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Event-Related Potential Studies of Cerebral Specialization during Reading

I. Studies of Normal Adults

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A number of methodological features were incorporated in a paradigm designed to maximize the likelihood of finding reliable event-related potential (ERP) signs of functional specializations between and within the cerebral hemispheres. Every subject was more accurate in identifying words presented to the right than to the left visual field. The morphology of the ERPs elicited by these words varied considerably as a function of electrode position both within and between the hemispheres. Amplitude asymmetries of ERP components recorded from occipital regions of the two hemispheres varied systematically with the position of the word in the visual field. On the other hand, ERPs from more anterior (temporal and frontal) regions displayed large asymmetries which were in the same direction regardless of the visual field of word presentation. The most prominent such asymmetry was in the negativity in the region 300–500 msec (N410) which was larger in the left than the right hemisphere in every subject. These results demonstrate that in this paradigm which demands specialized language processing ERPs are sensitive to aspects of cerebral organization both within and between the two hemispheres.

A large literature has documented the different functional specializations of the left and right cerebral hemispheres in man. While questions remain concerning the specific functions for which each hemisphere is dominant, most investigators concur that the left hemisphere plays a major role in reading, writing, and the production and comprehension of speech, while the right hemisphere is more important for the performance of nonlanguage tasks which require the perception of spatial re-

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lations (Hecaen & Albert, 1978; Heilman & Valenstein, 1979). Most of the evidence for hemispheric specialization has come from observations of the differential effects of damage to the two sides of the brain, and from studies of intact adults showing differential lateral asymmetries in the accuracy of reporting language and nonlanguage material presented to the two ears, visual fields, or hands.

It seems reasonable to expect that the different functional specializations of the two hemispheres would be reflected in electrophysiological recordings from over left and right brain regions. In principle, these electrophysiological measures could contribute to many issues in neuropsychology since they provide information about the sequence and timing of neural events which intervene between a stimulus and response. In particular, event-related brain potentials (ERPs) yield information complementary to that available from behavioral asymmetries, not only about the relative timing of activation of the two hemispheres, but also about the flow of information *within* a hemisphere. In addition, reliable ERP signs of lateralized processing could elucidate individual differences in hemispheric specialization. Thus, for example, paradigms producing lateral ERP asymmetries in intact adults could be employed to investigate the effects of different developmental histories on functional cerebral organization (see our companion paper reporting studies of congenitally deaf adults; Neville, Kutas, & Schmidt, 1982) and the effects of brain damage on cerebral function (Neville, Snyder, Knight, & Galambos, 1978; Neville, 1980).

However, recent reviews of the ERP literature agree that evidence for hemispheric specialization has been elusive and, when obtained, the ERP asymmetries appear small in relation to what one might expect based on the clinical and behavioral literatures (Galambos, Benson, Smith, Schulman-Galambos, & Osier, 1975; Friedman, Simson, Ritter, & Rapin, 1975; Donchin, Kutas, & McCarthy, 1977; Hillyard & Woods, 1979).

To maximize the likelihood of finding reliable ERP signs of hemispheric specialization, the present experiment incorporated a number of methodological features based on the behavioral and ERP literatures in a reading paradigm. First, to ensure active participation during ERP recording, subjects were required to identify in writing different words presented to the two visual fields. These written responses thus provided behavioral evidence for the functional interpretation of the ERP asymmetries obtained. Second, to avoid biases associated with direction of scanning or with ease of identifying words which begin (right visual field) versus end (left visual field) close to the fovea, words were presented in vertical orientation. Third, central fixation was monitored by requiring accurate discrimination of a colon (:) from a semicolon (;) presented in the center of the display. Fourth, in view of recent reports of reliable asymmetries in low-frequency, sustained ERP components (Desmedt, 1977; Kutas & Hillyard, 1980a; Neville, 1980) the EEG was amplified with a 0.01-Hz low-frequency cutoff. Fifth, in an attempt to reduce the amplitude of sensory evoked ("exogenous") ERP components in relation to those associated with linguistic processing (Hillyard & Woods, 1979), white words were presented on a darkened video screen. Finally, in view of the different morphology and functional relevance of ERPs recorded over anterior and posterior scalp regions (Callaway, Tueting, & Koslow, 1978), recordings were obtained over homologous frontal, anterior temporal, temporal, parietal, and occipital regions of the left and right hemispheres.

METHODS

Subjects

Ten right-handed subjects (six female, four male, mean age = 22, Edinburgh Laterality Quotient X = 0.86) were paid to participate in the experiment.

