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PROCESSING OF SEMANTIC ANOMALY BY RIGHT AND LEFT HEMISPHERES OF COMMISSURОТОMY PATIENTS

EVIDENCE FROM EVENT-RELATED BRAIN POTENTIALS

by MARTA KUTAS, STEVEN A. HILLYARD *and* MICHAEL S. GAZZANIGA

(*From the Department of Neurosciences, University of California, San Diego, California, and the Division of Cognitive Neuroscience, Department of Neurology, Cornell Medical Center, New York, USA*)

SUMMARY

The ability of 5 commissurotomized patients to appreciate semantic anomalies presented to their right and left hemispheres was tested using both electrophysiological and behavioural measures. In all cases, the patients heard sentence fragments that were completed either by semantically congruous or incongruous words briefly flashed to the left visual field, right visual field or to both fields simultaneously. A dissociation between behavioural and event-related brain potential (ERP) measures was observed. All 5 patients were able to indicate by a pointing response with greater than chance accuracy whether the terminal word of a sentence made sense (i.e., appropriate for the context) or was nonsensical. This was true regardless of the hemisphere receiving the terminal word. Likewise, all the patients responded to right visual field anomalies with a cerebral potential (N400) that was typically elicited by such words in control subjects. In contrast, only those 2 patients who developed an overt speech capability under the control of the right hemisphere produced N400 waves in response to left visual field anomalies. These findings were interpreted as suggesting possible relationships within language generation and semantic priming.

INTRODUCTION

In recent years there have been extensive neuropsychological and electrophysiological investigations of the brain processes subserving language comprehension and production (*see* Kertesz, 1979; Ojemann, 1983; Patterson *et al.*, 1985; Kutas and Van Petten, 1988). Many of these studies have been aimed at further delineating the respective contributions of the two cerebral hemispheres in speech and linguistic analyses. At the core of the neuropsychological approach has been the assessment of linguistic abilities and deficiencies of each of the cerebral hemispheres in persons with abnormal brain organization. Among the various types of patients that have been studied are those with discrete lesions in one of

Correspondence to: Dr Marta Kutas, Department of Neurosciences, M-008, University of California, San Diego, California 92093, USA.

the hemispheres, an entire hemisphere removed surgically, unilateral hemisphere anaesthesia with sodium amylobarbital, and surgical or congenital disconnection of the left and right cerebral hemispheres.

The neuropsychological evidence demonstrates that most language functions are asymmetrically distributed, with the left cerebral hemisphere bearing the greater share of the processing load. Assuming no early brain damage, the left hemisphere of most individuals appears to subserve both speech and language comprehension in written, oral and gestural form. The contribution of the right hemisphere during normal language processing, for other than the prosodic and pragmatic aspects of language processing, is controversial. The positions taken range from those in which the right hemisphere plays little or no role in normal language processing (Rasmussen and Milner, 1977; Gazzaniga, 1983), to those that suggest its contribution to semantic analysis may parallel that of the left hemisphere (*see* Zaidel, 1981, 1985; Lambert, 1982*a*, *b*, 1983; Patterson and Besner, 1984; Curtiss, 1985). Whatever the case may be, studies of right hemisphere language functions have reinforced the idea that 'language' is not a unitary phenomenon and that it is necessary to define the respective roles of the cerebral hemispheres in mediating different aspects of language (e.g., Coltheart *et al.*, 1980).

The lateralization of language processes has been investigated using a variety of techniques. In particular, experiments with split-brain individuals have allowed detailed comparisons of the language functions in the surgically separated hemispheres (*see* Gazzaniga, 1970; Sperry, 1974; Gazzaniga and LeDoux, 1978; Benson and Zaidel, 1985). In the national population of split-brain patients in the USA who have been extensively examined for right hemisphere language, 5 are of particular interest (Gazzaniga, 1983). While there is good evidence that the right hemispheres of all 5 of these patients can comprehend spoken and written language with some facility, it has proved difficult to establish the extent to which the operating principles of comprehension in the right hemispheres of the different cases are similar to one another or to those of their left hemispheres. A particularly vexing problem has been to compare semantic processing in the right hemispheres of the different patients when only the left was capable of verbal report. While some ingenious experimental techniques for tapping into the mute right hemispheres have been developed, indices of comprehension based on pointing and matching behaviours may not always reveal qualitative differences in the underlying operations.

Another approach towards assessing right hemisphere language is to supplement behavioural observations with electrophysiological recordings of the synchronized brain activity elicited across the scalp by words in a written or spoken message (for review, *see* Rugg *et al.*, 1986). These responses, known as event-related brain potentials (ERPs) are useful in that they allow on-line monitoring of brain activity during linguistic processing, whether or not the person responds overtly to the stimulus material. Of the available ERP measures, we chose a component that is elicited reliably during the processing of semantically incongruous or unexpected words in a sentence context; this negative wave, termed N400, is triggered by words that deviate from an established semantic context and shows a maximum amplitude at around 400 ms after word onset (e.g., Kutas and Hillyard, 1984; Neville *et al.*, 1986). For example, a nonsensical word at the end of a sentence ('Every Saturday morning he mows the *chair*') elicits an N400 that is not seen in the ERP elicited by a more predictable word such as 'lawn' at the end of this same sentence. The N400 appears to be a general response to semantic incongruity, regardless of the input modality, since it can be elicited by spoken and printed words as well as the signs of American Sign Language (Neville, 1985; Kutas *et al.*, 1987). In so far as it has been tested, the N400 seems to be elicited specifically by semantic rather than grammatical or physical incongruities within prose (Kutas and Hillyard, 1980*b*, 1983; McCallum *et al.*, 1984).

Whereas the largest N400s are elicited by semantic anomalies, words that are not anomalous also elicit N400s with an amplitude that corresponds to their unexpectedness or unpredictability within a given context (e.g., Fischler *et al.*, 1983, 1984; Harbin *et al.*, 1984; Kutas and Hillyard, 1984; Kutas *et al.*, 1984). Thus while some uncertainty exists as to the exact nature of the semantic analyses indexed by the N400, such findings have led to the proposition that N400 amplitude is an inverse function of the amount of semantic priming (or degree of semantic constraint) that a word has received from a preceding context (Kutas and Hillyard, 1984; Bentin *et al.*, 1985). According to this view, this ERP marker may well be tracking one of the more automatic language processes that are presumed to occur during semantic processing. Whether or not this conception of the N400 proves to be wholly correct, it is clear that the elicitation of large N400s by anomalous or unpredictable words reflects a fairly high level of semantic processing, namely, an ability to appreciate the semantic relationship between a word and the verbal context within which it occurs.

By examining the N400 wave in split-brain patients who differ in their right hemisphere language capacities, we hope to elucidate further the language function(s) that must be present in order for this ERP response to occur and thereby learn more about the nature of the processing events that underly the N400. Moreover, by presenting words separately to the left and right hemispheres and by recording the ERPs indicative of the semantic analyses initiated in each hemisphere, we can evaluate whether the separated right hemispheres of split-brain patients carry out the semantic analyses reflected in the N400 in the same manner as do their left hemispheres. An affirmative answer would argue for a qualitative similarity between the semantic systems of the right and left cerebral hemispheres.

