In: Right Hemisphere Language Comprehension: Perspectives from
Cognitive Neuroscience. M. Beeman, C. Chiarello, Eds. Lawrence
Erlbaum Associates, New Jersey. 1998.

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Potential Asymmetries in Language Comprehension: In Search of the Electrical Right

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Several different brain areas, including cortical regions in both hemispheres, contribute to language comprehension and production. This is not surprising given that a large number of brain areas are involved in cognitive tasks thought to be less complex than language, and that language comprises many different computations subserved by different neural substrates. For these reasons, it has proven difficult to give a satisfactory answer to the question of what specific contributions the right hemisphere makes to language processing. A completely satisfying account presupposes that we know what language is, the dynamics of language processing, and the intricacies of how these processes are knit into neural tissue. Therefore, we expect that the reader will be left somewhat unsatisfied, although excited by the possibility that electrophysiological data will ultimately help resolve the answer more clearly.

In this chapter, we show that patterns of voltage recorded from either the scalp or the cortical surface can highlight differences in the dynamics of the contributions of regions in the two hemispheres, but cannot be taken as signs of some absolute level of hemispheric contribution to processing. Nor do differences in hemispheric contribution necessarily reflect some neat dichotomy; those who seek grand differences between the hemispheres will soon discover that the left and the right, like the warp and the weft of the cloth, are both made of silk. The same might be said about the differences between linguistic and nonlinguistic processing independent of the issues surrounding laterality. The tapestry of language is remarkable in that so much of the fabric is woven from threads of perception and cognition and scraps of motoric processing. We fear that those who seek language and language alone in the brain may end up pulling out these slender threads one by one, and thereby completely unravel the cloth, which is not woven from purely linguistic silk.

It may surprise some readers that we are so wary of suggesting that the two separated hemispheres do not have discrete processing modes. Don't they? Would that it were that neat. We might like to respect some form of the verbal-nonverbal dichotomy, but we are unwilling to shrug off gesture (see McNeill & Pedelty, 1995). We also do not know just when a word becomes a picture, or when a picture becomes an icon, or even when a word ceases to become a word when the font becomes sufficiently obscure or false (see, e.g., Peterson & Fiez, 1993). In the auditory modality, *Stop* is a word, whereas the sound of a car horn is not, but they clearly have related meanings, and, as it happens, they elicit similar but not identical brain responses (Van Petten & Rheinfelder, 1995).

In psycholinguistics, the distinctions get finer although often no less fuzzy. In addition to the well-known debate about syntax versus semantics in parsing are whole-word versus morphemic decomposition theories of word recognition, rule-based versus item-based pronunciation theories, rule-based versus frequency-based theories of syntactic ambiguity resolution, and competence versus capacity theories of processing difficulty. Although some might see this as a list of "left-brain, right-brain" pairs, this is generally not how they are viewed in the literature.

To achieve a different perspective on the problem, let us very briefly consider neuroscientific data concerning the processing of language in a specific setting, namely, the reading of Japanese text. The Japanese writing system includes 3 distinct sets of codes. Most well-known is the large set of ideographic characters, the *kanji*, used to represent the bulk of the native, content words in the language. Less well-known are the two different syllabaries (the *hiragana* and the *katakana*) together known as the *kana*, which are used to spell out many other content words, functional particles, and recently borrowed foreign words. Conveniently for psycholinguists, *kana* can also be used to spell out words that are usually written as *kanji*. A naive guess may have predicted a large right hemisphere component in the processing of words written in the picture-like *kanji*, but not *kana*. Although this issue remains unsettled, it is not very obviously true for the case of *kanji*. Primarily left and not right hemisphere strokes lead to alexia for *kanji* (reviewed by, e.g., Sasanuma, 1994) and positron emission tomography (PET) studies have indicated that in some situations *kanji* processing has a bilateral activation, but distinctly larger activation in the left posterior inferotemporal cortex (Sakurai et al., 1992). But the issues involved are not quite this straightforward, since it is possible that simpler, more concrete, or more picture-like *kanji* could benefit more from right hemisphere processing. Although many of the obvious experiments have been done, the answers are. not identical across task domains (see, e.g., Nakagawa, 1994).