Stimuli

The stimuli were 60 high-frequency (AA according to the Thorndike–Lorge (1948) word count) four-letter English nouns. Words were presented for a 100-msec duration. Half of the words were presented unilaterally once to the left visual field and once to the right visual field. The remaining words were paired with a different word and were presented bilaterally; each word occurred once in each field. All stimuli were white letters, presented on a dark, 24.5 cm × 20.0 cm video monitor controlled by a microcomputer. The monitor was about 100 cm from the subject so that words were presented 1.6° to the left or right of a central fixation and subtended 2.2° of visual angle vertically.

Procedure

Subjects were seated comfortably in a copper shielded, soundproof room and were given written instructions describing the task. The timing of the stimulus presentations is diagrammed in Fig. 1. A trial began with the presentation of a 1.1° square in the center of the monitor followed by a small (0.2 × 0.5°) rectangle beneath it (a in Fig. 1). Subjects focused on the center of the square where a colon or a semicolon appeared simultaneously with a unilateral word or a bilateral word pair (b in Fig. 1). The interval between the presentation of the rectangle and word onset was varied randomly between 900 and 1100 msec in order to attenuate the negative shift (CNV) which often occurs during fixed intervals that separate warning stimuli and expected events. Two seconds after stimulus presentation, the small rectangle disappeared (c in Fig. 1), and the subjects pressed one of two buttons to indicate which fixation symbol they had seen. If the fixation symbol was entered correctly, a message appeared on the screen instructing the subject to write the word s/he saw. If the fixation symbol was entered incorrectly, the trial was excluded from further analyses. The mean accuracy for this discrimination was 97.1%. All trials were initiated by subjects' button press. Intertrial intervals ranged between 7 and 9 sec. All subjects received six practice trials followed by 30 unilateral right, 30 unilateral left, and 30 bilateral word presentations, all randomly intermixed.

ERP Recording

Scalp electrical activity was recorded with nonpolarizable electrodes from homologous positions over left and right occipital (01,02), parietal (P3,P4), temporal (33% of the interaural distance lateral to CZ), anterior temporal (1/2 of the distance between F7(8) and

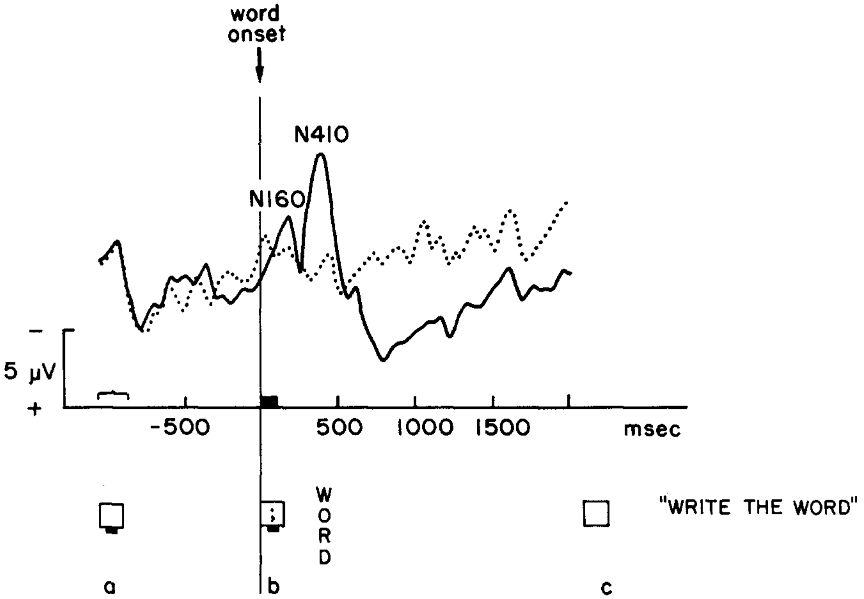

FIG. 1. ERPs from one subject (left and right temporal electrodes) averaged 1 sec prior to and 2 sec following presentation of a word to the right visual field. This shows the timing of stimulus sequences. Interval between a and b was randomly varied between 900 and 1100 msec to attenuate buildup of prestimulus negative shift (CNV).—, Left temporal; ..., right temporal.

T3(4)), and frontal (F7, F8) regions, and from the vertex (CZ). Recordings from these electrodes and the electrooculogram from beneath the left eye, were referred to the linked mastoids. Electrical activity was amplified with a bandpass of 0.01–100 Hz and was recorded on FM tape for off-line analysis on a PDP-11/45 computer.

