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Event-related potential asymmetries during the reading of sentences

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Summary This report is an overview of the lateral distribution of event-related brain potentials (ERPs) recorded during silent reading in 7 different experiments. Both single word and cross-sentence averages revealed the presence of several ERP asymmetries. The P1, P2 and a negativity between 300 and 500 msec were found to be larger over the right than left hemisphere. It was argued that this asymmetric negativity was due primarily to the contribution of the N400 elicited by all content words. The degree of N400 asymmetry was unaffected either by the rate of sentence presentation or the ratio of congruent to incongruent sentences but was quite sensitive to family history of left-handedness. In contrast, the P1 and P2 asymmetries were uninfluenced by lexical class or familial sinistrality.

Key words: Event-related brain potential asymmetries; Language; N400; P1; P2

Introduction

Over the past 5 years there has been a proliferation of event-related potential studies of word processing (for review see Kutas and Van Petten 1987). The majority of the experiments have examined the analysis of written English, although similar investigations have been carried out using speech (McCallum et al. 1984; Holcomb 1985) and American Sign Language (Neville 1985; Neville et al. 1986; Kutas et al. 1987). Within the visual modality language-related ERPs have been obtained with a variety of experimental paradigms. For example, Kutas and her colleagues (Kutas and Hillyard 1980a, b, 1984a) have recorded ERPs as subjects silently read sentences presented one word at a time while others have presented sentences or phrases and required subjects to decide about their validity (i.e., truth or falsity; Fischler et al. 1983) or congruity (i.e., sense versus nonsense; Neville et al. 1986). Yet other investigators have examined the ERPs to words presented in isolation for subsequent naming (Stuss et al. 1983), in lists or in pairs for word-non-word (Bentin et al. 1985), category (Boddy and Weinberg 1981; Harbin et al. 1984; Polich 1985) or rhyming judgments (Polich et al. 1983; Rugg 1984; Kramer and Donchin 1987).

Although each of these reports has mentioned a negativity between 250 and 600 msec which appears to be sensitive to some linguistic or semantic variable, it has been extremely difficult to compare the ERPs obtained across these different experimental procedures directly. The apparent scalp distribution of this language-related negativity has varied across studies in both its anterior-posterior and lateral dimensions. For example, Kutas and colleagues reported that the N400 elicited by a semantically anomalous word at the end of a sentence was larger over the central and parietal regions than over the frontal scalp and slightly larger over the right than the left hemisphere. In contrast, Stuss et al. (1983) found that a negativity of similar latency elicited by isolated words to be named was larger over frontal than parietal regions. Likewise, Boddy (1986) observed

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that a negativity between 300 and 500 msec in the ERP to the second word of an unrelated pair was larger over the left than the right hemisphere.

With few exceptions, the variable distribution of these language-related negativities has been attributed to measurement confounds produced by overlapping components rather than to the operation of distinct processing mechanisms. For example, Polich (1985) noted that, while it could be argued that various manifestations of the negativity reflect the activity of different functional brain processes, it was more parsimonious to assume one process invoked by a variety of task circumstances in a manner previously proposed for the P3 component. In this view, the scalp distribution of one negative component could vary considerably as a function of the other processes simultaneously active. Stuss et al. (1986) suggested that 'the asymmetrical (right greater) scalp distribution of the N400 reported by Kutas and Hillyard (1982) may possibly be related to its riding on an asymmetric left greater P3 wave.' In a similar vein, Boddy (1986) proposed that '... the right greater than left asymmetries in the earlier studies might be attributed to measuring N400 amplitude from a pre-S2 baseline, to which a left greater than right hemisphere asymmetric CNV had given a greater negative bias on the left than on the right, which consequently biased the N400 amplitude toward a right greater than left asymmetry.'

The present report is intended as an overview of the lateral distribution of the N400 elicited by words in visually presented sentences with special emphasis on possible measurement confounds. In some ways, it is a follow-up of a previous report from our laboratory concerning the lateral distribution of ERPs elicited by words during sentence reading (Kutas and Hillyard 1982). In that paper, we reported that the N400 component elicited by a semantically anomalous word at the end of a sentence was slightly larger and more prolonged over the right than the left hemisphere. Moreover, we noted that the ERPs elicited by intermediate words within 7-word sentences also were characterized by a lateral asymmetry, with the left hemisphere being more positive than the right in 400–700 msec region of the ERP.

Since that report, we have learned that the N400 is not specific to semantically anomalous words at the ends of sentences. First, we have shown that semantic anomalies occurring at intermediate sentence positions also elicit an N400 with a parieto-central, right hemisphere maximum (Kutas and Hillyard 1983). Second, we have found that semantically congruent sentence completions also can elicit N400 components to the extent that such words are unexpected. With semantic expectancy operationally defined in terms of a word's cloze probability (Taylor 1953) [1], we observed that N400 amplitude was largely an inverse linear function of expectancy for a given word to end a sentence (Kutas and Hillyard 1984a; Kutas et al. 1984). That is, sentence terminal words with a cloze probability of 0.70 or less elicited an N400 component whose amplitude increased as cloze probability decreased.

Given this relationship between N400 amplitude and semantic expectancy, it is not unreasonable to suppose that congruous intermediate words, insofar as they are not wholly predictable, also would elicit an identifiable N400 component. Accordingly, a second aim of the present paper is to show that the ERPs to many intermediate words are indeed characterized by an N400 component whose amplitude is influenced by degree of semantic expectancy. A re-examination of the ERPs in our previous publications indicates that this may be the case (Kutas and Hillyard 1983, 1984b). For example, inspection of the parietal recording presented in Fig. 5 of Kutas and Hillyard (1983) suggests that sentence intermediate words (especially the so-called content or open class words) elicit a small N400 component.

Overall, our intent is to show that the right-

[1] In a cloze probability procedure, a large group of subjects is asked to fill in the missing terminal word of a sentence. A word's cloze probability is defined as the proportion of subjects using that word to complete the sentence. The measurement of cloze probability for a particular word is dependent on the contextual constraint of the sentence. For a highly constrained sentence such as 'He mailed the letter without a ———,' the word 'stamp' might have a high cloze probability, while 'address' would have a low cloze probability. In contrast, a sentence such as 'There was nothing wrong with the ———' might have a number of equally acceptable endings, none of which would have an extremely high cloze probability.

more-negative-than-left asymmetry in the latency band of the N400 component of the ERP is a consistent, reliable response elicited by words throughout the course of visually presented sentences whether measured relative to a pre-word or a pre-sentence baseline. To this aim, many of the ERP data to follow will include averages across entire sentences or substantial portions of sentences. The data from 7 different experiments are described. It will be seen that while the amplitude asymmetry of the N400 is not large, and often only marginally significant, it is a highly replicable finding.

