THE LATERAL DISTRIBUTION OF EVENT-RELATED POTENTIALS DURING SENTENCE PROCESSING

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Abstract—Event-related brain potentials (ERPs) were recorded from adults as they read 160 different sentences, half of which ended with a semantically anomalous word. These deviant words elicited a broad, negative component (N400). Measured in the difference wave between ERPs to incongruous and congruous endings, the N400 was slightly larger and more prolonged over the right than the left hemisphere and diminished in amplitude over the course of the experiment. A left-greater-than-right asymmetry was again observed in the slow, positive ERP elicited by the first six words in the sentences, being most pronounced for subjects having no left-handers in their immediate family.

DESPITE an intensive search over the past decade for lateralized electrophysiological signs of linguistic processing in the brain, findings to date from investigations of event-related potentials (ERPs) do not form a coherent picture. A number of studies have reported an amplitude asymmetry in the ERPs recorded over the language areas and their right hemisphere homologues during tasks requiring linguistic or semantic analyses [1–7]. Others have observed that ERP activity over the left hemisphere is more sensitive to the linguistic properties of the eliciting stimuli than is right hemispheric activity [8–11]. However, a sizeable number of reports have noted an absence of hemispheric asymmetry in the ERPs obtained during the performance of language-related tasks [12–18].

Several reviewers of this literature have suggested that the paucity of reliable ERP asymmetries may be due at least in part to incomplete engagement of the language system by the tasks employed [14, 19, 20]. For example, the repeated presentation of isolated syllables, words, or a limited number of sentences may not tax language mechanisms as fully as would normal conversation or reading. Recently, we have reported a series of experiments involving recordings of ERPs from subjects as they read meaningful seven-word sentences, presented one word at a time [21–23]. Unexpected, semantically anomalous words placed at the ends of some sentences elicited a large negative wave (N400) having a parieto-central scalp distribution. We suggested that this N400 might be a marker of semantic evaluation processes following the interruption of the sentence analysis by the inappropriate word. While this particular interpretation may or may not be correct, the dependence of the N400 on linguistic analyses which are generally presumed to have lateralized cortical substrates led us to investigate whether this ERP would show lateral asymmetries at the scalp.

In our initial reading experiments [21, 22], the N400 was found to be virtually absent from lateral frontal scalp areas (F7 and F8). In a third experiment [23], recordings were made with a short time-constant from temporo-parietal leads, roughly over Wernicke's area and its right hemisphere homologue; both the N400 elicited by semantically incongruous words and the "difference N400" (incongruous minus congruous ERP) were slightly larger and more

prolonged over the right than the left side. That experiment also confirmed our earlier finding of a left-greater-than-right amplitude asymmetry in a slow positivity associated with the first six words in the sentences. This latter asymmetry was influenced by familial handedness, being attenuated for right-handed subjects who had left-handers in their immediate family. The present study was designed to evaluate the reliability of these laterally asymmetric ERPs during reading and to map their distributions more thoroughly.

A second aim of this study was to determine whether the N400 would be maintained when a substantial fraction (50%) of the sentences ended anomalously. In previous studies, the probability of a semantically incongruous ending was set at 0.25 because we had surmised that a higher frequency of deviant events might attenuate the associated endogenous components, as seems to occur with other late ERPs such as the P300 [24]. It was, therefore, of interest to see if N400 would be elicited at higher frequencies of semantic deviation, not only to contrast this effect with other expectancy-sensitive ERPs, but also to test the utility of N400 as a repeatable probe of semantic processing in a quasi-natural language context. Finally, increasing the proportion of anomalous sentences allowed a more precise examination of long-term changes in N400 amplitude across the test period.

METHODS

Subjects

Fourteen young adults (six female, age range 18-24 yr) were paid for participating in the experiment. Twelve of the subjects were right-handed according to self-report and the Edinburgh Inventory [25], and three of these had left-handed relatives in their immediate family. Of the remaining subjects, one was left-handed and the other ambidexterous; both had sinistral relatives.