Muddying the waters yet further is the fact many kanji have meaning ambiguities that are correlated with distinct pronunciations (known as *on* and *kun*), raising the question of whether the right hemisphere can access these distinct meanings even if only the left hemisphere can pronounce them. The remarkable subtleties and complexities involved in answering these questions (see, e.g., Sasanuma, 1994) do little to foster confidence in our ability to predict the hemisphericity of processing for the next experiment one might conduct.

As cognitive neuroscientists, we are somewhat disturbed by all of this precisely because (a) neurophysiological, neuroanatomical, and neuropsychological data have made us very aware that every neural function is computed somewhere in a physical system whose overall layout is far from arbitrary (e.g., Cherniak, 1990), (b) we have come to believe not that there are no localizable functions, but rather an extremely large number of them, and (c) the performance of any task can rely on a large (possibly redundant) subset of them. Moreover, these functions are computed in real if not always discrete time, so that the dynamics of processing is critical as well. It is in the elucidation of this aspect of processing perhaps even more than in physical localization of neural generators that the event-related potential (ERP) technique will prove immediately most useful.

HEMISPHERICITY AS LOCALIZATION

Questions about the hemisphericity of a given process are clearly just special cases of the more general question of mapping functions onto brain areas. There are two features that make hemisphericity a particularly interesting localization hypothesis. The first feature is that one seeks (and finds) differences in the computations performed by homotopic brain areas in the two hemispheres that, absent this asymmetry, would be expected to perform identical computations. The second feature is that, given a set of apparently lateralized computations, it is often assumed that all the differences between the two hemispheres can be attributed to one overarching, qualitative difference in their processing modes. ERPs are silent on this second issue, but can provide some information bearing on the first. Although ERPs provide no magical solution to the problem of localizing or lateralizing function, it is the case that ERP asymmetries do provide sufficient evidence that a generator, and therefore any function one might tentatively attribute to such a generator, is "lateralized" in some sense. But in a bioelectrical context, "lateralized" can mean just that otherwise identical cortical generators are oriented differently with respect to the scalp due to some accident of sulcal or gyral morphology. A related difficulty is that one cannot infer that an ERP component is generated in the hemisphere over which it is largest in amplitude. In particular, it is well known that generators on the medial surface of a hemisphere can be "paradoxically" lateralized-be larger over the contralateral than ipsilateral hemisphere (see, e.g., Regan, 1989). It is still the case, however, that all ERPs are a direct reflection of neural activity, and although we have little idea exactly where their sources are, we do know when they were active. ERPs are especially informative about the real-time temporal dynamics of processing. In the following paragraphs, we briefly review some basic ideas behind ERP recording techniques, and some practical pitfalls of their interpretation.

Ultrabrief ERP Tutorial

The electrical activity observed in individual neurons consists not only of the short-lived action potentials that propagate activity quickly through the axon of the cell but also of longer-lived modulations of voltage connected with activity in dendritic arbors that roughly constitute the "input" of a neuron. Depending on their polarity, these voltages can make a given neuron either more or less likely to fire an action potential, and are thus known as excitatory or inhibitory postsynaptic potentials (i.e., EPSPs or IPSPs). Small patches of cortex generally contain large numbers of pyramidal cells whose cell bodies are aligned in a consistent orientation, so that their activity adds up to create the effect of an equivalent dipole that describes the activity of the whole patch. The brain, of course, contains many such patches whose combined activity is a complex and time-varying electrical field. We can study this electrical field by calculating the voltage difference between a recording site and a "reference" site over time to generate the electroencephalogram (EEG). The EEG can be recorded from the surface of the cortex (i.e., intracranially) or at the scalp surface. In both cases, the activity observed at a given site reflects electrical activity directly beneath the recording electrode in addition to electrical activity that has been volume conducted from other patches of cortex via the fluid-filled brain case. In scalp recordings, further attenuation and smearing of the activity occur due to the fact that the skull is a poor conductor.