Methods

The majority of subjects for these experiments were young, right-handed adults with no left-handed relatives in their immediate families. A minority were right-handers with at least one left-handed relative in their immediate family; their data will be described separately.

The electroencephalogram (EEG) was amplified with Grass 7P511 and 7P122 amplifiers with an 8 sec time constant or DC. Recordings were taken from midline and lateral sites, referenced to linked mastoids or to an average of left and right mastoids (created off-line). Electrode sites included standard 10–20 sites (Jasper 1958) as well as anterior and posterior temporal sites approximately overlying Broca's and Wernicke's areas and their right hemisphere homologs, and central sites approximately overlying Brodmann's area 41. For experiments 1–6, the EEG was recorded with Ag-AgCl electrodes attached to the scalp with collodion. For experiment 7, the EEG was recorded with tin electrodes mounted in an Electro-Cap (Polich and Lawson 1985).

Horizontal eye movements and blinks were monitored in various experiments via either (1) an electrode placed on the lower orbital ridge referred to a right external canthal electrode or (2) an electrode placed below the eye referenced to mastoids and a bipolar right-versus-left external canthus montage. Trials with excessive vertical or horizontal electro-oculographic potentials were rejected as were trials with amplifier blocking. Determinations of artifact contamination were made off-line on digitized data stored on a magnetic tape by means of computer algorithms which calculated peak-to-peak voltage amplitudes, voltage deviations from baselines and polarity inversions between the lower eye and frontal recordings, whenever possible. ERPs were averaged on 2 time scales: so-called short averages of 1–1.5 sec which included the responses to individual words within sentences and longer averages of 4–7 sec which included either entire sentences or 5–9 words of each sentence.

In each experiment, subjects silently read sentences presented 1 word at a time on a CRT. In experiments 1 through 6, subjects were instructed to read for meaning in order to complete a subsequent recognition memory, cued recall or multiple choice questionnaire. In experiment 7, subjects were required to make a response at the end of each sentence. In no case, however, were the subjects required to make any overt responses while reading. All of the ERPs to be described were responses to congruous error-free sentences, unless otherwise noted.

The experiments described varied in the proportion of congruous to incongruous sentences, word presentation rate, lateral recording sites, sampling rate, and number of subjects. These are detailed in Table I.

Results

Hemispheric asymmetry across the course of a sentence

For the across-sentence averages, ERPs were quantified by means of computer-implemented algorithms as the mean voltage from 300 to 700 msec after the presentation of each word, relative to a baseline consisting of the average EEG activity 100 or 200 msec immediately preceding the first word of the sentence or a warning signal. For the experiments in which the sentences were presented at a rate of 1 word every 500 msec, the mean voltage measurement was restricted to the 300–500 msec region of the ERP. In all cases, these measures were analyzed via a repeated-measures analysis of variance using position of the

TABLE I

Exp. and figs. in text	Prev. report	Percent semant. incon. sents.	Word exposure duration (msec)	Word onset to onset (msec)	Intersentence interval (msec)	Sampling rate for across sentence averages (Hz)	Lateral electrodes	Ref.	No. of subs. (with left-handed relatives)
No. 1 1	Kutas and Hillyard (1983)	26.6	200	640–760	2100	36.6	ant. temp. pos. temp.	link. mast.	14 (5)
No. 2 2, 7, 9	–	50	150	500	2000	62.5	F7, F8 ant. temp. central pos. temp.	avg. mast.	14 (5)
No. 3 3, 7, 9	Van Petten and Kutas (1987a)	0	200	900	4000	50	ant. temp. C3, C4 pos. temp.	avg. mast.	20
No. 4 4	Kutas and Hillyard (1982)	50	100	1000	2000	32	C3, C4 T3, T4 pos. temp.	link. mast.	13 (3)
No. 5 5	Kutas and Hillyard (1982)	25	100	500	2000	32	C3, C4 T3, T4 pos. temp.	link. mast.	5
No. 6 6, 7, 9	Kutas and Hillyard (1984a)	0	132	700	2800	62.5	ant. temp. pos. temp.	link. mast.	14
No. 7 8, 10	–	50	150	700	2700	56	F3, F4 C3, C4 P3, P4 T5, T6 O1, O2	avg. mast.	13

Abbreviations: semant. incon. sents. = semantically incongruous sentences, Ref. = reference electrodes, subm. = submitted, ant. temp. = anterior temporal sites approximately over Broca's area, pos. temp. = posterior temporal sites approximately over Wernicke's area, central = central sites approximately over Brodmann's area 41, link. mast. = linked mastoids, avg. mast. = averaged mastoids.

word in the sentence, electrode site along the anterior-posterior dimension, and hemisphere (left-right) as factors.

Fig. 1 shows the ERPs from left and right hemisphere sites recorded over the first 9 words of a subset of the sentences described in Kutas and Hillyard (1983), averaged separately for right-handed subjects with and without a left-handed family member. Although an occasional sentence in this experiment contained either a semantic anomaly or grammatical error, the present analysis is restricted to those sentences that were 9 words or longer and did not contain any violations. Visual inspection of these data reveals a clear right-more-negative-than-left asymmetry in the ERP to the second word of the sentence and evident in the response to every word thereafter. The ANOVA indicated no significant main effect of hemisphere. However, there was a significant interaction between word position and hemisphere (F (7, 91) = 2.75, $P < 0.012$), reflecting the fact that the responses to first words exhibited only a very slight asymmetry relative to the other words in the sentences.

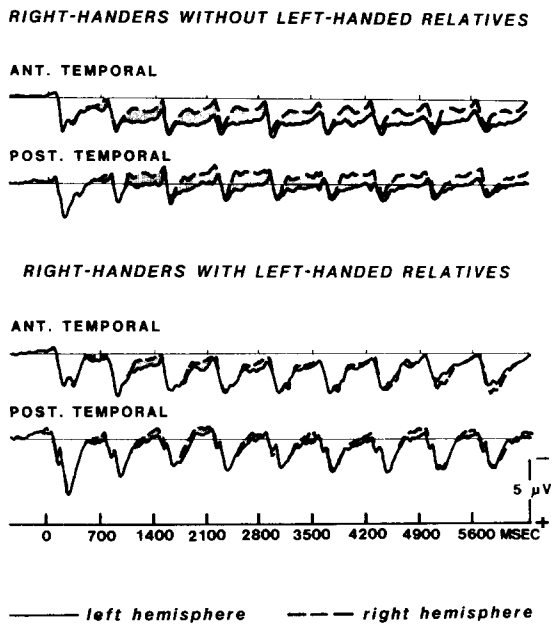

Fig. 1. Grand average ERPs for the first 9 words of the sentences in experiment 1. Anterior and posterior temporal sites are shown. The top part of the figure is for the 9 right-handed subjects without left-handed family members, the bottom is for the 5 right-handers with left-handed family members. The asymmetric late negativity is shaded in this and subsequent figures.