Stimuli

Words were displayed in the form of brightened dot matrices on a CRT controlled by an Apple II microcomputer. All words lasted 100 msec and subtended a vertical angle of 0.4° with the subject sitting approximately 53" from the screen.

Recording system

EEG activity was recorded from seven scalp electrodes, each referred to linked mastoids. Five were placed according to the International 10-20 convention [26] at Cz and at left and right central (C3, C4), and temporal (T3, T4) locations. Symmetrical temporo-parietal electrodes were placed lateral (by 30% of the interaural distance) and 12.5% posterior to the vertex. These placements were situated approximately over Wernicke's area and its right hemisphere homologue. Eye movements and blinks were monitored via an electrode placed on the lower orbital ridge referred to linked mastoids. A right vs left external canthal montage was used to record lateral eye movements.

The Cz, C3 and C4 leads and the lateral eye recordings were amplified with Grass 7P1 preamplifiers (system bandpass DC to 40 Hz, half-amplitude cutoff). The other lateral scalp placements were amplified with Grass 7P1 preamplifiers having 8 sec time constants. Lower eye activity was amplified with a Grass 7P5 preamplifier (system bandpass down 3dB at 0.15 and 150 Hz).

The EEG, EOG and stimulus trigger codes were recorded on FM tape, and analog to digital conversion was performed off-line by a PDP 11/45 computer. A 1024 msec epoch of EEG data beginning 100 msec before the onset of each stimulus was analyzed at a sampling rate of 4 msec per point.

Procedure

Subjects were tested in one session that lasted $2\frac{1}{2}$ -3 hr, while reclining in a comfortable chair. They were informed that they would be presented with a series of simple, English sentences, one word at a time, and that each sentence would form a grammatically correct, meaningful unit. They also were told that the sentences were similar to one another in grammatical structure and that some might seem very familiar. Their instructions were to read each of the sentences silently in order to answer questions about their contents at the end of the experiment.

The start of each sentence was signalled by a warning stimulus consisting of XXXXX. This was followed 1 sec later by the sequential presentation of seven words at intervals of 1 sec, the last of which was followed by a period to indicate sentence completion. After a 2 sec delay the next sentence was presented, and so on.

ERP ASYMMETRIES

At the beginning of the session, subjects were exposed to 10 practice sentences with no ERPs recorded. Two of these were completed by a semantically anomalous word. The practice trials were followed by eight experimental series of 20 sentences each. Each sentence was unrelated to the others. Of these 160 sentences, half were completed by semantically appropriate (congruous) words and half by inappropriate words (e.g. "There are too many people in *wallet.*" and "He listed his occupation as a *chocolate.*") These two types of sentences were presented in random order. Each series of 20 sentences was followed by a 2–3 min rest period.

Following the ERP recordings, subjects were given a memory recognition questionnaire on the sentences. The first test listed the first six words of 42 different sentences, 31 of which were selected from the sentences just seen and 11 of which had not been shown. The subject's task was to check whether each sentence was "old" or "new" and to fill in the word they remembered as completing each of the "old" sentences. The subjects were then shown a list of all 160 of the completed sentences and were asked to rate each of the last words as to their unexpectedness on a seven-point scale.

RESULTS

General characteristics of ERPs

Figure 1 shows the superimposed ERPs from individual subjects to the four different classes of stimuli. The corresponding grand average waveforms over all subjects are shown below. The ERPs to all stimuli were characterized by a negative peak at 120–150 msec (N136) and a positive peak at 180–250 msec (P220). The responses to the warning stimulus (WS) included a small and highly variable positivity at around 400 msec (P400).



FIG. 1. ERPs to the warning stimulus (WS), to words 1-6 (averaged together), and to the congruous and incongruous seventh words. Each of the superimposed tracings in the top row is the averaged ERP from a different subject. The ERPs in the bottom row are the corresponding "grand average" waveforms over all subjects (N = 14), recorded at the vertex.