METHODS

Control subjects

Nine normal young adults (5 male, age range 18-32 yrs) were paid for participating in this experiment. All of the subjects were right-handed according to self-report and the Edinburgh

Inventory (Oldfield, 1971). Only 1 of these subjects had a member of their immediate family who was left-handed.

Commissurotomized patients

The case histories of the 5 split-brain patients are summarized below (for further details, *see* Gazzaniga *et al.*, 1984*a*).

Case 1. P.S. is a right-handed male, 20 yrs of age at the time of testing (Wilson *et al.*, 1977). He experienced a series of right-sided motor seizures at 20 months of age. He was without seizures until aged 4 yrs, when he experienced 'absences' about twice a month. At the age of 10, he began to have right-sided partial seizures and was found to have an abnormal EEG over the left hemisphere; seizures recurred over the next 5 yrs and proved intractable. At aged 15, he underwent complete surgical section of the corpus callosum. Since his operation, he has remained largely free of seizures. Magnetic resonance imaging (MRI) showed the callosum to be fully sectioned with no evidence of other brain damage.

Case 2. V.P. is a right-handed female (27-yrs-old when tested) who had experienced recurrent seizures starting at 9 yrs of age (Sidtis *et al.*, 1981). Anticonvulsant drugs controlled the seizures until the age of 27 yrs, when she began experiencing grand mal, petit mal and myoclonic episodes while on multiple anticonvulsants. That year she underwent partial anterior callosal section at the Medical College of Ohio; the resection of her corpus callosum was completed in a second operation 7 wks later. She was tested 6 months after this second operation. MRI has since revealed sparing of a few fibres both in the rostrum and splenium (Gazzaniga *et al.*, 1984).

Case 3. J.W. is an alert right-handed male (26-yrs-old when tested) with a history of staring spells, reportedly since the age of 13 yrs (Sidtis *et al.*, 1981). After his first major motor seizure at 19 yrs of age, frequency of the seizures increased and they became intractable (Wilson *et al.*, 1982). Midline section of the corpus callosum was performed in two stages by Dr Donald Wilson of the Dartmouth Medical School at the age of 25 yrs. The posterior half of the corpus callosum, including the splenium, was sectioned first, with the remaining anterior portion sectioned in a second operation 10 wks later. MRI has verified complete callosal sectioning.

Case 4. N.G. is a right-handed woman who was tested at the age of 47 yrs. She had a left temporal EEG focus and evidence for a right central lesion in the form of rolandic calcification 1 cm wide, as well as left-sided numbness preceding some of her preoperative convulsions. As a result of intractable epilepsy that began when the patient was 18 yrs of age, a single stage complete cerebral commissurotomy (including the anterior commissure, corpus callosum, massa intermedia and right fornix) was performed at 30 yrs of age. The operation was performed by Drs P. J. Vogel and J. Bogen at the White Memorial Medical Center in Los Angeles (Bogen *et al.*, 1965).

Case 5. L.B., a right-handed male, 28-yrs-old at testing, had demonstrated generalized EEG abnormalities. His epilepsy began at $3\frac{1}{2}$ yrs of age. Surgery was performed by Dr Vogel and his colleagues at age 13 yrs. The approach for the complete single-stage commissurotomy was, as with Case 4, by retraction of the right hemisphere.

Procedure

All experiments were conducted with the informed consent of the subjects and patients.

During all runs, subjects sat in a reclining chair in an unshielded experimental room. At the start of each trial block they were asked to fixate a dot in the centre of either (1) a translucent screen on which visual stimuli (terminal words of sentences) were back-projected from a slide projector, or (2) a video monitor on which the words were flashed under the control of a microcomputer.

Each of the split-brain subjects and the 9 control subjects were presented with 319 seven-word sentences in 16 blocks of 20 each, following a block of 20 practice trials. A warning tone preceded each sentence by approximately 1 s. The first 6 words of each sentence were presented auditorily (binaurally), through headphones, at interword intervals of about 600 ms. Each sentence was completed by a 180 ms duration flash of a pair of words, one in each visual field. The words

TABLE 1. EXAMPLES OF INCOMPLETE SENTENCES AND WORDS PRESENTED FOR COMPLETION TO THE LEFT AND RIGHT VISUAL FIELDS

	Visual terminal words	
Auditory phrase	*LVF*	*RVF*
1. The mechanic decided to join a	union	union
2. She ran the mile in four	candies	minutes
3. The two suspects were arrested for	murder	cereal
4. He towed the car from the	juice	juice

LVF = left visual field; RVF = right visual field.

averaged 5.16 letters in length and were 1.2° high. The medial aspect of each word was situated 1.5° lateral to the fixation point. Maintenance of fixation was monitored by the horizontal electroculogram (EOG).

For 204 of the sentences, the words in the two visual fields were identical to one another and were congruous with the preceding auditory context. The remaining 115 sentences were completed by word pairs in which the word in the left visual field (LVF, N = 38), right visual field (RVF, N = 39) or both fields (N = 38) was semantically inappropriate to the preceding context. A congruous word of equal length was shown in the opposite field for each of the unilateral incongruous words. Examples of the four sentence types are given in Table 1. The 2 obvious choices for visual completion of these sentences were to present a single word randomly in either the right or the left visual field (i.e., unilaterally) or to present 2 words simultaneously in each field (i.e., bilaterally). For the present experiment, we decided to complete the auditory sentence fragments with bilateral word presentations for several reasons. First, experience has shown that control subjects and patients alike are much less prone to make disruptive horizontal eye movements when they are required to read 2 words, one in each visual field, at the same time (especially for exposure durations of less than 200 ms). Secondly, since each sentence frame was presented auditorily (binaurally) we assumed that each hemisphere was awaiting a visual completion. By providing a completion for both hemispheres, we hoped to reduce the effect of ERP components known to be associated with the surprise at receiving nothing (Renault, 1983) and to increase our control of the stimuli that each hemisphere received. In future work, we also plan to evaluate ERP changes with unilateral visual presentations.

After each block of 20 trials during the ERP recording session, the subject was asked to recall by verbal report the terminal words of several of the sentences they had just received. Control subjects were tested for recall on all of the sentences. In this delayed recall task, the experimenter read the first 6 words of the sentence, and the patient was asked to report the word or words they remembered as having completed that sentence. Since the commissurotomized patients had a tendency to report a congruent ending regardless of the word actually presented, they were given occasional reminders that some of the sentences were terminated by nonsensical words. In addition, for a few of the sentences chosen at random, the patients' word recognition was probed by asking them to write the word they had seen (presumably the one presented in the left visual field), on a piece of paper with their left hand. These tasks served to keep the subject attentive to the stimuli and provided further information about how well the visually presented words were being perceived.

In addition, in separate sessions without ERP recordings, the split-brain subjects were presented a series of unilateral words flashed for 180 ms to the left or right visual fields at random. Their task was to name the word seen as quickly as possible. Common words, 3–5 letters in length, were flashed with the medial aspect located 1.5° from the fixation point. This task was aimed at testing for the possibility of expressive speech under the control of the right hemisphere (as would be evidenced by the ability to name left-field words).