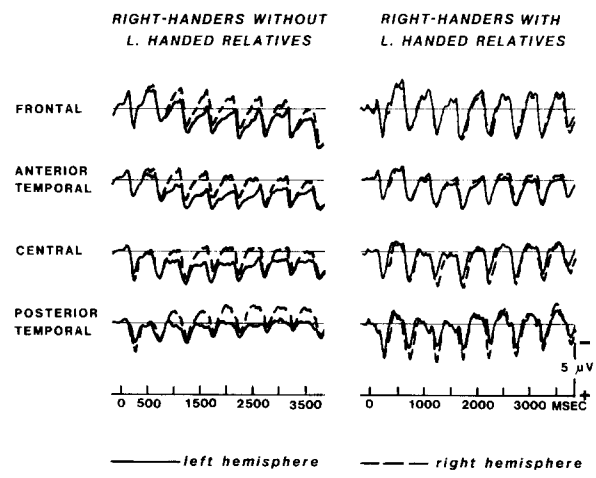

Fig. 2. Grand average ERPs for the first 7 words of the sentences in experiment 2, separately for the 9 right-handed subjects without, and the 5 right-handed subjects with left-handed relatives. Right and left hemisphere sites are overlapped. Electrode sites are, from top to bottom, F7 and F8, anterior temporal, central sites approximately over Brodmann's area 41, and posterior temporal.

While there were not enough subjects to make a statistical comparison between the subjects with and without left-handed family members, it is clear from the figure and an ANOVA of only those 9 subjects who did not have left-handed relatives, that the ERP asymmetry was more robust in the absence of familial left-handedness (word position by hemisphere, F (7, 56) = 3.89, $P <$ 0.002).

These findings were replicated in experiment 2 with a different group of 14 subjects reading a series of isolated sentences presented at a faster rate (e.g., 1 word every 500 msec). Their wave forms show a very striking difference in the asymmetry of the 300–500 msec region of the ERPs as a function of their family history of left-handedness (see Fig. 2). The 9 right-handed subjects without left-handed relatives showed a right-greater-than-left negativity (main effect of hemisphere, F (1, 8) = 6.15, $P < 0.038$). There was also a significant 2-way interaction between word position and hemisphere indicating that the asymmetry was not as evident in the first word ERPs (F (6, 48) = 4.05, $P < 0.002$). In sharp contrast, right-handers with a left-handed family member showed no such asymmetry for any word in the sentence (main effect of hemisphere, F (1, 4) = 0.013, N.S.; word position by hemisphere F (6, 24) = 1.99, N.S.). Instead, these subjects seemed to elicit asymmetric P2 components, with the right hemisphere being more positive in the recordings over the back of the head. However, this asymmetry did not distinguish those subjects with left-handed relatives from those without, because the latter also appeared to have asymmetric P2s if the preceding negativity is taken into account.

These results were again replicated in experiment 3 wherein 20 right-handed subjects without any left-handed family members read 240 congruous sentences presented at a slower rate (e.g., 1 word every 900 msec). Their responses averaged across the first 6 words of the sentences are presented in Fig. 3. The right hemisphere is more negative than the left for all but the first word of the sentence (word position by hemisphere inter-

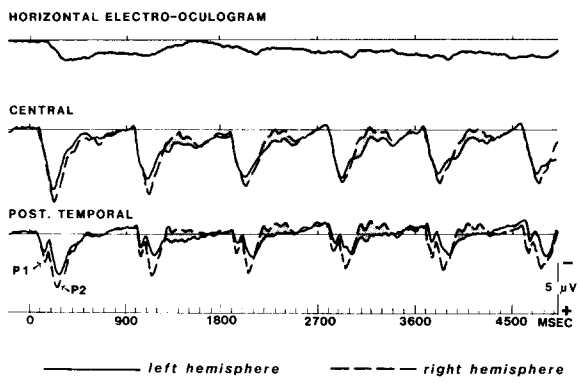

Fig. 3. Grand average ERPs for the first 5 words of the sentences in experiment 3, recorded from C3 and C4, and posterior temporal sites. The larger P1 and P2 seen at right hemisphere sites are indicated by arrows. At the top of the figure is a recording of the horizontal eye movement taken between the right and left external canthi.

action, F (4, 76) = 5.52, $P < 0.001$). In addition, as in the previous experiment, the P2 components of the ERP are larger (i.e., more positive) over the right than the left hemisphere. In this case, the P1 also appears to show a similar right hemisphere preponderance.

Effect of sentence congruity

Experiments 4 and 5, previously reported in Kutas and Hillyard (1982), allow a direct comparison of the asymmetries between intermediate and final words of congruous and incongruous sentences. All of the sentences were 7 words long. As evident in Fig. 4, there is a right-more-negative-than-left asymmetry in response to each of the words across a substantial portion of the sentences regardless of their eventual congruity (main effect of hemisphere, F (1, 12) = 6.4, $P <$ 0.026). There is, however, an effect of sentence congruity on the asymmetry of the responses to final words. An analysis of variance which excluded the ERP to the sentence-initial words resulted in a significant interaction between congruity, word position and hemisphere, F (5, 60) = 3.65, $P < 0.006$. The ERPs to incongruous endings show an asymmetry which is not distinguishable from that obtained to the preceding words (main effect of hemisphere, F (1, 12) = 10.36, $P < 0.007$).

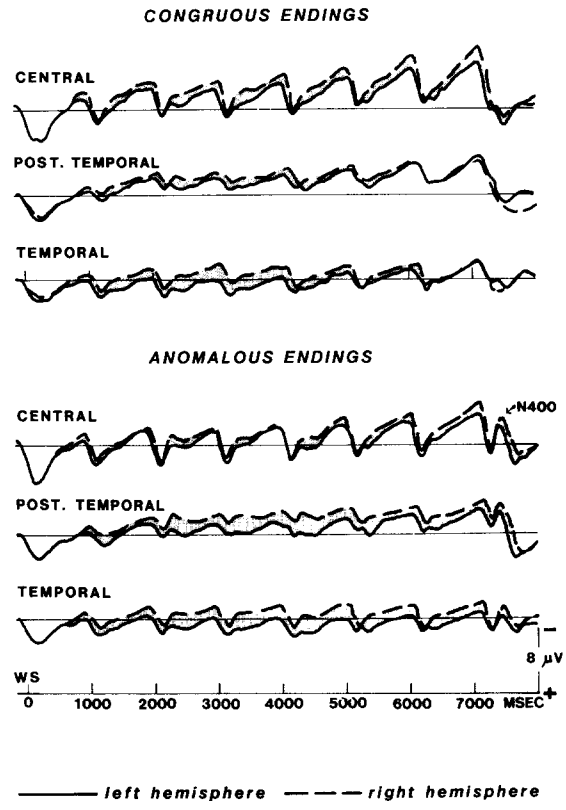

Fig. 4. Grand average ERPs for the warning signal (WS) and 7-word sentences of experiment 4, shown separately for sentences which ended congruously and incongruously. Left and right hemisphere recordings are shown for C3 and C4, posterior temporal, T5 and T6. Unlike previous figures, the ERP to sentence terminal words is shown. The N400 to incongruous terminal words is labeled.

