modality only, and who display deficits relative to native-speaking, hearing subjects in reading fluency and knowledge of English grammar, nonetheless displayed ERPs to open class words and to semantically anomalous words that were similar qualitatively and quantitatively to those of normal-hearing subjects. The morphology and distribution of the N350 response to open class words and of the N400 semantic anomaly effect were the same in the two groups, while the latency of the N400 "difference wave" was slightly prolonged. A similar latency shift has been reported by Ardal et al. (1990) in bilingual subjects and may indicate a slight slowing of the semantic processes indexed by the N400. These results suggest that the processes indexed by the N350 to open class words and the N400 to semantic anomalies develop rather normally under the markedly altered language experience typical of congenitally deaf subjects.

In contrast to these results, closed class words, which provide much grammatical information in English, elicited ERPs that were qualitatively different in deaf and hearing subjects. In hearing subjects, ERPs to closed class words were characterized by a negative peak, N280, that was asymmetrically distributed over anterior temporal and frontal regions of the left hemisphere. This component was absent in the deaf subjects. Additionally, a negative shift from 400 to 700 msec, also apparent over anterior regions of the left hemisphere, was present in hearing subjects but was absent in deaf subjects.

These results suggest that the aspects of semantic processing, indexed by the ERPs to open class words and the N400, are very robust under the conditions of different early language experience of the deaf. By contrast, the hypothesized processes central to grammatical processing and indexed by the N280 and N400–700 responses to closed class words appear to be highly vulnerable to this early experience. More specifically, these results raise the hypothesis that the development of specialized processing within anterior regions of the left hemisphere may depend upon exposure to and acquisition of the grammar of a language at an earlier age than typically occurs for deaf subjects (i.e., before the early teens). Early and complete exposure to the grammar of English occurs very rarely in deaf subjects, perhaps due to the difficulty of teaching English grammar through the picture–word association method. Over the past several years we have tested a few congenitally deaf subjects who have mastered the essentials of English grammar, as measured on tests of grammar. In each of these subjects, ERPs to closed class words display the N280 peak and its characteristic asymmetry. The numbers of subjects are small and preclude statistical analysis, but are consistent with the working hypothesis that the acquisition of the grammar of a language is an important factor in the development of the special-

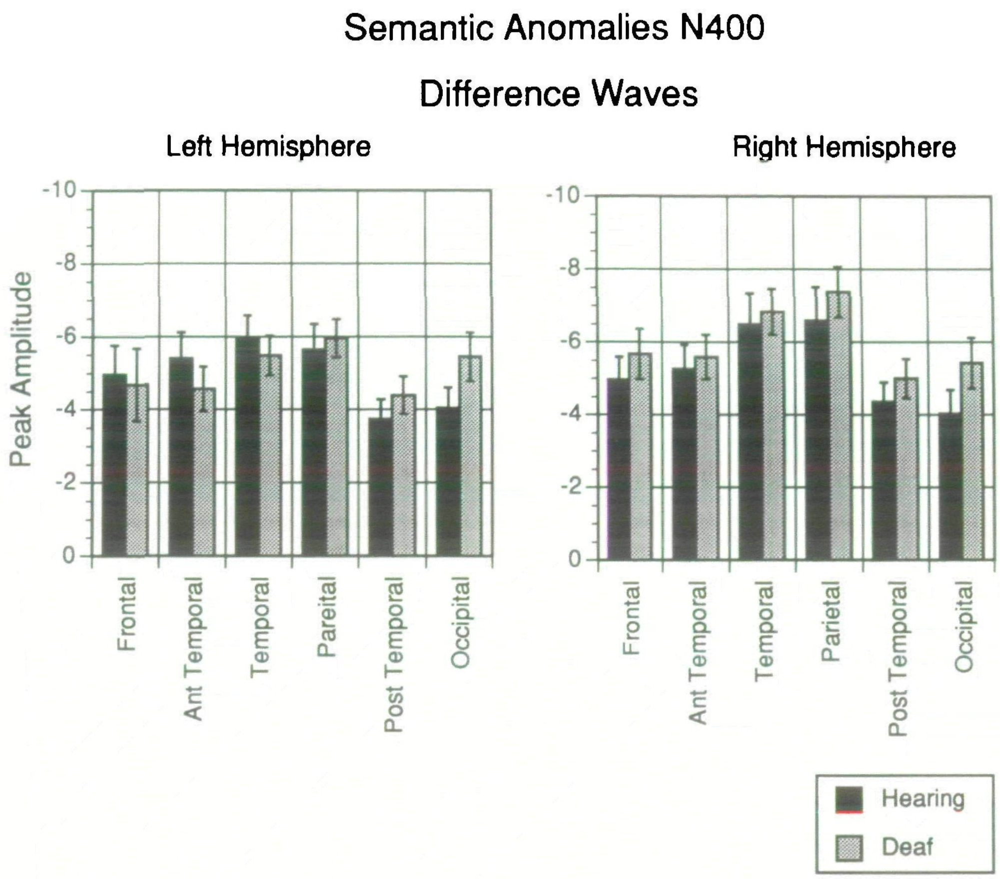

Figure 13. Amplitude of the N400 (±SE) peak to semantic anomalies in the difference ERPs from 17 hearing and 10 deaf subjects. The amplitude and distribution of N400 were the same in deaf and hearing subjects.

ized neural systems that mediate aspects of language processing in hearing adults.

In addition to group differences that were selective for certain types of language processing, we also observed differences between deaf and hearing subjects that were present in the ERPs to both open and closed class words. The anterior N100 component was significantly earlier in deaf subjects, and the responses beyond 200 msec were consistently more positive in deaf than in hearing subjects. These specific changes are similar to differences between deaf and hearing subjects that we have observed in other experiments requiring nonlanguage visual processing. We have linked such changes to experience-dependent alterations in visual sensory processing due to auditory deprivation since birth (Neville and Lawson, 1987a,b; Neville, 1990). Future research with appropriate control groups will determine whether the group differences in this study that occurred independently of word type can also be attributed to the effects of auditory deprivation.

In summary, the results from the hearing subjects demonstrate that nonidentical neural systems mediate the processing of words that provide primarily semantic and grammatical information. Moreover, the observed differences could not be accounted for by general factors including word frequency, length, imageability, or some combination of these variables. These results, then, do not support the proposal that different levels of similar and general functions can account for differences in the processing of these types of information. Rather, they are consistent with proposals that semantic and grammatical processes are biologically and functionally distinct subsystems within the language domain. Further evidence for this view comes from the results from deaf adults showing the different developmental vulnerabilities of these specific subsystems.

The working hypothesis that the group differences raise is that these distinct neural systems develop along different time courses and that they are differentially affected by the acquisition of specific language skills in development. Important further tests along these lines will include studies of cerebral organization in normally developing children as they acquire different language capabilities. In addition, an important test of these hypotheses, and of the hypothesis that similar neural systems mediate all formal languages, will be results from deaf subjects in their native language, ASL.

Most generally, the present results strengthen the proposal that the combined behavioral–electrophysiological approach, when utilized in a developmental context, can contribute to the identification and characterization of different functional subsystems within a neurocognitive domain.

Notes

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