Also in a separate session, the ability of the split-brain subjects to appreciate semantic anomalies with the right and left cerebral hemispheres separately was tested. The subjects were presented with a series of sentences one at a time. All but the final word of each sentence was presented auditorily. The final word was flashed unilaterally for a duration of 180 ms randomly either to the right or the left visual field. The subjects' task was to point to the word SENSE or NONSENSE written on a card in their lap, depending upon whether or not the flashed word made sense as a completion to the preceding sentence fragment. Half the sentences were semantically congruous and half were semantically anomalous. Of the anomalous sentences, half were completed by a word semantically related to the expected completion for that sentence whereas the other half were completed by a word that was semantically unrelated to any word in the sentence.

Our primary aim with this behavioural test was to find out whether each hemisphere could determine, in isolation, whether sentences did or did not make sense. Experience with bilateral stimulation (a sensible word in one field and a nonsensical one in the other) indicated that the patients found making an overt judgement (e.g., pointing or verbal report) under such conflicting conditions to be difficult and disturbing. The emotionality observed under bilateral conditions was not observed during the ERP recordings when the subjects' task was only to read for comprehension and subsequent recognition or recall. Also, with a pointing response under bilateral conditions, it was impossible to determine which hemisphere was controlling the response. Since neither horizontal eye movements after 180 ms nor the surprise of the unstimulated hemisphere posed any problem for interpretation of these behavioural results, we decided to probe the comprehension of each hemisphere's ability by completing the auditory sentence fragments with random unilateral visual presentation.

Recording system

For the patients, the EEG was recorded from 6 electrodes, each referred to linked mastoid electrodes, placed according to the International 10-20 convention (Jasper, 1958) at central (C3, Cz, C4) and parietal (P3, Pz, P4) midline and lateral locations. For the control subjects, the EEG was recorded from 14 electrodes, each referred to the left mastoid, placed at frontal (Fz, F7, F8), central (Cz, C3, C4), temporal (T5, T6), parietal (Pz, P3, P4), occipital (O1, O2) and the right mastoid (A2) locations. Nonpolarizable Ag-AgCl electrodes were secured to the subject's scalp with collodion. Electrode impedances did not exceed 2 kΩ. Eye movements and blinks were monitored via an electrode placed on the lower orbital ridge, referred to linked mastoid electrodes in the patients and to the left mastoid electrode in the controls. In addition, a bipolar right external canthus to left external canthus montage (horizontal EOG) was used to record lateral eye movements. Midline and horizontal EOG channels were recorded with d.c. preamplifiers (high frequency cut-off 40 Hz), and lateral channels with an 8 s time constant (high frequency cut-off 100 Hz).

RESULTS

Control subjects

Behavioural performance

The control subjects' performance data (mean percentage correct and SD) on the delayed recall of sentence completions are presented in Table 2. In general, terminal words were better recalled if they were congruous than if they were incongruous. In addition, more endings (whether congruous or incongruous) were recalled (by about 15%) if the same word had been presented in each visual field than if 2 different words were shown. There was no interaction between visual field and congruity in determining recall accuracy.

TABLE 2. CONTROL SUBJECTS: PERCENTAGE CORRECT FOR CUED RECALL OF SENTENCE TERMINAL WORDS PRESENTED TO LEFT (LVF) AND RIGHT VISUAL FIELD (RVF). MEANS (±SD)

Terminal word pair RVF/LVF	*LVF*	*RVF*
Cong./Cong.	93.5 (0.1)	93.5 (0.1)
Cong./Anom.	77.4 (13.7)	37.4 (25.0)
Anom./Cong.	34.7 (21.8)	74.0 (15.2)
Anom./Anom.	52.2 (18.0)	52.2 (18.0)

ERP findings

The grand average ERPs (n = 8) recorded from the central electrode locations in response to the visually presented terminal words of the sentences are shown in fig. 1. One subject's data were not included because of excessive artifact. In each column, the ERPs elicited by bilaterally congruous endings are compared with the ERPs elicited by unilateral or bilateral incongruous endings, with the incongruity presented either in the right, left or both visual fields, respectively. In all cases the ERP waveform was dominated by a broad positive (downward)

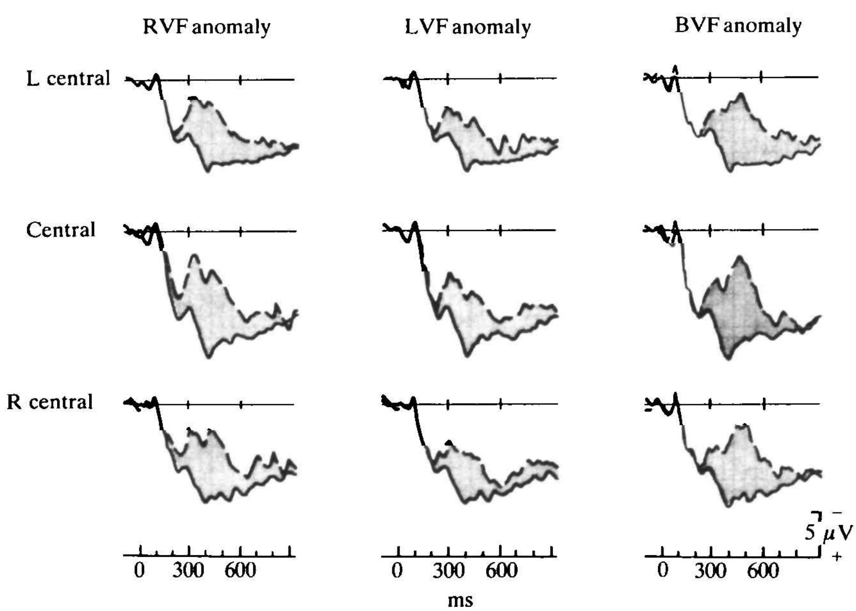

FIG. 1. Grand average ERPs from control subjects (n = 8) elicited by sentence terminal words from midline (central, Cz), left central (C3) and right central (C4) scalp locations. In each column the response to bilateral congruous endings (solid tracings) is compared with the response to the indicated type of anomalous ending. The anomalous endings also consisted of a bilateral word pair with the word in either one (LVF or RVF) or both (BVF) visual fields being semantically anomalous relative to the preceding sentence context. In this and all subsequent figures negativity is plotted upwards. Continuous line = congruous; broken line = semantically anomalous.

deflection that represents, in part, the termination of the sustained negativity (Contingent Negative Variation) that develops during sequential word presentations (e.g., Kutas and Hillyard, 1980*a*, *b*). For congruous endings, this late positivity peaked at around 380 ms at the centroparietal sites where it was the largest.

The late positive complex appeared to be composed of early (300-600 ms) and late (600-900 ms) subcomponents having different scalp distributions. Both the early and the late phases were most positive at the vertex site. For the early phase, the potential at the remaining sites expressed as a percentage of maximum amplitude, was as follows: Fz (65), Pz (92), L frontal (33), R frontal (43), L central (77), R central (85), L temporal (29), R temporal (36), L parietal (61), R parietal (69), L occipital (29) and R occipital (38). The amplitude of the later phase fell off more rapidly towards the back of the head than did the earlier positivity. The late phase potential expressed as a percentage of maximum amplitude was as follows: Fz (71), Pz (70), L frontal (50), R frontal (52), L central (79), R central (80), L temporal (17), R temporal (12), L parietal (47), R parietal (48), L occipital (8) and R occipital (9).