In contrast, the ERPs to congruous endings show no such asymmetry but rather a slight tendency for the right hemisphere to be more positive than the left. In the analysis limited to congruous sentences, this is reflected in the lack of a main effect of hemisphere but a significant interaction between word position and hemisphere (F (6, 50) = 14.90, $P < 0.001$). As previously noted for other data sets, excluding the subjects (n = 3) with left-handed family members from the statistical analyses enhances the amplitude of asymmetries obtained.

Effect of contextual constraint and cloze probability

Bilaterally symmetric ERPs were also obtained

in response to congruous final words in experiment 5 (Kutas and Hillyard 1982, exp. 2). While the ANOVA indicated no main effect of hemisphere, there was a significant interaction between word position and hemisphere (F (5, 20) = 3.23, $P < 0.027$). Again, this analysis did not include sentence-initial words and the interaction reflected the lack of the right-more-negative-than-left asymmetry in the congruous final word ERPs. The congruous sentences in this experiment were subdivided into several types: cliches and nursery rhymes (e.g., 'Roses are red and violets are blue'), factual statements (e.g., 'Sacramento is the state capital of California'), and some more open-ended (i.e., less contextually constrained) sentences (e.g., 'He returned the book to the library'). It is clear that the reduction or reversal of the asymmetry in the congruous ending ERPs was primarily due to the final words of the cliches and factual sentences, albeit evident in the ERPs to open-ended congruous final words as well. The reduced asymmetry for the final words of the cliches may have been due to their predictability.

In experiment 6, the factors of contextual constraint and cloze probability were manipulated more explicitly. The stimuli in this experiment consisted of 321 sentences, none of which were anomalous. They did, however, vary systematically in their degree of contextual constraint and the cloze probability of their final word (see footnote 1). ERPs to the final words of these sentences were described in Kutas and Hillyard (1984a). The top row of Fig. 6 shows the average ERP across the first 5 words of all the sentences; the left and right hemisphere recordings from the temporoparietal sites are superimposed. As noted in the previous studies, all but the first word of the sentence was associated with an ERP more negative over the right than left hemisphere between 300 and 700 msec following word onset (main effect of hemisphere, F (1, 13) = 12.56, $P < 0.003$; word position by hemisphere interaction, F (4, 52) = 19.35, $P < 0.001$).

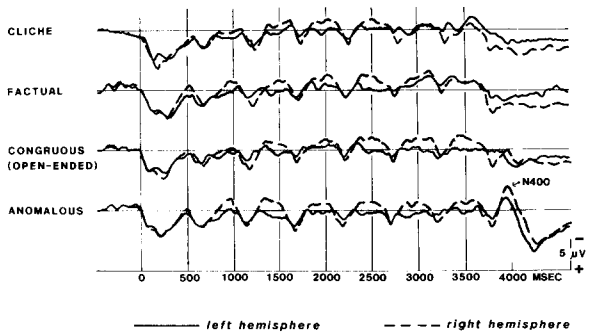

Fig. 5. Grand average ERPs for the warning tone and 7-word sentences of experiment 5, recorded from left and right posterior temporal sites. Three different types of congruous sentences are shown in addition to incongruous sentences.

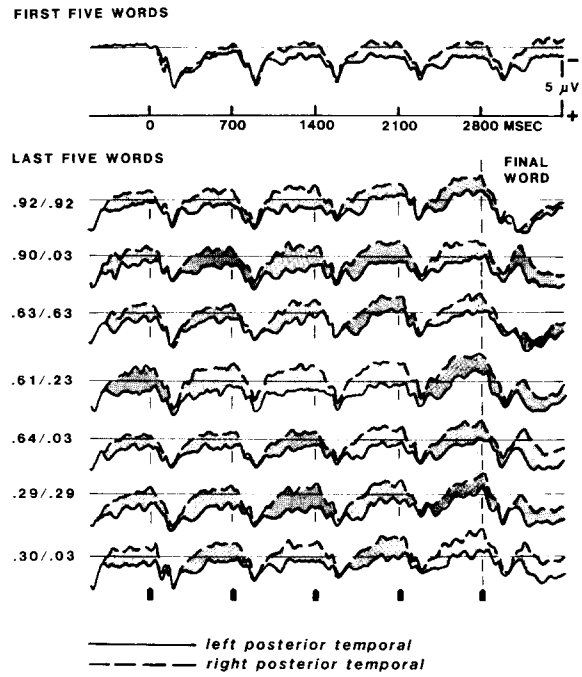

Fig. 6. Grand average ERPs from experiment 6 recorded from posterior temporal sites. The sentences in this experiment were of variable length and separate averages were required to obtain responses to the beginnings and ends of sentences. In the first row is shown the response to the first 5 words, collapsed across experimental conditions. Rows 2–8 show the responses to the last 5 sentence words as a function of experimental condition. The onset of each of the last 5 words is indicated by a vertical bar. The labels indicate the proportion of respondents using a given word to complete the sentences in each experimental condition. The first part of each label represents the contextual constraint of the sentences, i.e., the cloze probability of the *most probable* terminal word. The second part of each label represents the cloze probability of the terminal word *actually presented* (see footnote 1 for definition of cloze probability).

The ERPs in rows 2–8 are the grand average ERPs in each of the 7 experimental conditions (e.g., degree of contextual by final word cloze probability combination) recorded from over left and right temporoparietal sites. The wave forms include the responses to each of the 5 words leading up to the final word as well as the response to the final word itself. The choice of baseline for overlap was extrapolated from the average across the first 5 words. The hemispheric asymmetry of the 300–700 msec negativity characterizes the ERPs to all non-terminal words regardless of the experimental condition (main effect of hemisphere, F (1, 13) = 12.60, $P < 0.003$). Only some of the terminal word responses showed this asymmetry, as revealed by a significant 3-way interaction between experimental condition, word position and hemisphere (F (24, 312) = 3.62, $P <$ 0.001). In specific, the final word ERPs that did not contain N400 components (e.g., those in the hi/hi and med/hi conditions) were not asymmetric.