The ERPs to the final words in the sentences were also marked by appreciable inter-subject variability, but in each case the semantically congruent ERPs were associated with a sustained late positivity in the 300–900 msec range. The ERPs to the incongruous words, on the other hand, included an additional negative-going wave between 300 and 600 msec (N400). Thus, the ERPs elicited by the congruent and incongruent seventh words differed significantly in the 300–600 msec zone [F(1,13)=73.19, P < 0.001, for area measure relative

to 90 msec pre-stimulus baseline]. This difference was maximal around 380 msec at the vertex and averaged $-8.63\pm0.65\,\mu\text{V}$ relative to the baseline. The congruous and incongruous seventh word ERPs did not differ significantly from one another in the 600–900 msec region.

Comparison of ERPs over left and right hemispheres

Warning stimulus and words 1–6. The ERPs from the lateral electrodes averaged across all 14 subjects are depicted in the first two columns of Fig. 2. The ERPs elicited by the WS were



FIG. 2. Superimposed ERPs over the right and left hemispheres from three pairs of homologous locations. Comparisons are shown for ERPs elicited by the warning stimulus (WS) and by words one-six (averaged together). The ERPs in the first two columns are averages across all 14 subjects. The ERPs in the last two columns are segregated according to whether the subjects did (N=9) or did not (N=5) have any left-handed relatives in their immediate family.

nearly symmetrical, whereas the ERPs averaged over the first six words in the sentences showed a prolonged positivity that was larger over the left than the right hemisphere, particularly over the temporo-parietal sites.

This left-right hemispheric difference, quantified as the area of the region 400-700 msec post-stimulus relative to a 90 msec pre-stimulus baseline (shaded region between vertical lines), was evident in each of the electrode pairs, but specific comparisons indicated that this lateral asymmetry was significant only at the temporo-parietal sites [F(1,13)=6.22, P<0.03]. Inspection of the individual subjects' waveforms revealed that the left-greaterthan-right positivity to words 1-6 was larger in the right handers without left-handed relatives. While this difference between the groups was present at all of the electrode pairs, planned comparisons showed that significant asymmetry was restricted to the temporoparietal locations [F(1,8)=7.24, P<0.02]. There were no significant sex differences in ERP laterality. Seventh words. In contrast to the ERPs elicited by words 1–6, the late positive shift in the ERPs to the congruent seventh words was approximately 1 μ V larger over the right than the left hemisphere for each of the lateral electrode pairs (P < 0.01 for each pair for the area measure between 300 and 900 msec) (see Fig. 3). The degree of asymmetry was not influenced



FIG. 3. The grand average ERPs (across all 14 subjects) elicited by the semantically congruous and the semantically incongruous seventh words. In each case, the ERPs recorded from homologous sites over the two hemispheres are superimposed.

by subjects' familial handedness. The ERPs elicited by the incongruent seventh words also showed a slight tendency for a right-more-positive-than-left asymmetry in the 200-400 msec and 600-900 msec ranges, while the N400 itself (at 400-500 msec) appeared slightly more prolonged over the right hemisphere. However, none of these asymmetries were significant.

Difference waves. The lateral distribution of the N400 difference waves obtained after a point by point subtraction of the congruent from the incongruent seventh word ERPs is shown in Fig. 4. Although the N400 difference wave averaged over all subjects was approximately 1 μ V larger over the right than the left hemisphere at each pair of lateral electrode sites, neither a base-to-peak nor an area measure of the negativity revealed a significant lateral asymmetry. The N400 was approximately 1 μ V larger at the central than at the temporo-parietal sites, which in turn were some 2 μ V larger than at the anterior temporal sites [anterior-posterior electrode main effect, F(2,26)=28.79, P < 0.001].

A significant electrode location by hemisphere interaction was found for subjects without left-handers in their immediate family [for area 300-600 msec measure, F(2,16)=3.72, P < 0.05]. This was due to a right-greater-than-left negativity that was significant only at the temporo-parietal locations [F(1,8)=5.90, P < 0.04].