Data Analysis

ERPs were digitized for 100 msec prior to and 924 msec after stimulus presentation at a sampling rate of 1 point/4 msec. Trials on which excessive eye movement or muscle artifact occurred were rejected (approximately 3% of trials). For each subject, average ERPs were computed for left visual field, right visual field, and bilateral word presentations. ERP components were quantified by computer as either peak amplitudes within a latency range or as area measures (the mean voltage within the same latency range). Both measures were computed relative to 100 msec of prestimulus baseline voltage; the same latency windows were used for all subjects' ERPs. Since the morphologies of ERPs from anterior and posterior electrodes were different (see Fig. 3) different measures were taken and separate analyses were performed on them. Similar methods were employed to quantify "difference waveforms" computed by subtracting the averaged ERPs recorded over the right hemisphere from those recorded over homologous locations of the left hemisphere. The ERP data were analyzed by a four-way analysis of variance with repeated measures on two levels of hemisphere (left, right), three levels of field (left visual field, right visual field, bilateral), and three anterior (temporal, anterior temporal, frontal) or two posterior (occipital, parietal) levels of electrode. The difference ERP data were analyzed with a three-way analysis of variance with repeated measures on three levels of field and three anterior or two posterior levels of electrode. Subanalyses of variance were performed to further clarify significant interaction effects.

RESULTS

Behavioral Results

Subjects correctly identified significantly more words presented to the right than to the left visual field (field effect $F(1,9) = 93.0$, $p < .001$). This asymmetry was observed in every subject after unilateral (mean percentage correct left visual field 58 versus right visual field 74) and bilateral word presentations (left visual field 27 versus right visual field 50; see Fig. 2).

Event-Related Potentials

Figure 3 presents ERPs (averaged across all subjects) from all electrode locations elicited by words presented to the right visual field. It is clear that the morphology of the ERPs elicited by these words varied considerably as a function of electrode position both within and between the cerebral hemispheres. While some of these ERP components were similar to those reported in studies employing complex visual stimuli, others were not readily equatable with previously named components. Thus,

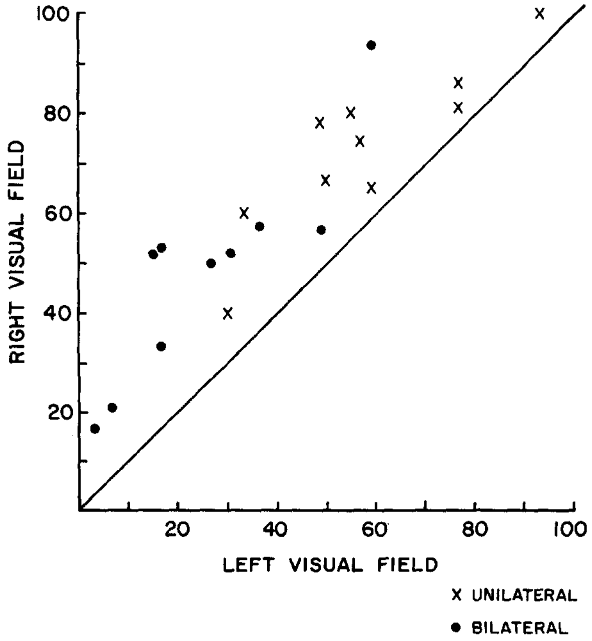

FIG. 2. A scatter plot showing percent correct identification of words after unilateral (left or right visual fields(×)) and bilateral (●) word presentations. Points fall above the diagonal line if accuracy was greater after right visual field (left hemisphere) presentations.