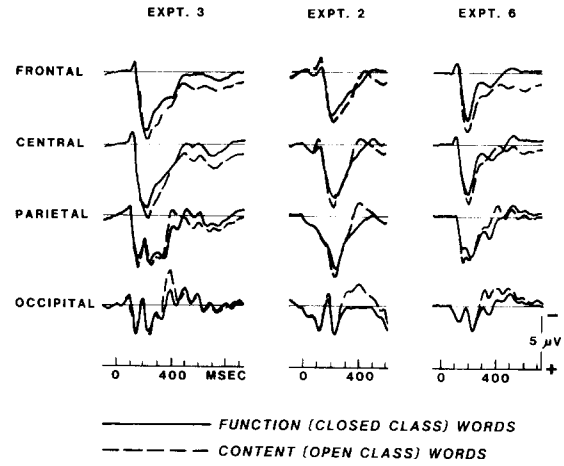

Fig. 7. Grand average ERPs to sentence intermediate words, recorded from midline sites in 3 experiments. ERPs to content and function words have been overlapped. The across-sentence averages for these experiments are shown in Figs. 2, 3 and 6. Note the posterior N400 to content words.

ERPs by lexical class

One general trend that emerges from the studies discussed thus far is the lack of a significant asymmetry in the negativity to sentence initial words. One possible explanation for this may be that for many of the experiments the first words of sentences were comprised primarily of articles (e.g., 'a,' 'the') or pronouns (e.g., 'he,' 'she,' 'it,' 'they'). It may be that the responses to articles and pronouns, as well as those to other 'function' or closed class words (e.g., prepositions, conjunctions, auxiliaries), do not show this asymmetric negativity whereas those to 'content' or open-class words (e.g., nouns, verbs, adjectives, and adverbs; see Clark and Clark 1977) do. While it is difficult to test this hypothesis in the across sentence averages, such a comparison can be made in the ERPs elicited by individual words in the sentences sorted as a function of lexical category.

Before examining the lateral distributions of the ERPs to function and content words, we can determine whether content words elicit larger N400s than do function words. In Fig. 7, the midline ERPs to intermediate content and function words from 3 different experiments (nos. 2, 3 and 6) are superimposed. The wave forms indicate that the ERPs elicited by these lexical categories when they occur in sentence intermediate positions differ in a number of respects.

Over the frontocentral regions of the scalp, content words are associated with greater positivity than function words, starting around the P2 and lasting throughout the recording epoch. Over the centroparietal regions of the scalp, the greater positivity for content words relative to function ones is interrupted or reversed in the 250–400 msec region of the ERP by the presence of an N400 to content words. Following the N400 at the centroparietal sites, content word ERPs again become more positive relative to function ones. While the relative amplitude of the N400 to intermediate words varies across different experiments, these data argue that it is primarily the content words which elicit an N400 wave. The next section examines the extent to which this N400 to intermediate content words is sensitive to semantic context.

Influence of semantic expectancy on ERPs to intermediate content words

For sentence terminal words we operationally

defined semantic expectancy in terms of a word's cloze probability (see footnote 1). However, it is relatively impractical to obtain cloze probabilities for sentence intermediate words. We can, however, make a rough division into high and low expectancy words based on their position within individual sentences. When experimental stimuli consist of a set of unrelated sentences, the first few words of each sentence are highly unpredictable, while later words should be subject to greater contextual constraint by the ongoing sentence.

Thus, in experiment 7, we subdivided intermediate content words into 2 sets: those which were the first content word in their sentence ('early') and those which appeared later ('late'). Note that no first word ERPs were included into the 'early' averages and no terminal word ERPs were included into the 'late' averages. We excluded sentence initial words for a variety of reasons, primary among them the fact that our inter-sentence intervals were generally 3–4 times longer than our inter-word intervals (see Table I); in so doing, we avoided confounding the effect of word position with refractoriness of ERP components. Similarly, final word ERPs were excluded from the 'late' average because of the possible confounds with electrical and cognitive resolution effects. The possible influence of syntactic role was controlled by averaging only those words which were the subjects and predicates of the sentences in which they appeared. For instance, in the sentence 'The hunters shot two elk and a deer' the subject 'hunters,' although it is the second word in the sentence, is the first content word and would be included in the 'early' average. The next content word, 'shot,' was the predicate of the sentence and would be included in the 'late' average. In the sentence, 'He can run the mile in under four minutes,' the first content word is the predicate ('run'), occupying the third position in the sentence and would have been included in the 'early' average. 'Early' and 'late' words did not differ significantly in frequency of usage within written English (Kucera and Francis 1967; mean frequency for 'early' = 159, 'late' = 187, t (137) = 0.66, N.S.) or word length (mean length = 6.5 letters for both word types).

The ERPs elicited by these 2 sets of words are shown in Fig. 8. Although both classes of content words elicited some N400 activity, the N400 was significantly larger in the responses to the words occurring 'early' as opposed to 'late' in the sentences. The N400 difference between word types was largest at posterior electrode sites (mean voltage 300–700 msec, word type by anterior/

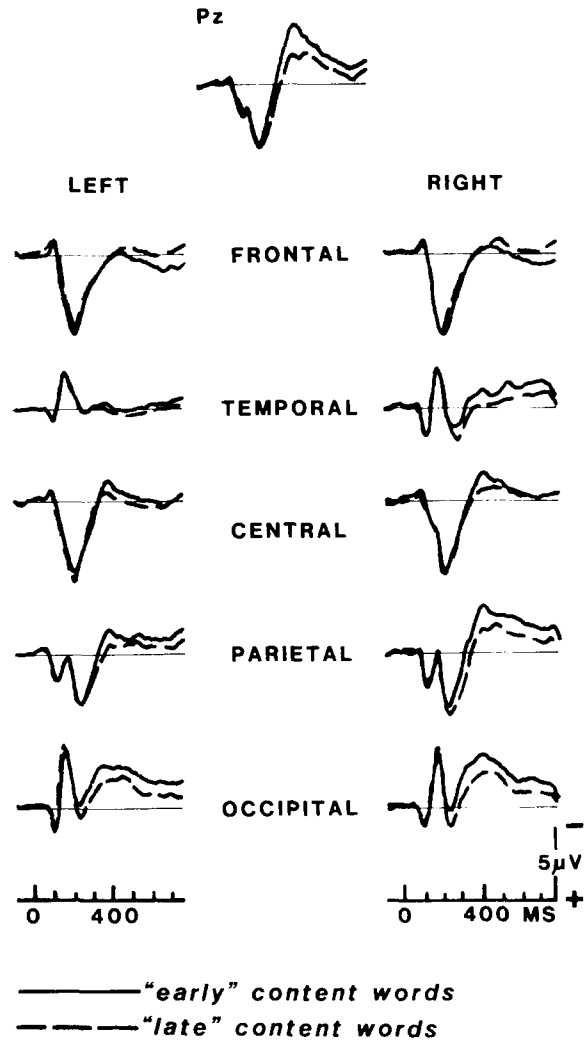

Fig. 8. Grand average ERPs to intermediate content words in experiment 7. The recording sites shown are Pz, F3 and F4, T5 and T6, C3 and C4, P3 and P4, O1 and O2. 'Early' words are those which were the first content appearing within a sentence, 'late' words are those which appeared at some later point in a sentence.

posterior interaction, F (4, 48) = 6.5, $P < 0.001$), and greater over the right hemisphere (word type by hemisphere interaction, F (1, 12) = 6.5, $P < 0.025$).