Seventh word ERPs by quarters

The ERPs to the congruent and incongruent seventh words and their difference waveforms were averaged separately for each quarter of the experiment (Fig. 5). Visual inspection of these data indicates that the ERPs elicited by the semantically incongruent words remained essentially unchanged while the amplitude of the late positivity elicited by the congruent







FIG. 5. The grand average ERPs (N = 14) elicited by semantically congruent and incongruent seventh words, and the difference waveform obtained by subtracting them, shown as a function of the quarter of the experiment in which they were recorded. Each ERP represents an average over 15-20 trials/subject.

words declined systematically. As a result, the amplitudes of the corresponding N400 difference waves also declined over the experiment.

The ERPs to the incongruous final words differed between quarters only in the amplitude of the N136 component, which was significantly larger (by 1–1.5 μ V) during the second than the first half of the experiment [for base-to-peak measure, main effect of quarter was F(3,39) = 3.49, P < 0.03]. Measures of the N400 remained unchanged across quarters.

The N136 elicited by the congruent final words was also largest towards the end of the recording session [F(3.39) = 3.15, P < 0.04]. In addition, the amplitude of the late positivity in the ERPs to congruent words was reduced significantly in the course of the experiment [for area 300-600 measure, F(3.39) = 5.31, P < 0.003; for area 600-900 measure F(3.39) = 6.67, P < 0.001].

The N400 difference waves similarly were reduced in amplitude from the first to the last quarters [for area 300-600 measure, F(3.39) = 3.99, P < 0.02]. In peak amplitude, the N400 difference wave decreased by approximately 2 μ V from the first to the second quarters, and by 0.5-1.0 μ V thereafter. The amplitude of the late negativity in the region 600-900 msec post-stimulus also declined during the experiment [F(3.39) = 5.75, P < 0.002].

Behavioral data

Semantic incongruity ratings. Behavioral assessments of the subjects' reactions to the last words were derived from their responses on a seven-point rating scale, where 1 indicated that the word was "expected" and 7 that it was "totally unexpected". The mean ratings for congruous (1.61 ± 0.13) and incongruous words (6.28 ± 0.17) diverged sharply (Mann-Whitney U, P < 0.001). These ratings did not differ over quarters for the congruous (1.58, 1.61, 1.63, 1.71) or for the incongruous (6.27, 6.18, 6.39, 6.31) words.

Memory/recognition questionnaire. The subjects correctly identified an average of 65% of the "old" six word sentences and misclassified an average of 24% of the "new" sentences on the list as belonging to the set they had just seen. They correctly filled in the seventh word that was actually shown for 84% of the sentences that had ended appropriately. However, while they recognized 39% of the sentences that had ended inappropriately, they were able to fill in the correct word for only 10% of them.

DISCUSSION

As in previous reports, words presented in this silent reading task elicited long latency ERPs that differed as a function of word position and meaningfulness [16, 21–23, 27]. Each of the initial six words in these sentences was associated with a small positive ERP sustained over 300–900 msec post-stimulus, while the final words were followed by considerably larger positive baseline shifts. In addition, when the last word was semantically inappropriate to the context of that sentence a negative component (N400), of maximal amplitude over central-parietal scalp regions, was superimposed upon the positive-going shift.

As reported previously [22–23], the late positivity elicited by words 1–6 in the sentences was larger over the left than the right temporo-parietal scalp. The size of this asymmetry was again found to be relatively smaller for subjects having left-handers in their immediate families. While this small, highly consistent ERP asymmetry may be a sign of lateralized linguistic processing, this remains speculative in the absence of appropriate control evidence from non-language tasks. Nonetheless, since the asymmetry was not present in the ERPs to the warning stimuli and has not been observed in studies employing repetitive sentences [16], it is reasonable to suggest that these slow shifts may be associated with the active assimilation

of natural language. Furthermore, the reduction of this ERP asymmetry in subjects with lefthanded relatives parallels the observations of smaller laterality effects in such persons on a variety of behavioral measures that have been taken to reflect hemispheric specialization for language [28, 29].