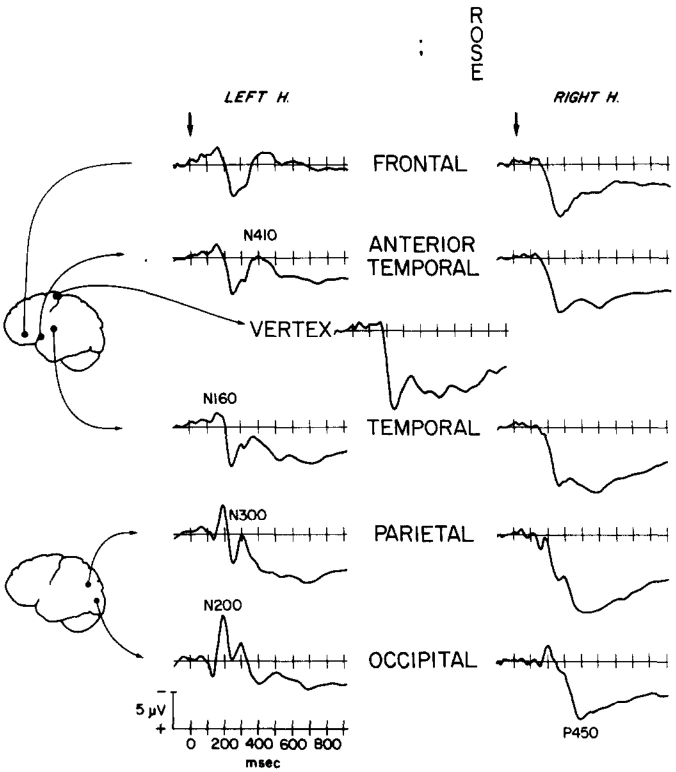

FIG. 3. Grand mean ERPs (averaged across all 10 subjects) from homologous locations over the left and right hemispheres and the vertex, elicited by vertically oriented words presented to the right visual field. Negativity is upward on this and all subsequent figures. The dots on the schematics of the brains at the far left of the figure represent approximate locations of the various recording electrodes over the left-hemisphere scalp.

we adopted the convention of labeling the ERP peaks in terms of their polarity (or the polarity of their initial direction of movement) and mean latency.

Several of the ERP peak measures showed amplitude asymmetries over the two hemispheres. The direction of some of these asymmetries (as in the N200, P450) varied systematically with word position in the visual field. Other asymmetries as in the N160, N300, and N410 components were constant in direction but varied in degree as a function of the visual field of presentation.

Posterior ERPs (Occipital and Parietal Regions)

A comparison of the ERPs recorded over the left and right occipital regions during right, left, and bilateral visual field word presentations is provided in Fig. 4. Visual inspection of these ERPs revealed that each

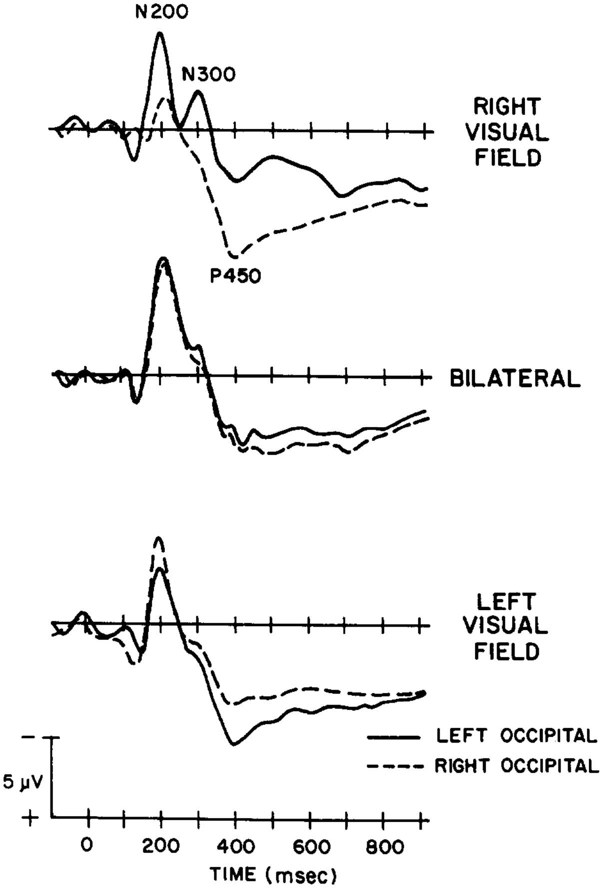

FIG. 4. A comparison of the grand mean ERPs recorded over the left (solid line) and right (dashed line) *occipital* regions during right, left, and bilateral visual field word presentations.

of the three major components at these sites, the N200, the N300 and the P450, was asymmetrically distributed across the two hemispheres, particularly for words presented to the right visual field. The nature of the amplitude asymmetry, however, varied with the component in question.

N200. At the *occipital* sites, the lateral distribution of the N200 varied according to the position of the word in the visual field (see Fig. 4). That is, N200 amplitude (measured as the area 150–220 msec) was approximately 2–3 μV larger over the hemisphere contralateral to the visual field for unilateral word presentations, and was symmetric for bilateral word presentations (hemisphere × field $F(2,18) = 37.4$, $p < .00001$). At *parietal* sites, N200 was 1–3 μV larger from the left than the right hemisphere after both right visual field and bilateral word presentations, and was symmetric after left visual field presentations (hemisphere × field $F(2,18) = 14.9$, $p < .0002$).