The ERPs elicited by incongruous endings included a broadly distributed negativity between 250 and 600 ms (i.e., the 'N400 effect') superimposed on the late positive deflection. The N400 effect (fig. 1, shaded area) began at a latency of around 200 ms, peaked between 400 and 450 ms and lasted for 300 to 400 ms. The amplitude of the N400 effect was quantified from the 'difference waves' formed by subtracting the ERPs to the congruous endings from those to the anomalous endings (Table 3). These data were analysed by repeated measures ANOVA, with factors of visual field of anomaly (left, right, both) and electrode site (13 levels). These analyses employed the Greenhouse-Geisser correction for inhomogeneity of covariance (Keselman and Rogan, 1980).

On the whole, the amplitude, latency and scalp distribution of the N400 effect in the control subjects was similar whether the anomalous word was presented to the right or left visual field (*see* Table 3). The slight tendency for the N400 to be larger in response to anomalies in the right visual field was not statistically significant. Likewise, while there was a slight tendency for the difference wave to begin earlier (between 100-200 ms) following right than left visual field anomalies at the frontocentral sites, this was not statistically significant; it is possible that with many more trials this difference would have proven real. In contrast, the peak amplitude of the N400 difference wave following bilateral anomalies was significantly larger than that following either of the single visual field anomalies (peak amplitude between 300-600 ms relative to 100 ms prestimulus baseline, $F(2, 14) = 5.37$, $P < 0.024$, epsilon = 0.61; mean amplitude 300-600 ms, $F(2, 14) = 5.43$, $P < 0.048$, epsilon = 0.76). There was also a slight tendency for the N400 difference wave in association with bilateral anomalies to peak somewhat later (427 ms at Cz) and to be more prolonged than that to either right visual field (403 ms) or left visual field (391 ms) anomalies.

TABLE 3. CONTROL SUBJECTS: PEAK AMPLITUDE OF N400 DIFFERENCE WAVE* IN μV (SE) OVER THE RANGE 300-600 ms POSTSTIMULUS

	Anomalous word in:		
Electrode site	*RVF*	*LVF*	*Both VF*
Frontal	−9.57 (1.13)	−7.33 (0.60)	−8.95 (0.97)
Central	−10.90 (1.58)	−8.28 (0.55)	−11.75 (1.13)
Parietal	−9.12 (1.35)	−7.82 (0.85)	−11.10 (1.28)
L frontal	−5.51 (0.73)	−4.45 (0.29)	−5.15 (0.77)
R frontal	−6.81 (1.12)	−5.80 (1.04)	−6.57 (1.03)
L central	−9.19 (1.21)	−7.39 (0.66)	−10.55 (1.09)
R central	−9.67 (1.22)	−7.73 (0.89)	−10.79 (1.15)
L temporal	−4.85 (0.80)	−4.05 (0.74)	−6.82 (0.94)
R temporal	−6.42 (0.67)	−5.27 (0.74)	−7.44 (1.19)
L parietal	−7.91 (1.00)	−7.03 (1.16)	−9.54 (1.22)
R parietal	−8.37 (0.84)	−7.23 (1.06)	−9.62 (1.16)
L occipital	−5.81 (0.44)	−5.11 (0.96)	−7.52 (0.92)
R occipital	−6.09 (0.73)	−6.02 (1.05)	−7.40 (1.07)

* Difference waves calculated by subtracting the ERPs to the bilateral congruous endings from those to the indicated type of anomalous ending. Peak amplitude is relative to 100 ms prestimulus baseline.

Split-brain subjects

ERP findings

Substantial N400 waves were elicited in all the split-brain patients by word pairs when the right visual field contained an anomalous word (*see* figs 2, 3). Thus when the language dominant hemisphere saw the anomaly, an N400 of near normal amplitude but of somewhat prolonged latency was elicited (Table 4). In contrast, the patients varied considerably in the amplitude of the N400 elicited by left visual field anomalies. To illustrate these differences, the ERPs were averaged separately for the 2 subjects (Cases 1, 2) who showed sizeable N400s to left field anomalies (fig. 2) and for the 3 subjects (Cases 3-5) who showed much smaller N400s for anomalies flashed to the right hemisphere (fig. 3). The N400 difference waves for Cases 1 and 2 (fig. 4, middle traces) show the N400 effect to be of relatively similar amplitude for left and right visual field anomalies and slightly larger over the right than the left hemisphere at the central and parietal scalp sites; this lateral asymmetry did not differ according to the visual field in which the triggering anomalous word was presented. For the other 3 patients (fig. 4, lower traces), the N400 was also slightly larger over the right hemisphere for right field anomalies, whereas its amplitude was near noise levels for left field anomalies.

Although statistical analyses of data from so few subjects are lacking in power, the difference between the two groups of patients was verified by testing whether the N400 (area measure 300-600 ms at the P4 electrode site) elicited by the right and by the left field anomalies was significantly greater than zero. This was true

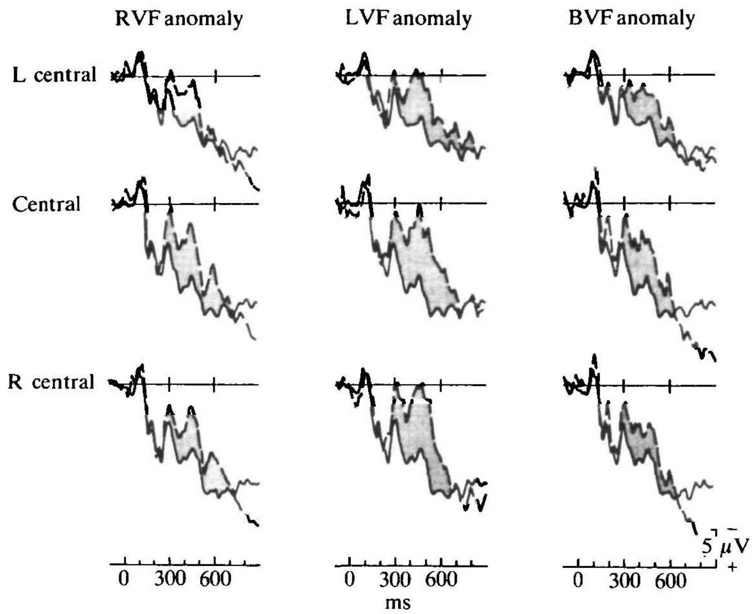

FIG. 2. Comparison of ERPs recorded at central scalp locations following semantically congruous and anomalous sentence endings. ERPs are averaged across commissurotomized *Cases 1 and 2* (P.S. and V.P.), who showed a similarly enlarged late negativity (shaded areas) to semantic anomalies presented to the left visual field. Continuous line = congruous; broken line = semantically anomalous.