These data are in line with several recent reports of a prolonged positive electrogenesis in the later regions (post 300 msec) of the ERP, larger over the left than the right hemisphere for language-related tasks [7] and larger over the right than the left in tasks requiring tactile discrimination [30] or spatial analysis [31]. While these asymmetries appear to have an opposite laterality for language and non-language tasks, our present understanding of scalp ERPs does not permit a definite interpretation of such asymmetries in terms of specific hemispheric functions.

A significant lateral asymmetry was also observed in the N400 difference waves (incongruous minus congruous endings). This hemispheric difference was quite small, but it has also been observed consistently in two prior studies [23, 32]. Figure 6 shows the right-greater-than-left asymmetry in the N400 and in the difference waves in a previous study by KUTAS [32] which differed from the present one in two minor ways: (a) the words were presented at a rate of 2 per sec, and (b) the probability of a sentence ending with a semantically anomalous word was set at 0.25. Again, the N400 was larger and more prolonged over the right side of the head. (The area of the difference wave between 500 and 700 msec averaged $28 \pm 194 \ \mu$ V msec at the left temporo-parietal site and $-458 \pm 101 \ \mu$ V msec at the right temporo-parietal site [F(1,6)=9.59, P < 0.02]). While this asymmetry may derive in part from overlap with other late components, it appears that the negativity associated with semantic anomaly has a right hemispheric preponderance.

It should be noted that the asymmetry of the N400 difference wave is a function of asymmetries in the ERPs to both the incongruous and congruous final words. While the



FIG. 6. The grand average ERPs (over all seven subjects in this experiment) elicited by semantically incongruous seventh words (left) and the incongruous minus congruous difference waves (right). In each case, the ERPs recorded from homologous sites over the two hemispheres are superimposed. These data are from KUTAS [32].

difference N400 has consistently been larger over the right hemisphere in all experiments, the ERP to the congruent endings has shown different directions of asymmetry in different experiments [22, 23]. Whether this variation represents different processing strategies or individual differences between subjects remains to be determined. Interpretation of these asymmetries is doubly difficult because of the likelihood that several overlapping (and possibly interacting) components are produced at the end of the sentences.

If the greater right-sided negativity seen in the N400 difference wave reflects a preferential processing of semantic incongruity in the right hemisphere, such an effect would appear to be at odds with the generally accepted specialization of the left hemisphere for most aspects of language processing. However, several lines of recent evidence point to an important role for the right hemisphere in the comprehension of high-level semantic, conceptual, and contextual relationships [33-35]. For example, WAPNER et al. [35] found that patients who had sustained brain damage restricted to the right cerebral hemisphere showed no deficiencies in their phonology, syntax or word memory, but did experience difficulty in appreciating the overall contextual framework of narrational and humorous material. WAPNER et al. suggested that right-lesioned patients are impaired at using the normal "plausibility metric", whereby words and statements are judged as being appropriate to a particular context. Since the present experiments also involve judgements about the plausibility of words in sentence contexts, it is conceivable that a right hemispheric specialization for this type of activity may be manifest in a lateralized N400 component. This interpretation of the cognitive functions of the right hemisphere is consistent with findings that patients with right-sided cortical damage are impaired at understanding humor [36], at interpreting metaphors and figures of speech [37], and in appreciating affectively toned situations [38, 39]—all of which share features in common with the type of semantic anomalies that elicit the N400.