N300. N300 was also prominent in the ERPs recorded over parietal and occipital regions and was most clearly defined over the left hemisphere in response to words presented to the right visual field (see Fig. 4). Thus, over posterior regions, the N300 (measured as the area 250–400 msec) was significantly larger from the left than the right hemisphere for right visual field presentation, but was symmetric across the two hemispheres for left visual field and bilateral word presentations (hemisphere $F(1,9) = 8.2$, $p < .01$, field $F(2,18) = 6.1$, $p < .009$; hemisphere × field $F(2,18) = 39.0$, $p < .00001$).

P450 and sustained positivity. Following N300, posterior ERPs displayed a positivity peaking around 450 (450 ± 27) msec, which was followed by a positive shift sustained throughout the epoch (see Fig. 4). The area measure between 500 and 900 msec was systematically related to the visual field of word presentation and was larger over the hemisphere ipsilateral to the word during unilateral field presentation and was symmetrically distributed for bilateral presentations (hemisphere × field interaction $F(2,18) = 19.6$, $p < .00001$).

Anterior ERPs (Frontal, Anterior Temporal and Temporal)

N160. The first negative component over the anterior sites, an N160 (mean peak latency 162 ± 6 msec; measured between 100 and 200 msec) was larger over the left than the right hemisphere (mean peak amplitude left $-2.3 \pm .05$ μV; right $-0.8 \pm .05$ μV) regardless of the field of word presentation (hemisphere effect $F(1,9) = 68.0$, $p < .00001$).

N410 (Area 300–500). Beginning around 250 msec after word presentation, ERPs from frontal and temporal regions of the left hemisphere were consistently more negative than those from the right hemisphere (see Fig. 3). The negativity was maximal around 410 (409 ± 17) msec. The nature of the lateral asymmetry of N410 in response to unilateral and bilateral word presentations can be seen in Fig. 5, where the ERPs from the anterior temporal regions of the two hemispheres are superimposed. First, it is clear that this region (300–500 msec) was more negative over the left than the right hemisphere whether words were presented to the right visual field, left visual field, or bilaterally. Analyses of two different measures of the N410, the peak negativity and the mean voltage between 300 and 500 msec relative to a prestimulus baseline, indicated that the N410 was significantly larger over the left than over the right hemisphere for each type of presentation at the frontal, anterior temporal, and temporal sites (hemisphere effect $F(1, 9)$ base–peak $= 38.4$, area $= 40.0$, $p < .0001$).

The consistency of this asymmetry is evident in the scatter diagram in Fig. 6 where the mean voltage of the areas in the region 300–500 msec

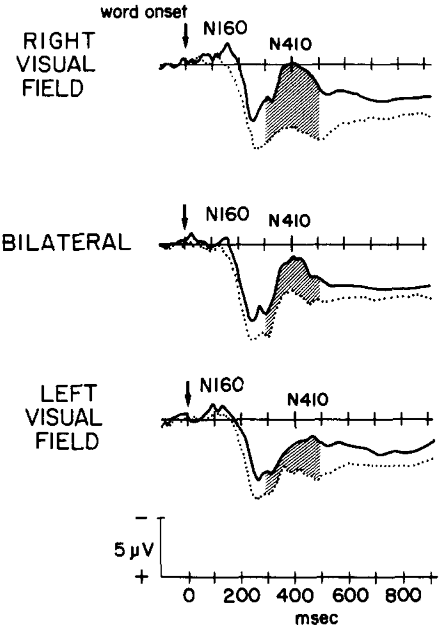

FIG. 5. A comparison of the grand mean ERPs recorded over the left (solid line) and right (dotted line) *anterior temporal* regions during right, left, and bilateral visual field word presentations.

from the right and left hemispheres are plotted against each other for the different word presentations for each subject. Thus, this region was more negative from the left than the right anterior temporal locations in *every* subject after right visual field and bilateral word presentations and in 8 of 10 subjects after left visual field presentations. Figures 5 and 6 also demonstrate that the difference between the two hemispheres in the region of the N410 was greater for right visual field presentations than for either left visual field or bilateral word presentations (hemisphere × field interaction $F(2, 18)$ base–peak = 9.3, area = 12.4, both $p <$ .001).

Sustained positivity. The positivity after N410 averaged 3–5 μV in amplitude and tended to be larger from the right than the left hemisphere, but this effect was not significant (area 500–900, NS).