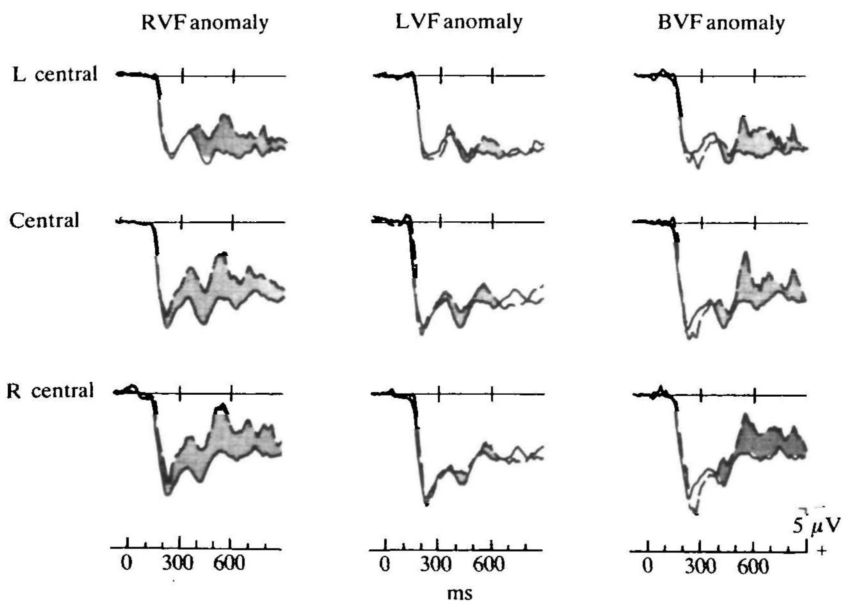

FIG. 3. Comparison of ERPs recorded at central scalp locations following semantically congruous and anomalous sentence endings. ERPs are averaged across commissurotomized *Cases 3-5* (J.W., L.B. and N.G.), who showed a similarly reduced late negativity (shaded areas) to semantically anomalous endings presented in the left visual field. This pattern was distinct from that shown by *Cases 1 and 2* (P.S. and V.P.). Continuous line = congruous; broken line = semantically anomalous.

TABLE 4. MEAN AMPLITUDE* OF N400 DIFFERENCE WAVE AT DIFFERENT ELECTRODE SITES FOR SEMANTIC ANOMALIES IN RIGHT, LEFT AND BOTH VISUAL FIELDS

	Semantic anomaly in		
	RVF	*LVF*	*Both VF*
Control Ss (n = 8)			
Cz	−6.05 (1.25)	−4.11 (0.37)	−6.94 (1.02)
Pz	−4.40 (1.53)	−3.43 (0.57)	−6.64 (1.16)
C3	−5.11 (0.69)	−3.66 (0.49)	−5.88 (0.64)
C4	−5.35 (1.11)	−3.62 (0.71)	−6.33 (0.98)
P3	−3.71 (0.93)	−2.98 (0.95)	−5.51 (0.78)
P4	−3.80 (1.08)	−2.87 (0.46)	−5.78 (1.02)
Commissurotomized patients (Cases 1, 2)			
Cz	−5.27 (0.69)	−7.24 (2.23)	−4.97 (1.96)
Pz	−4.66 (1.61)	−4.27 (1.20)	−4.70 (1.86)
C3	−2.88 (1.70)	−4.50 (2.97)	−3.27 (2.02)
C4	−3.90 (1.80)	−7.24 (2.39)	−3.51 (1.62)
P3	−3.92 (0.87)	−4.13 (0.98)	−2.97 (1.70)
P4	−5.62 (1.12)	−5.04 (1.05)	−4.06 (3.21)
Commissurotomized patients (Cases 3–5)			
Cz	−4.17 (0.36)	−1.45 (0.89)	−1.82 (2.08)
Pz	−4.73 (1.11)	−1.20 (1.00)	−2.86 (1.71)
C3	−2.24 (0.56)	−0.81 (0.70)	−1.14 (0.66)
C4	−4.03 (1.11)	−0.52 (1.15)	−1.66 (2.29)
P3	−2.62 (0.59)	−1.31 (0.96)	−1.97 (0.84)
P4	−4.11 (0.39)	−0.75 (1.06)	−2.19 (1.30)

* N400 amplitude measured as mean voltage in μV (SE) in difference waves over the interval 300–600 ms poststimulus relative to 100 ms prestimulus baseline.

for Cases 1 and 2 for both right ($t(1) = 27.0$, $P < 0.02$) and left ($t(1) = 45.8$, $P < 0.01$) field anomalies; for Cases 3–5, however, the N400 was significant for right ($t(2) = 10.56$, $P < 0.01$) but not for left ($t(2) = 0.71$, n.s.) field anomalies. Calculated a different way, the parietal N400 amplitude for Cases 1 and 2 did not differ significantly between right and left field presentations (−5.62 versus −5.04 μV), whereas for Cases 3–5 this difference (−4.12 versus −0.75 μV) was significant ($t(2) = 4.79$, $P < 0.05$). The N400 difference waves for left and right field anomalies are shown individually for each of the subjects in fig. 5.

As previously noted, for the control subjects the bilateral anomalies elicited N400 amplitudes that were larger and somewhat later than either single field anomalies. Among the patients, Cases 2 and 5 showed a pattern similar to the controls. The remaining patients generated either a very small N400 apparently overlapped by a large late positivity (Case 1), a very late response between 500 and 900 ms (Case 3) or none at all (Case 4) in response to bilateral anomalies. Because of the lack of N400 in Case 4, the ERP averaged over the second group of split-brain subjects (fig. 3) shows the bilateral anomalies to elicit smaller N400 amplitudes than the right field anomalies. In no group did the amplitude of the N400 to bilateral anomalies approach the sum of the 2 unilateral responses; such a result would have suggested that the stimuli in the 2 fields activated wholly independent cerebral systems.

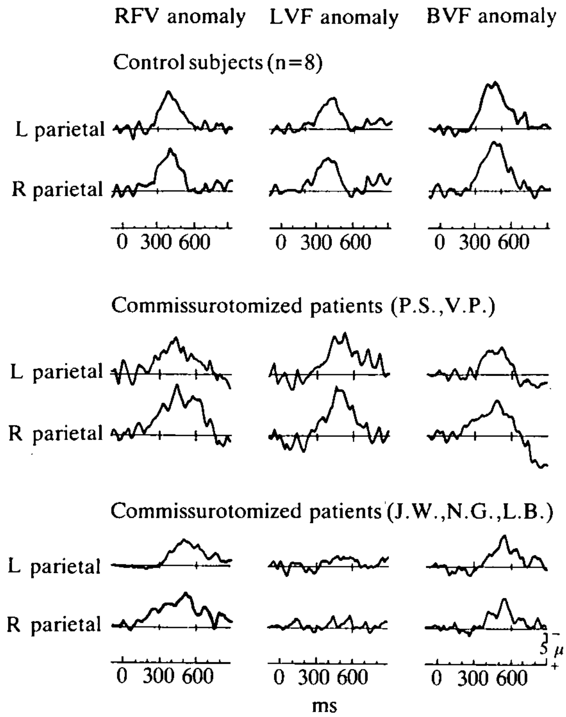

FIG. 4. Grand average difference waveforms for control subjects, for *Cases 1 and 2* (P.S. and V.P.), and for *Cases 3-5* (J.W., N.G. and L.B.). In each case the difference wave represents a point-by-point subtraction of the ERP elicited by bilaterally congruous endings from the ERP to the indicated type of anomalous ending.