The N400 amplitudes were substantial in this experiment, even though half of the sentences were completed by semantically anomalous words. In fact, the mean N400 difference wave was equal in amplitude to those observed in two previous experiments in which the probability of an incongruous ending was 0.25 [20, 22]. This suggests that the N400 may be less sensitive to changes in the probability of occurrence of the eliciting events than are other late components such as the N200, P300 and slow wave, the amplitudes of which are inversely related to stimulus probability over the range 0.25-0.50 [39]. However, it should be noted that subjective expectancy seems to be a more potent factor than simple event frequency in determining the amplitude of the P300 complex. As yet, no metric exists for comparing the expectancies formed during natural language processing with those formed during a random sequence of tones. It may be that highly salient events like semantic anomalies have the same psychological impact over a wide range of probabilities. Furthermore, since linguistic messages are highly constrained and redundant, the persistence of the N400 at higher probabilities of anomaly may reflect the automatic, overlearned character of semantic analyses during reading. Whatever the explanation, the maintenance of a robust N400 in the face of frequent semantic anomalies should make this ERP useful in reading studies where semantic analyses are tested repeatedly.

Although the N400 persisted at the 50% anomaly rate, its amplitude as measured in the incongruous minus congruous difference wave decreased over trials. The nature of this decrement is difficult to evaluate, since the ERP waveforms to the congruous endings were characterized by a late positive shift that also declined steadily throughout the experiment. This positive shift probably consists, at least in part, of the resolution of the CNV that

develops throughout each sentence [21]. The inference that the CNV and, hence, its resolution are habituating over the course of the experiment is consistent with the parallel increase that was observed in the amplitude of the N136 component of the ERPs to the final words. The N136 (also termed N1 or N100) is reportedly larger when superimposed on a reduced CNV [40, 41].

The ERPs to the terminal words may also include an additional positive component related to "syntactic closure" [16] or some other aspect of sentence completion. If such a positive wave were elicited as a "latent" component at the end of incongruous sentences and habituated over the experiment, then the reduced amplitude of the N400 difference wave would indicate that the N400 process itself was habituating. On the other hand, if such a positive-going component was not a constituent of the ERP to the incongruous endings or did not decrement over trials, this would imply that the N400 effect itself was stable, as seen in the actual ERPs to the incongruous words (Fig. 5, left).

Another possible interpretation of this long-term change would be to assume that subjects altered their expectations and processing strategies as they learned that many of the sentences were going to be semantically anomalous. Future studies which independently manipulate the various overlapping ERP components and associated psychological processes may clarify these alternatives.

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Resume :

On a enregistré les potentiels évoqués cérébraux chez des adultes tandis qu'ils lisaient 160 phrases différentes dont la moitié finissait par un mot sémantiquement anomal. Ces mots déviants déterminaient une composante négative étendue (N 400). Mesuré dans l'onde de différence entre les potentiels évoqués selon les terminaisons, congruente ou incongruente, N 400 était légèrement plus grand et plus prolongé sur l'hémisphère droit que sur l'hémisphère gauche et diminuait d'amplitude au cours de l'expérience. On observait à nouveau une asymétrie plus grande à gauche qu'à droite dans les potentiels évoqués positifs lents produits par les six premiers mots des phrases, asymétrie plus prononcée chez les sujets n'ayant pas de qauchers dans leur famille immédiate.

Zusammenfassung

Ereignis-korrelierte Hirnpotentiale wurden bei Erwachsenen registmiert, als sie 160 unterschiedliche Sätze lasen, von denen die Hälfte mit einem semantisch inakzeptablen Wort endete. Diese abweichenden Wörter lösten eine breite negative Komponente (N400) aus. Verglich man den Unterschied der Potentiale bei passenden und unpassenden Satzendigungen, war die N400 etwas breiter und länger über der rechten als über der linken Hemisphäre und verminderte sich in ihrer Amplitude während des Experimentes. Eine Asymmetrie links größer als rechts fand sich wiederum bei den langsamen positiven Reaktionspotentialen, die durch die ersten 6 Wörter in den Sätzen ausgelöst wurden, sie war am deutlichsten bei Versuchspersonen, die keine Linkshänder in ihrer unmittelbaren Familie hatten.

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