Difference ERPs

Many aspects of the asymmetries obtained in this study are summarized in the left minus right hemisphere difference ERPs. As seen in Fig. 7a, the asymmetries in occipital ERPs reflected the position of the word in the visual field: N200 was larger (more negative) contralateral to field of word presentation, P450 was larger (more positive) ipsilateral to field of word presentation and both were symmetric during bilateral word

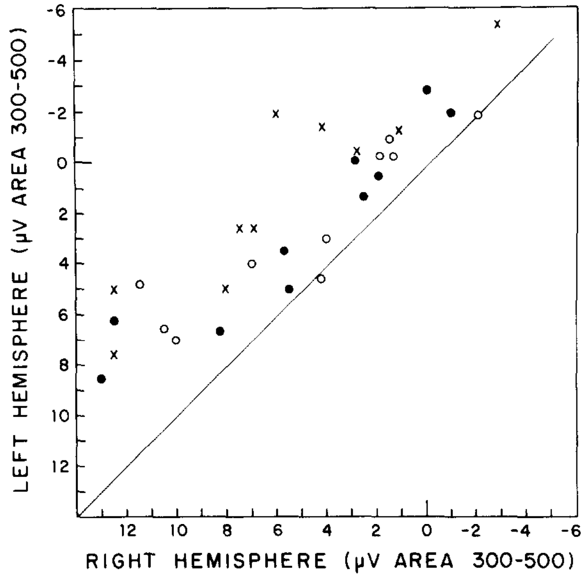

FIG. 6. A scatter plot comparing the amplitude of N410 from the left and right anterior temporal sites for words presented in the left or right visual fields or bilaterally. Points fall above the diagonal if the left hemisphere was more negative than the right. The N410 was measured as the area under the ERP in the region 300–500 msec post stimulus relative to a prestimulus baseline. Each mark represents data from an individual subject. The different symbols represent the values obtained from ERPs elicited by left visual field (open circle), right visual field (×), and bilateral word presentation (closed circle).

presentations (N200 field $F(2, 18) = 19.4$, $p < .00001$; P450 field $F(2,18) = 72.6$, $p < .00001$). In contrast, as seen in Figs. 7b and c, the differences between the hemispheres at temporal and frontal electrodes were in the same direction regardless of field of word presentation. The N410 was more negative from the left than the right hemisphere and this asymmetry was largest for right visual field word presentations (mean hemisphere difference area 300–500 RVF = 5.2 µV, LVF = 2.3 µV, bilateral = 2.4 µV; field $F(2,18) = 12.4$, $p < .0004$).

DISCUSSION

The goal of this study was to determine whether reliable ERP evidence for cerebral specialization could be demonstrated in a paradigm designed to maximize the appearance of functional asymmetries. The fact that every subject exhibited behavioral asymmetries consistent with a specialized role for the left hemisphere in this task (i.e., greater accuracy in identification of words presented to the right visual field) testifies to the efficacy of these procedures in inducing lateralized cerebral processing. In parallel with these behavioral asymmetries, the N410 from every subject was larger over the anterior regions of the left than the right

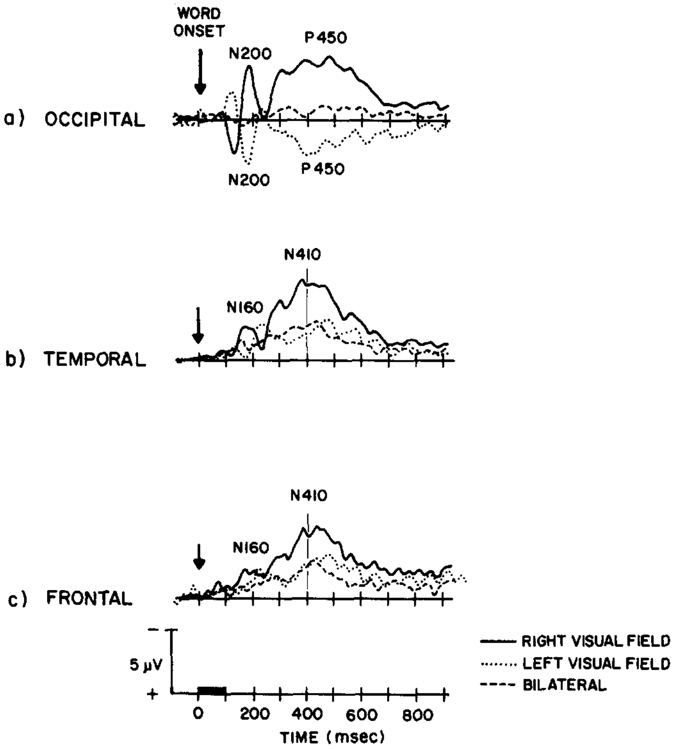

FIG. 7. Difference ERPs obtained by subtracting ERPs recorded over the right from those recorded over the left (a) occipital, (b) temporal, and (c) frontal regions.

hemisphere. Moreover, the asymmetries in the ERPs were greatest when identification of words was best (i.e., after unilateral presentation of words to the right visual field). Therefore, the N410 appears to be a likely candidate for an index of lateralized cerebral processing during reading.