Behavioural observations

In the tests where unilateral words were flashed and immediate verbal responses were given, all split-brain subjects accurately reported more than 75% of the words that were flashed in the right visual field. The errors made were reports of visually similar words or word fragments, as would be expected with brief visual presentations. Case 1 was unique, however, in also being able to name immediately the word flashed to the left visual field on over 80% of the trials. This is consistent with previously reported observations on this subject during this period (Gazzaniga *et al.*, 1979). Case 5 reported verbally the left field word correctly about half the time (7/16 trials), but he only did so after a response delay of 10–15 s, suggestive of a cross-cueing strategy (*see* Discussion). Cases 2, 3 and 4 were unable to name the words flashed to the left visual field.

During the ERP recording runs when subjects were questioned about a few of the terminal words they had seen after each block of 20 sentences, there was a

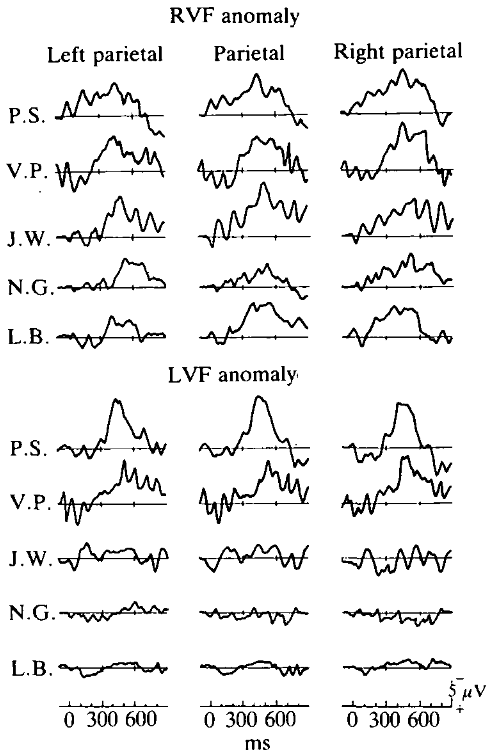

FIG. 5. Difference waves (anomalous minus congruous) for each of the commissurotomized patients obtained from recordings taken over midline (Pz), left parietal (P3) and right parietal (P4) scalp. The upper and lower halves of the figure show responses to semantically anomalous endings presented in the right and left visual field, respectively.

strong tendency to report the most probable and expected terminal word for a given sentence frame, even when an anomalous word had actually been presented. For example, when the sentence frame 'We want to buy a new microwave . . .' was read to the subjects in the delayed recall task, the majority responded they had seen 'oven', even though 'road' had actually been presented in both visual fields. This illustrates the difficulty the patients had in remembering the anomalous endings over a number of intervening sentences together with the strength of context in provoking a congruous response. Thus the subjects reported the congruous words presented to the right visual field with a mean accuracy of 88% correct (range 78-96%), whereas only 22% (range 13-32%) of the incongruous words shown to the right field were reported correctly. Erroneous congruous responses were given on 61% of the trials with right field anomalies, and failures to respond occurred on 16%. The fact that subjects were as accurate as 13 to 32% in this difficult memory test, however, does indicate that they were generally attentive to the stimuli.

Except for Case 1, there was not a single instance in this recall test of a subject reporting verbally an incongruous word that had been delivered only to the left visual field (i.e., when the right field word was congruous). This indicates that the delayed verbal report was completely under the control of the left hemisphere in

Cases 2-5. Case 1 verbally reported incongruous endings correctly 13% of the time for right field presentations and 22% of the time for left field presentations, indicating participation of both hemispheres.

TABLE 5. PERCENTAGE CORRECT OF SENSE/NONSENSE JUDGEMENTS FOR AUDITORY SENTENCES COMPLETED BY UNILATERALLY PRESENTED WORDS

Case	*1*	*2*	*3*	*4*	*5*
LVF	91	80	76	70	75
	(125)	(127)	(129)	(43)	(32)
RVF	75	92	90	87	95
	(131)	(127)	(126)	(45)	(39)

Numbers of trials in parentheses.

All the commissurotomized patients were above chance at indicating by a pointing response whether a word presented to the right or left visual field completed a spoken sentence fragment sensibly or nonsensically. All the patients were significantly ($F(1, 4) = 10.58$, $P < 0.03$) more accurate in judging sense than nonsense (LVF: congruous endings 83% correct, anomalous endings 73%; RVF: congruous 95%, anomalous 79%). Across all subjects judgement accuracy was only slightly worse for semantically related than unrelated anomalies (LVF: related 70%, unrelated 76%; RVF: related 79%, unrelated 80%). With the exception of Case 1, all the patients showed a right visual field advantage (*see* Table 5).

DISCUSSION

The ERP results from this experiment are in line with the view that the language systems of the right cerebral hemisphere are quite variable among split-brain patients (Gazzaniga, 1983). Only 2 of the 5 patients (Cases 1, 2) demonstrated N400 amplitudes in the normal range in response to semantically anomalous words presented to the right hemisphere; in fact, at some electrode sites these N400s were slightly larger than those following anomalous words presented to the patients' left hemispheres. In contrast, all patients showed sizeable N400 waves when the left hemisphere encountered an anomalous sentence ending. Taking the N400 as an index of a language processing capability that is reliably present in the vast majority of normal individuals (Kutas and Hillyard, 1980*a*, 1983), it would appear that this capability is less fully developed in the right hemispheres of Cases 3-5 than in the right hemispheres of Cases 1 and 2 or in the left hemispheres of either patients or controls.

If we assume that similar electrophysiological configurations imply a qualitative similarity of underlying processing mechanisms, it would follow that the right hemispheres of Cases 1 and 2 possess a language analysis system that is similar in kind to that employed by their left hemispheres (and also by normal brains).

Indeed, in these 2 patients the N400 waves were highly similar in morphology (monophasic negativity), amplitude and scalp distribution for right and left visual field anomalies. The extent to which this similarity of their left and right hemisphere processing systems extends to aspects of language other than the subset that is manifested in the N400 is unclear, but it does not appear to hold for all aspects of syntactic processing. Although Cases 1 and 2 have demonstrated more syntactic competence with their right hemispheres than Cases 3–5, the left hemisphere of Case 1 is appreciably more sophisticated in dealing with syntactic constructs than is her right hemisphere (Baynes and Gazzaniga, 1988). It is also unclear whether the lack of N400 in response to right hemisphere anomalies in Cases 3–5 is due to a reduced capacity (i.e., quantitative in nature) or to a qualitatively different language analysis system that does not engender a robust N400 wave. It should also be noted that the N400 latencies were somewhat longer in the patients than in the normal control subjects. This may be a consequence of the patients anticonvulsant medication and/or processing delays associated with their neurological conditions, which in all cases involved chronic epilepsy.