Thus, content words not only elicit more negativity than function words in the 300–700 msec region of the ERP, but the amplitude of this negativity varies with semantic expectancy. In the next section, we return to the question of whether the asymmetry observed over the course of sentence is due primarily to the contribution of content (open-class) words.

Asymmetry by lexical class

The data in Fig. 9 (top row) show a comparison of the lateral distribution for the intermediate content and function words of the sentences in experiment 3 (also see Fig. 3). This display indicates that the right hemisphere negativity seen in the across sentence averages is indeed primarily the contribution of the responses to content words (for mean amplitude 300–700, lexical class by hemisphere, F (1, 19) = 16, $P < 0.001$).

This observation is corroborated by the data shown in the second and third rows of Fig. 9, which are comparisons of the lateral distributions of the intermediate content and function words from experiment 2 (also see Fig. 2). These data demonstrate that the right hemisphere negativity for individual content words, like that observed in the across-sentence averages, is most pronounced for right-handed subjects without left-handed family members (mean voltage 300–500 msec, lexical class by hemisphere, F (1, 8) = 7.2, $P < 0.03$). There appears to be no late negative asymmetry in the ERPs of subjects with left-handed relatives for either lexical class (lexical class by hemisphere, F (1, 4) = 0.02, N.S.).

While only those ERPs elicited by content words tend to have a posterior N400 asymmetry, there are ERP components which appear to be asymmetric for all words. For example, an enhanced P2 over the right hemisphere is shown in Fig. 9 for 3 experiments. This effect was significant in all three and did not interact with lexical class (base-to-peak amplitude in a 190–250 msec window, main effect of hemisphere, exp. 3: F (1, 19) = 8.6, $P < 0.01$; exp. 2: F (1, 13) = 6.9, $P < 0.03$; exp. 5: F (1, 13) = 8.5, $P < 0.02$). This P2 asymmetry appeared to be unaffected by family history of left-handedness (see Fig. 9, third row), but the small number of subjects of this type made this possibility difficult to evaluate statistically (exp. 2: main effect of hemisphere in subjects with left-handed relatives, F (1, 4) = 3.7, $P < 0.15$). Additionally, there was a tendency for the P1 component to be larger over right than left temporoparietal sites. However, this effect reached significance in only 1 of the 3 experiments displayed in Fig. 9 (base-to-peak amplitude in a 120–180 msec window, main effect of hemisphere, exp. 3: F (1, 19) = 5.3, $P < 0.05$).

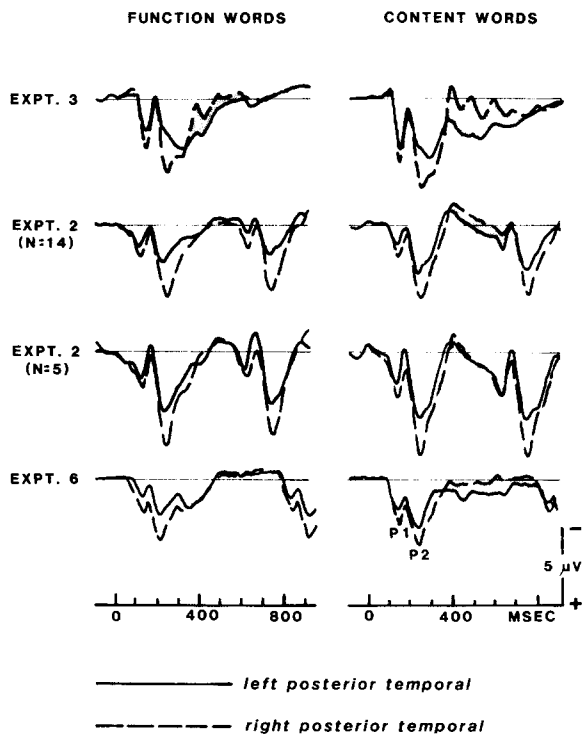

Fig. 9. Grand average ERPs from right and left posterior temporal sites. Responses to intermediate content and function words are shown for the same experiments as in Fig. 7. Note that for experiments 2 and 6, part of the ERP to subsequent words is also visible. For experiment 2, subjects with left-handed family members are shown separately in the third column. The across-sentence averages for these experiments are shown in Figs. 2, 3 and 6.

Discussion

In a number of previous reports we have noted that the N400 elicited by semantically anomalous and congruous but unexpected endings was larger (more negative) over the right than the left hemisphere. This asymmetry, while sometimes largest over temporoparietal areas, was generally widespread in its appearance. In the present paper we have demonstrated that this N400 asymmetry is observed whether the baseline for measurement is the activity preceding the eliciting word (as in previous reports) or the first word of a sentence (as in the present report).

We have also found that the same subjects who responded to unexpected sentence endings with a centroparietal, right hemisphere N400, also produced a posterior, asymmetric negativity to other words within sentences. Across several subject samples, we observed a right more negative than left (or left more positive than right) asymmetry in association with words in intermediate sentence positions. This hemispheric asymmetry was generally not as evident in response to the first word of a sentence, but was clear and consistent in the ERPs elicited by all of the following words. Our various analyses indicated that this asymmetric response could be seen up through the eighth word of a sentence (as far as we could analyze). Again, this asymmetry in the negativity associated with each word was obtained whether the baseline was the EEG activity preceding each word or the activity preceding the sentence. Within the data sets described here, the two different baselining procedures led to similar conclusions about the laterality of the negativity. However, it should be noted that, in general, a pre-sentence baseline yielded larger asymmetries whenever the responses to the intermediate words did not resolve from one word to the next (see the posterior temporal recordings in Fig. 4).

Neither the presence nor the amplitude of asymmetric negativity appeared to be dependent upon the rate of sentence presentation or the proportion of congruous to incongruous sentences. For example, we obtained an essentially similar pattern of lateralization whether the inter-word intervals were 500 msec (e.g., exp. 2 and 4), 700 msec (e.g., exp. 1, 5 and 7), 900 msec (e.g., exp. 6) or 1000 msec (e.g., exp. 3). Similarly, the asymmetry was evident across experiments which included no semantic anomalies (e.g., exp. 5 and 6), less than 50% anomalies (e.g., exp. 1 and 4), or 50% anomalies (e.g., exp. 2, 3 and 7). In contrast, the amplitude of this asymmetry was influenced by family history of left-handedness; this will be discussed in detail later.