We also observed large differences in the morphologies of ERPs within the hemispheres from electrodes separated by only a few centimeters. For example, the N410 component was prominent at the temporal region of the left hemisphere but was not observed over the parietal region of the left hemisphere. Since we did not observe this component in earlier studies employing similar tasks (Neville, 1980), the long time constant of the recording system and the choice of electrode sites may have been important variables in revealing the N410.

Other asymmetries in the ERPs could be interpreted as consistent with the language processing required and the behavioral performance of the subjects. Thus, the asymmetric N160 and N300 are also candidate ERP components which may reflect specific aspects of the specialized role of the left hemisphere in this reading task.

These results demonstrate that under certain conditions one can obtain reliable ERP asymmetries which may reflect the different functional specializations of the two hemispheres. However, further research is required to clarify the functional significance of the different patterns of activity recorded from the two hemispheres. While various ERP components from regions of the left hemisphere were more negative, ERPs from the right hemisphere displayed sustained positive shifts, which may have prevented the appearance of negative components in the ERPs. It is conceivable that asymmetries observed in ERPs to the words may have been due in part to asymmetries in the prestimulus ''expectancy''-related baseline shifts of the two hemispheres (Walter, Cooper, Aldridge, McCallum, & Winter, 1964; Hillyard, 1973); however, Fig. 1 demonstrates that this was not a prerequisite for the appearance of asymmetries to the words. At this time we can hypothesize only that the pattern of hemispheric differences observed in this task reflects aspects of lateralized hemispheric processing during the identification of words. On the basis of the behavioral data and results from previous clinical studies we may propose further that this organization includes a specialized role for the left hemisphere which, in this situation, was reflected in the greater left-hemisphere negativity of several ERP components.

To test this proposal further we recorded ERPs from four subjects (two of these subjects had previously participated in the study with words) on a version of this task in which all stimulus parameters and response requirements were similar, but in place of words, vertical strings of nonalphabetic symbols were randomly presented to the LVF, RVF, or bilaterally. Subjects indicated in writing whether all four symbols in a string were the same or different. The ERPs to the symbols are shown in Figs. 8 and 9 (averaged over all subjects). The N200 from the occipital regions displayed a contralateral dominance as for the word presentations. However, the N300 (prominent in the left hemisphere when words were presented to the RVF) was not observed (see Fig. 8). Moreover, as seen in Fig. 9, at the anterior electrodes the region from 300–500 msec was symmetrical for nonalphabetic strings presented to each visual field, in marked contrast to the results with words.

While these data further substantiate the hypothesis that the ERP asymmetries to the words reflected cerebral specializations related to reading, the precise functional significance of the different asymmetries is obscure. Both clinical and theoretical considerations suggest that reading involves a number of separable processes. These have been hypothesized to include the discrimination and identification of visual form (i.e., letters, or ''graphemes''), the conversion of visual information to auditory representation (''grapheme to phoneme conversion'') and the synthesis of individual components (letters) into a symbolic unit (word) that conveys meaning. Clinical studies have documented the selective disruption

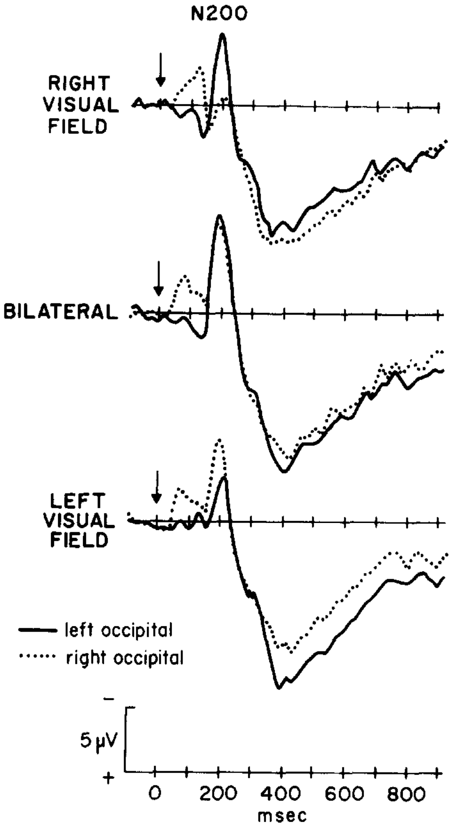

FIG. 8. A comparison of the grand mean ERPs recorded over the left (solid line) and right (dotted line) *occipital* regions to the presentation of *nonalphabetic* symbols (e.g., =, −) to the right, left, and bilateral visual fields.

of these aspects of reading after lesions of the left hemisphere (Heilman & Valenstein, 1979). While anatomical correlations for these processes within the left hemisphere are not well established, lesions to the left occipital, parietal, temporal, and frontal areas have been implicated in these varieties of alexia.