The ERP data reported here are consistent with behavioural studies showing that Cases 1 and 2 possess more highly developed right hemisphere language than do the other patients. Unlike the other 3 patients, they were able from the time of their operation to respond to written commands and to judge whether or not written words rhymed, and they have shown some degree of syntactic competence for material presented to the right hemisphere (Gazzaniga *et al.*, 1984; *see also* Levy and Trevarthen, 1977). Most dramatically, Case 1 showed evidence for overt speech under the control of the right hemisphere, both in the present test of naming words flashed to the left visual field and in previous studies of a similar nature (Gazzaniga *et al.*, 1979). Although Case 2 was not able to name left visual field stimuli at the time of the present experiments, she did show a relatively high degree of 'generative capacity' with respect to written output (Sidtis *et al.*, 1981). Starting about 6 months after our tests, she began to develop an overt right hemisphere speech capability which was fully developed 2 years later (Gazzaniga *et al.*, 1984). Thus, by several criteria, Cases 1 and 2 both have right hemisphere language systems more akin to those of the normal intact brain than any of the other split-brain patients studied.

There is some early (Butler and Norrsell, 1968; Gazzaniga and Hillyard, 1971; Levy *et al.*, 1972) and more recent (Johnson, 1984*a*, *b*; present study) evidence that Case 5 can name letters, numbers and words presented to the left visual field with better than chance accuracy. It is not clear, however, to what extent this capacity represents speech controlled by the right hemisphere as opposed to an unusual degree of interhemisphere transfer of visual information together with elaborate cross-cueing strategies (Gazzaniga and Hillyard, 1971). In any case, there is no evidence that he has developed the ability to give an immediate and accurate vocal response to words flashed in the left visual field, as do Cases 1 and 2 (Gazzaniga *et al.*, 1984). In our tests of his word naming capabilities, we found

Case 5 to be relatively accurate in naming words flashed briefly to left visual field, but his verbal responses were several orders of magnitude slower than when he named right visual field words. He was consistently and equally slow to name a left visual field word whether or not he was accurate in his report; his naming latencies for a monosyllabic word ranged between 1.5 to 10 s. In addition, unlike his immediate verbal reports of right visual field words, he tended to report left visual field words as a series of individual letters which culminated in the naming of a word. There is even less evidence that Case 4 has the capacity for right hemisphere expressive language (Johnson, 1984*b*), and virtually none for Case 3. Thus there appears to be a general correlation between the generative capacity of the right hemisphere for speech together with at least a moderate level of syntactic competence and its production of an N400 wave to semantic anomalies.

Since our sample size is limited to 5 commissurotomized patients with different medical and experiential histories, it is possible that this correlation between syntactic/generative competence and N400 elicitation is coincidental. However, if we assume that this observed relationship has general validity, some interesting implications may be drawn concerning the organization of language in the brain, in particular about possible relationships between processes of semantic priming and those of comprehension and expression. The first step in this line of reasoning is to document the N400 wave as a reliable index of semantic priming in language and possibly of more general priming processes as well. (Note that we do not use the term priming necessarily to imply an automatic or unconscious mechanism.) Evidence for this relationship comes from several sources. First, studies of ERPs to semantic anomalies at the ends of sentences have shown that N400 amplitude is reduced if the anomaly bears some semantic relationship to the expected completion of the sentence (Kutas *et al*., 1984). For example, the amplitude of the N400 elicited by a semantically anomalous completion of the sentence fragment ('The pizza was too hot to . . .') was smaller if the anomaly (e.g., 'drink') was associated in meaning with the expected completion ('eat') than if it was not ('cry'). Similarly, Fischler *et al*. (1983) showed that false statements with a high degree of semantic association between the major words of the sentence did not elicit large N400s (e.g., 'A robin is not a bird'), whereas true statements with little semantic association between the major lexical items did (e.g., 'A robin is not a truck'). Further work confirmed that semantic anomaly is not a necessary condition for N400 elicitation; semantically congruent but relatively unexpected or unpredictable words within a sentence context also elicit N400 waves having an amplitude that varies inversely with semantic expectancy, operationally defined in terms of 'cloze' probability (Kutas and Hillyard, 1984). The results of such experiments have led to the proposition that the amplitude of the N400 wave under such conditions provides an index of the degree of association between words, in particular of the extent to which the eliciting item has been primed or constrained by the preceding context (Kutas and Hillyard, 1984). This idea has received additional support from findings that N400 amplitudes to words preceded by semantically related words are reduced relative to when those words are preceded by semantically unrelated items in semantic categorization and lexical decision tasks (Boddy and Weinberg, 1981; Harbin *et al.*, 1984; Bentin *et al.*, 1985; Kutas, 1985; Rugg, 1985; Boddy, 1986).

In studies to date, manipulations of semantic priming have produced the greatest alterations of N400 amplitude. However, it is important to note that semantically anomalous words in sentences generally fail to match a person's expectancies along other linguistic dimensions as well. The appearance of a semantic anomaly may violate orthographic, phonological and grammatical expectancies, and these factors might also make some contribution to overall N400 amplitude. There are indeed reports that N400-like waves are sensitive to phonological (rhyme/nonrhyme) and other forms of expectancy (Stuss *et al.*, 1983; Rugg, 1984; Kramer and Donchin, 1987). Nonetheless, available evidence is consistent with the proposition that semantic anomalies at the ends of sentences elicit large N400s by virtue of their being unprimed, primarily in the semantic realm.

According to this view, a failure to produce an N400 in response to a semantically anomalous word would imply an abnormality of semantic priming mechanisms. Thus the finding that the right hemispheres of Cases 3-5 did not generate an N400 wave following a semantically anomalous word presented to the left visual field suggests a differential organization or utilization of semantic priming operations in their two hemispheres. However, since their right hemispheres were shown to be capable of judging whether or not a word was semantically anomalous when tested behaviourally, there appears to be a dissociation between comprehension and semantic priming mechanisms.

This dissociation holds whether the apparent comprehension of sense/nonsense by the right hemisphere here reflected a true integration and understanding of sentence meaning or semantic association between key words in the sentences. Since many of the congruous sentences in this experiment included a word that was a semantic associate of the sentence terminal word, the patients could have performed with reasonable accuracy without a full understanding of sentence meaning, for example, by deciding to respond 'sense' whenever a semantic relationship was noted and 'nonsense' otherwise. Such a strategy, however, seems to be insufficient to explain their performance completely. For example, the patients were able to decide that sentences were sensible with greater than chance accuracy even if the sentence did not contain a lexical associate of the congruous terminal word (e.g., 'Fred put the worm on the *hook*'; 'Most cats can see very well at *night*'). Moreover, all the patients were more accurate in judging sensible than nonsensical sentences. Had the patients based their judgements solely on the presence or absence of semantic association, they would have been more accurate on the semantically unrelated anomalous than the congruous sentences; this was not the case. Finally, with the exception of Case 4 all of the patients could indicate above chance that a left field terminal word was anomalous even if that word was semantically related either to a previous word or the expected completion of the sentence. Thus whether the accurate sense/nonsense judgements were based on lexical association or the appreciation of syntactic structure and semantic content, there appears to be a dissociation between the behavioural and electrophysiological indicators of meaning.