Relationship of the asymmetry over the course of a sentence to the N400

Based on its latency and scalp distribution, we will argue that a substantial portion of the asymmetric negativity over the course of a sentence is due to the presence of N400s elicited by congruous intermediate words. In some experiments, the asymmetric negativity observed in across-sentence averages appears to be more broadly distributed across the anterior-posterior scalp than does the N400 response to incongruous words which is typically of greatest amplitude at posterior sites. In Fig. 2, for example, the right-greater-than-left negativity is nearly as large at the frontal sites as it is at the posterior temporal sites. Such frontal recording sites are particularly vulnerable to contamination by electro-oculographic (EOG) potentials produced by eye movements. While we routinely reject trials with large saccadic eye movements from our averages, we have observed that many individual subject averages include a sustained potential of 2–5 μV in the horizontal EOG channel. Given our horizontal recording montage, this potential probably reflects a tendency for subjects to move their eyes slightly to the left at the beginning of a sentence. A small but systematic eye movement of this sort does result in an artifactual right-greater-than-left asymmetry at frontal sites. However, the potentials generated by such eye movements cannot account for the asymmetries we observe over the back of the head. We believe that the scalp distribution of the right-more-negative-than-left asymmetry in the across-sentence averages closely resembles the posterior distribution of the N400. This can be seen in the wave forms obtained from those few subjects who showed little horizontal EOG activity (see Fig. 10). In contrast, when subjects do

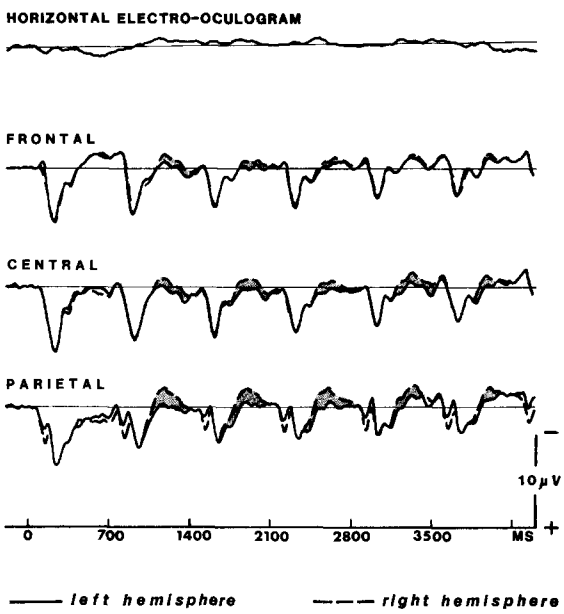

Fig. 10. Grand average ERPs from 9 right-handed subjects with no left-handed family members recorded from a right-to-left montage at the external eye canthi and scalp sites F3, F4, C3, C4, P3 and P4. Shown are responses to the first 6 words of sentences from experiment 7.

make lateral eye movements then the posterior N400 asymmetry adds to the frontal asymmetry created by shifts in horizontal eye position, thereby leading to an apparently equipotential distribution of the lateral asymmetry.

A number of the present findings suggest that the asymmetric negativity is sensitive to the same semantic variables as the terminal word N400 which has been the focus of most previous research. First, the hemispheric asymmetry present throughout the sentence ERP becomes much reduced or absent upon the presentation of a highly predictable final word. In the case of nursery rhymes or cliches, in which the final words could be predicted well before the sentence's end, the right more negative than left asymmetry seems to disappear several words before the end of the sentence. While at first glance this result may seem at odds with our finding that the amplitude of the asymmetry was not significantly different for intermediate words within sentences of high, medium or low constraint, close scrutiny indicates that the conflict is more apparent than real. Although the terminal words of cliches, nursery rhymes and highly contextually constrained sentences all have high cloze probabilities, these sentence types vary in another dimension of expectancy. Cliches and nursery rhymes are highly overlearned, resulting in high predictability for several of the words leading up to the final word as well as for the final word itself. We assume that, by virtue of their overall predictability, cliches and nursery rhymes were comprehended in their entirety before their actual completion. This may have been especially so in experiment 5 since none of them were ever completed unexpectedly or incongruously. This was in sharp contrast to experiment 6 in which half of the highly contextually constrained sentences were completed by low cloze probability endings. This line of reasoning would predict that, regardless of contextual constraint, a repeated sentence which the subject recalled from previous presentations should elicit little N400 asymmetry. We plan to test this prediction in future investigations.

Second, more detailed analyses showed that there was some specificity to the laterality observed over the course of a sentence. Not all types of words within a sentence elicited ERPs with asymmetries in the N400 range. In specific, it was predominantly those words in the sentences which bore meaning, namely the content words, that elicited asymmetric ERPs within 300–700 msec of word onset. In sharp contrast to these content word responses, the ERPs elicited by function words, which bear little semantic content but play important grammatical roles, lacked the asymmetric late negativity.

Finally, our proposition that all content words elicit N400s predicts that the amplitude of these potentials should be modulated by semantic expectancy on a moment-to-moment basis as a sentence progresses. And, in fact, we have seen that the amplitude of the negativity elicited by intermediate content words is modulated by semantic expectancy in much the same way as the N400 to terminal words. When we compared the ERPs to content words matched for word frequency and syntactic role as a function of their position in the sentence, we found significantly

larger N400s in association with the 'early' than 'late' occurring words. The only apparent difference between 'early' and 'late' content words was that the 'early' words, by virtue of being the first content words in their respective sentences, were unpredictable and unprimed, while 'late' words were subject to at least some degree of contextual constraint by the preceding portion of each sentence.

ERP asymmetries and family history of left-handedness

One intriguing aspect of our N400 data was its sensitivity to familial handedness (see also Kutas and Hillyard 1980c; Kutas 1985). The amplitude of the N400 asymmetry was greatly influenced by a subject's family history of left-handedness: right-handed subjects with at least one left-handed family member showed a substantially smaller N400 asymmetry than those of right-handed subjects without a left-handed family member. Our results are in line with a number of reports of less reliable or smaller perceptual asymmetries in right-handed subjects with left-handed relations than in those without (Varney and Benton 1975; McKeever and Van Deventer 1977; Kraft, 1981). Such findings are generally offered as evidence in favor of greater bilateralization of function in right-handers with a family history of left-handedness than those without (Hardyck and Petrinovich 1977). However, since several studies have failed to support this purported relationship between hemispheric specialization for language and familial sinistrality, alternative interpretations have been offered (e.g., Orsini et al. 1985).