As speculative as we must be at this time, the N160 and N410 over the left temporal regions are possible indices of subprocesses in reading. Since N160 amplitude did not vary systematically with visual field of presentation, the standing, left greater than right, asymmetry of this relatively early component may reflect attentional priming of the left hemisphere such as has been postulated to underlie the behavioral asymmetries observed in this kind of task (Kinsbourne, 1970, 1975). The N410 also appears as a good candidate process related to reading since the degree of asymmetry of its amplitude varied systematically with subjects' performance.

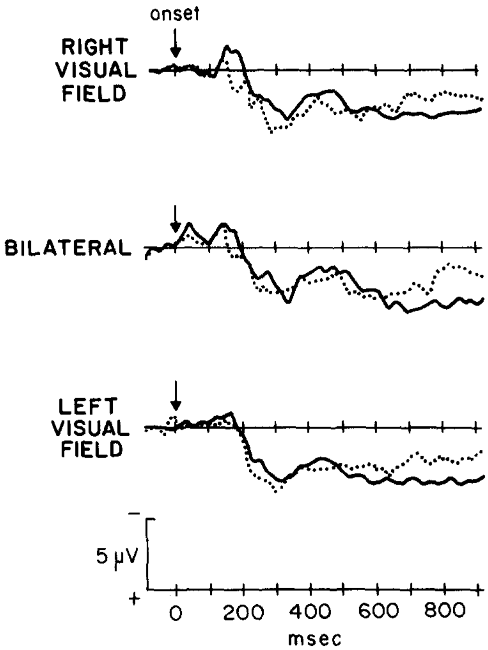

FIG. 9. A comparison of the grand mean ERPs recorded over the left (solid line) and right (dotted line) *anterior temporal* regions during the presentation of *nonalphabetic* symbols to the right, left, and bilateral visual fields.

This N410 is probably not equivalent to either similarly named components in children (Neville, 1977) or to the N400 obtained in response to semantically inappropriate words at the end of a sentence (Kutas & Hillyard, 1980b). Since the amplitude of the latter was largest from central and parietal sites (while the N410 was largest anteriorly) and was recorded primarily to incongruous words (while the N410 appeared to all words), it is likely that different neural systems underlie the two components.

In contrast to these results, the occipital N200 component demonstrated asymmetries which were consistent with the known anatomy of the visual system, being larger over the hemisphere contralateral to the visual field of word presentation. The amplitude of the P450 and subsequent positive shift at the occipital regions, however, was larger over the hemisphere ipsilateral to unilateral word presentations. Although the P450 is similar in some respects to the P300 component elicited by infrequent, unexpected stimuli (for review, see Donchin, Ritter, & McCallum, 1978), it has generally been reported to be bilaterally symmetric (for review, see Hillyard & Woods, 1979). Perhaps P450 amplitude in this situation reflects a "surprise" reaction lateralized to the contralateral hemisphere on those relatively rare (33%) occasions when a word is not present in a visual field. This could be tested by presenting words in a predictable sequence, e.g., in blocks of right visual field, left visual field, or bilateral presentations.

Clearly, further research is required to relate the distinct components observed in this study to specific aspects of reading. Potentially informative approaches to these questions include the study of individuals with specific acquired or developmental reading deficits. For example, the study of patients with alexia without agraphia, who demonstrate a marked and isolated deficit in reading secondary to a localized brain lesion (Dejerine, 1892), should provide information as to the neural origins and functional significance of reading-related ERP components. Indeed, in an early study along these lines, we observed very reliable alterations in the N100 and P300 components elicited by words in such patients (Neville et al., 1978; Neville, 1980).

The study of people who have learned to read with different strategies also may contribute to these and other issues. For example, we have employed the paradigm reported here to study cerebral organization in congenitally deaf adults who by all indications do not perform a phonological conversion on the individual letters in written words (see companion paper, Neville et al.).

In summary, the results from this study demonstrate that in this paradigm which demanded specialized language processing, ERPs were sensitive to aspects of cerebral organization both within and between the two hemispheres. Therefore, this approach to the study of brain–behavior relations promises to contribute to investigations of the development of cerebral organization underlying language, and to the study of the processes underlying the recovery of language after brain damage.

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