A similar dissociation was observed by Milberg and Blumstein in investigations of semantic priming in aphasics. Of relevance here is their finding that Wernicke's aphasics exhibited large semantic priming effects in both auditory and visual lexical decision tasks in the face of severe comprehension deficits, whereas Broca's aphasics with almost no comprehension deficits exhibited small priming effects in the auditory modality and none in the visual modality (Milberg and Blumstein, 1981; Blumstein *et al.*, 1982). A related dissociation between the ability to comprehend syntactically-constrained sentences and the ability to judge their grammaticality has also been observed for agrammatic aphasics (e.g., Linebarger *et al.*, 1983) and Case 3 (Baynes and Gazzaniga, 1988). In both instances, patients who could not comprehend semantically reversible active and passive sentences with sufficient accuracy to choose an appropriate pictorial representation were nonetheless able to judge whether the sentences were grammatical or not.

The finding that N400 could only be elicited by right hemisphere anomalies in patients who either showed overt right hemisphere speech (Case 1) or were on the way to developing it (Case 2) might indicate that a hemisphere can best subserve language generation if it contains a semantic organization that permits semantic priming to occur. Typically, discussions of the role of semantic priming in language processing have focused on comprehension (in particular, during reading and listening) rather than on production. This has been true despite the belief of some investigators that lexical spreading activation can be disregarded as a fundamental mechanism for facilitating lexical access in the reading of sentences (e.g., Henderson, 1982). In so far as it has been investigated, the same variables (e.g., concreteness, frequency, semantic relatedness) that influence lexical access and semantic priming in comprehension also exert similar effects during production—for example, by shortening the latency to speech onset (Taylor, 1969; Rosenberg, 1977). Moreover, there is evidence to indicate that semantically primed words can, on occasion, influence the order in which words in a particular sentence are uttered (Bock, 1986).

Clearly, further experiments need to be carried out to clarify the relationship between semantic priming operations and language production, both spoken and written. Nonetheless, we view our data as consistent with the hypothesis that semantic priming might play a crucial role in successful language output. Within the split-brain population, this proposition would lead to the prediction that the right hemispheres of Cases 1 and 2 would yield strong semantic priming effects whereas those of Cases 3-5 would not. In so far as evidence is available, this appears to be the case (Zaidel, 1983; Baynes and Gazzaniga, 1988). Whatever the nature of the priming/speech production turns out to be, the present results suggest that a hemisphere which can subserve speech has a different functional organization of the semantic lexicon than does a hemisphere which cannot.

Since the split-brain surgery in Cases 1 and 2 left their anterior commissures intact, the possibility must be considered that visual information presented to the right hemisphere might be transferred to the left for the production of linguistic and/or ERP responses. A recent MRI examination in Case 2 further shows the presence of some remaining callosal fibres in the rostral and splenial regions

(Gazzaniga *et al.*, 1984). Behavioural tests in both patients, however, showed an inability to cross-compare 2 visual patterns (i.e., judge them same or different) when presented separately to the left and right visual fields (Gazzaniga, 1987). This suggests that the word stimuli used in the present study were lateralized to the directly stimulated hemisphere.

Several recent reports have argued that split-brain patients can cross-integrate some visual information. For example, Ramachandran *et al.* (1986) reported that the split-brain patient was capable of perceiving apparent motion when the 2 visual stimuli were flashed alternately, one to each half brain. Likewise, Sergent (1983, 1986) reported that J.W., N.G. and L.B. (Cases 3–5 in the present study) could indicate whether 2 letters, 1 in each visual field, included a vowel or not. She interpreted their ability to produce a single response in the face of contradictory information as evidence for integration in the brainstem. Gazzaniga (1987), however, has argued that Sergent's results can be interpreted without invoking interhemispheric integration. Whatever the explanation, there is general agreement that only rudimentary visual information is transferred between the hemispheres of a split-brain patient, even those with anterior commissures intact (e.g., Holtzman, 1984).

It should also be noted that Case 3 has an intact anterior commissure and showed no evidence either of an interhemispheric visual matching capability or of vocal responses to left-field stimuli except under certain conditions. Specifically, he can report verbally which of 2 stimuli were flashed to his right hemisphere as long as both the stimulus and response options are binary (Gazzaniga *et al.*, 1987). Despite this ability, however, he cannot indicate whether 2 numbers flashed simultaneously 1 to each hemisphere are the same or different or report verbally the outcome of any operations performed on the contents of information presented to the left visual field. Whether such information transmission between the hemispheres is mediated by the anterior commissure or brainstem is unknown; however, it is clear that the nature of the information transmitted in this manner is relatively limited in detail.

These ERP recordings from the commissurotomy patients shed some light on the nature of the cerebral generators of the N400 component. In normal subjects the N400 typically has a widespread bilateral scalp distribution, with a slight tendency to be higher in amplitude and more prolonged over the right hemisphere (Kutas and Hillyard, 1982, 1983; Kutas *et al.*, 1988). In the present experiment, the N400 also had a bilateral distribution regardless of the field of presentation. Surprisingly, there was no consistent shift in the lateral distribution of the N400 as a function of the visual field receiving the anomaly either for the control or the commissurotomized subjects. Although the individual patients differed somewhat in the degree and direction of N400 asymmetry, these data are difficult to reconcile with the idea of independent cortical generators for the N400 in each of the cerebral hemispheres. Two alternative mechanisms seem reasonable to consider: first, it may be that the N400 is generated by deep structures within the stimulated hemisphere in such a way that a unilateral activation produces a bilateral scalp field. This view is consistent with the reports of depth recorded N400-like activity localized to subcortical generators within anterior temporal lobes (McCarthy and Wood, 1984; Smith *et al.*, 1986). In this case the slight right hemisphere preponderance of the N400 generally observed with normal subjects might reflect the contribution of a deep medial source in the left hemisphere orientated so as to make the potentials at the right scalp appear more negative than those at the left scalp. A second possibility would be that the scalp-recorded N400 emanates from bilateral activation of the cerebral hemispheres for anomalies presented to either hemisphere. According to this view, semantic analyses of anomalous words performed separately in either hemisphere of Cases 1 and 2 would trigger the activation of a common bilateral system (presumably via subcortical pathways), which then gives rise to the N400 recorded at the scalp.

The ERPs elicited on the trials where an anomalous word was presented to both visual fields simultaneously provide further evidence against there being independent generators for N400 in each hemisphere. If each hemisphere generated an N400 wave independently according to the type of word seen, the N400 difference wave to the bilateral anomalies should constitute a simple summation of the amplitudes of the difference waves engendered by the single right and left field anomalies. This clearly was not the case in either the split-brain subjects or the normal controls (*see* fig. 4). Indeed, in Cases 1, 3 and 4, the N400 difference wave was smaller for the bilateral anomalies than for the summed unilateral responses; in Case 3 the bilateral difference wave was also delayed. This is a puzzling result that suggests considerable interhemispheric interaction in the production of N400, perhaps including some interference between the hemispheres in these patients. The presence of a somewhat larger N400 in response to bilateral anomalies may reflect the partial cancellation of the N400 to unilateral anomalies by the positivity elicited by the congruous words simultaneously flashed to the other visual field. The observed ERP pattern for bilateral anomalies in the patients and controls is consistent with the view that the N400 arises from (or is dependent upon) a bilaterally projecting system that can be activated fully by semantic processing in either hemisphere for Cases 1 and 2, but only by processing events within the left hemisphere alone for the others. Future research may help to differentiate between these alternative generator proposals.

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