Our ERP results in this regard were not gathered in experiments explicitly designed to assess cerebral specialization or its relation to familial handedness. Nonetheless, we have consistently observed reduced N400 asymmetries in response to content words elicited from right-handed subjects who (as far as we know) differed from right-handers with larger asymmetries only in having a left-handed family member. These data were obtained during silent reading, which by many lines of reasoning would preferentially engage left-hemisphere language mechanisms and be in some way related to the functional organization of the brain for language.

The relationship between N400 asymmetry and familial sinistrality may be especially interesting in light of the fact that other ERP components elicited by visually presented words showed a pattern of lateralization which was uninfluenced by the presence of left-handed family members. Both the P1 and P2 components of the ERPs elicited by sentence intermediate words were larger over the right than left hemispheres. Neither of these asymmetries were affected by familial sinistrality or the lexical class of the eliciting words. At present, we do not know the cognitive or electrophysiological mechanism generating either of these asymmetries. Our P1 asymmetries were most pronounced at the temporoparietal sites and absent at occipital sites in the single study (exp. 7) which used such sites. A similar P1 asymmetry '... of questionably significant right-sided predominance ...' was observed by Goodin et al. (1985) in lateral parietal ERPs elicited by 60 repetitions of 7 words. Both the P1 and the P2 asymmetries await further study.

Finally, although we have provided some evidence that the N400 asymmetry may be related to cerebral specialization, the right hemisphere predominance of a component elicited in a language-processing paradigm may be seen as problematic. A similar argument could be offered for the P1 and P2 asymmetries as well. However, it should be remembered that our descriptions of ERP components are relative in nature. Greater right hemisphere negativity could just as easily be described as greater left hemisphere positivity. Our data do not allow a specific statement about polarity and hemispheric engagement as reflected at the scalp, or about the locus (or loci) that generate these potentials. They do however indicate that reading differentially engages the two hemispheres and that the mechanisms underlying the P1, P2 and N400 components are different.

ERP negativities and task structure

Our working hypothesis relating the N400 wave to semantic priming effects predicts that an N400 would be elicited by an unprimed word whether it occurs in sentences, in isolation or in a random list. Insofar as this prediction has been tested, it has been upheld; the 300–500 msec region of a word-elicited ERP has been found to be more

negative for semantically unprimed than primed words regardless of experimental conditions. This general finding has obtained whether the task instructions required reading for content (e.g., this paper), determining whether a sentence or phrase was true or false (i.e., sentence verification) (e.g., Fischler et al. 1983; Neville et al. 1986), determining whether or not an item was a member of a semantic category (semantic categorization) (e.g., Boddy and Weinberg 1981; Harbin et al. 1984; Polich 1985), or deciding whether a letter string was or was not a bona fide English word (i.e., lexical decision-LDT) (Bentin et al. 1985; Holcomb 1985; Boddy 1986).

Together with this consistency, however, there have been notable differences in the morphological and distributional characteristics of this negativity (leading to the term N200/N400). For example, some N200/N400s have been reported to be quite anterior (e.g., Stuss et al. 1983) while others have been characterized by their distinctly posterior distribution (e.g., Kutas and Hillyard 1983). Likewise, some N200/N400s have been found to be larger over the right hemisphere, some larger over the left hemisphere while still others have exhibited no lateral asymmetry. These inconsistencies in anterior-posterior and lateral distributions of the N200/N400 across the scalp have (1) led to considerable controversy as to the nature of the underlying cognitive operation/process, (2) made it difficult to use this ERP as a specific marker of a specific cognitive operation, and (3) underscored our lack of definitive criteria for determining the equivalence of a wave recorded in one situation with that of another recorded under different circumstances (similar problems have arisen in investigations of the various late positivities that fall under the P3/P3b/P300/LPC umbrella).

To deal with this problem, we have opted for a weighted combination of wave form morphology, scalp distribution, and task specification parameters with the weights of each at the discretion of the experimenters. To the extent that the task structure across experiments has been held constant or similar, we have placed a greater weight on wave form morphology and distribution; however, in general, equivalence of task structure has received the greatest weight. Thus, it has been reassuring that the various silent reading paradigms of Kutas and her colleagues and relatively similar paradigms by Fischler et al. and Neville et al. have yielded N400s with a centroparietal, slightly right hemisphere distribution. However, even under conditions of silent reading, the centroparietal distribution of the N400, characteristic of incongruous or unrelated words presented at relatively slow rates (that is, between 500 and 1150 msec between words), has been found to be altered when the same words were presented at faster rates (e.g., with 200 msec or less between words). Insofar as it has been examined, anomalous or unprimed words presented at very fast rates elicited N400s with a relatively more frontal distribution than those presented at slower rates; that is, N400s elicited at high rates tended to be more evenly distributed along the anterior-posterior dimension (see Figs. 1 and 2 in Kutas 1987; Figs. 2 and 3 in Van Petten and Kutas 1987b). Experiments which have required subjects to make a decision or a response concerning the validity or appropriateness of an incongruous phrase or sentence also have resulted in a somewhat different appearing N400 than that observed under silent reading conditions. In particular, the N400s recorded in these situations have been characterized by a negativity that had a slightly earlier peak latency, was somewhat less prolonged in duration and was slightly more frontal in distribution than those recorded in the silent reading situation without a response (Fischler et al. 1985; Neville et al. 1986; Neville unpublished data). These changes appear to be due to the overlap of a decision/response-related componentry; large posterior positivities would tend to cancel at least part of the N400, making its distribution appear less posterior. However, this is an empirical issue which must await further experimentation and/or the development of new techniques for component separation and identification. In any case, it should be clear that scalp distribution is not a hard and fast criterion for component identification.

Our general feeling is that the underlying negativities in the Kutas and Hillyard silent reading studies, Fischler et al.'s sentence verification studies and Neville et al.'s (1986) study of congruous

and incongruous phrases are the same and somehow reflect activity of semantic priming mechanisms. In any case, it should not be surprising that more drastic variability in the experimental situation, as in the comparison between silent reading and lexical decision, would result in more dramatic wave form variability. The change in task parameters, together with changes in their associated componentry, may well explain the fact that lexical decision tasks are associated with N200/400s with an apparently different distribution than the N400s recorded during silent reading. To the extent that the N400 is related to semantic priming and that semantic priming is built into a lexical decision task, an N400 should be and probably is elicited. However, without a better understanding of the number and similarity of all the processing operations involved in LDT and silent reading, predicting the morphology and scalp variation of the resultant ERP wave form is a shot in the dark. The equivalence of silent reading ERPs to ERPs in studies which are even more different in task requirements, such as those involving rhyming judgments (Rugg 1984) or mental rotation (Stuss et al. 1983), has been even more difficult to assess. A definitive statement as to their equivalence would be premature.

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