By recording the scalp EEG from a large number of sites we can generate a spatial map of electrical activity. Such maps usually show clear regional differences. For our current purposes, the fact that there are quite often pronounced hemispheric differences in electrical activity is of fundamental importance. However, because the brains of humans are quite convoluted not only figuratively but physically, any and all differences seen on the scalp are generally very difficult to trace to particular generators. Indeed, without additional constraints, the problem cannot be solved (Nunez, 1981). In particular, the polarity observed for the EEG anywhere on the skull depends on the position of the generator(s) with respect to the "recording" electrode and the "reference." A trivial case of this ambiguity can be seen by exchanging the identity of the recording and reference electrodes; the waveform will have the same shape, but be of the opposite polarity.

In the event-related potential (ERP) approach, the EEG is recorded from individuals performing multiple trials on some task involving stimuli occurring at known times, and analyzing that part of the brain response that is time-locked to the stimulus by averaging activity over the multiple trials. In such time-locked averages, it is customary to use a brief, pretrial interval (e.g., 100 or 200 msec) as the "baseline" against which the voltage fluctuations in the poststimulus region are compared. Just like the EEG, ERPs can be obtained from different scalp sites, with observable differences in the timing, polarity, and morphology of the peaks and troughs of the waveform. Not infrequently, spatially and temporally defined features of the ERP (usually peaks of either positive or negative polarity) vary systematically as a function of both stimulus and person variables; such features are usually referred to as *components* (see Regan, 1989, for an extensive review).

Figure 8.1 shows a grand average (across stimuli and subjects) ERP elicited by midsentence content words presented with a 200 msec stimulus duration and a 500 msec interword interval. Marked on the figure are several commonly discussed components of the ERP from two temporoparietal and two frontal electrode sites, showing the hemispheric and regional differences in brain responses. The labels on the waveforms indicate the polarity (e.g., N for negative or P for positive) and either the actual or normative latency (in milliseconds) of the labeled "peak" in the waveform. Thus, the P100 is a positivity with a peak latency of 100 msec, whereas the N400 is a negativity with a peak latency of 400 msec. A common alternative method for labeling ERPs is to number the positive troughs and the negative peaks in order of their appearance; using this nomenclature, the P100 would be referred to as the P1. Returning to Fig. 8.1, we note the visual P100 and N170, which are sensitive to attentional manipulations (reviewed by Mangun, Hillyard, & Luck, 1993), the P200, and a subsequent frontal negativity that we refer to as the Lexical processing negativity (or LPN). As the latency of the LPN varies with word type, word length, and word frequency (King & Kutas, 1995; Neville, Mills & Lawson, 1992), this name reflects its proposed functional significance rather than its latency. Last but not least is the N400 component, whose amplitude and latency are sensitive to relative differences in semantic congruity, repetition of words within a discourse, and the degree of semantic priming between words in unstructured lists, among others (reviewed by, e.g., Kutas & Van Petten, 1994).

Substantial research in both the auditory and visual modalities has revealed that the ERPs to words vary in amplitude between 250 and 550 msec as a function of their "fit" within the current context. Words that readily fit a context do not elicit much if any N400 activity; the less expected the word, the larger the N400. Note that expectancy can be influenced by both global and local contexts and is modulated by frequency of occurrence/usage, and repetition. Thus, although semantic anomalies yield the largest N400s, they represent an endpoint on a continuum reflecting varying degrees of probability for a particular word in a particular sentence context. The visual N400 is usually larger in amplitude over the right hemisphere, but the results described next should prevent the reader from thereby assuming that it is the reflection of a right hemisphere generator. Thus, although the hemispheric asymmetry of this component at the scalp may indicate an asymmetry in the responsible sources, the pattern alone cannot be used to localize the generator.

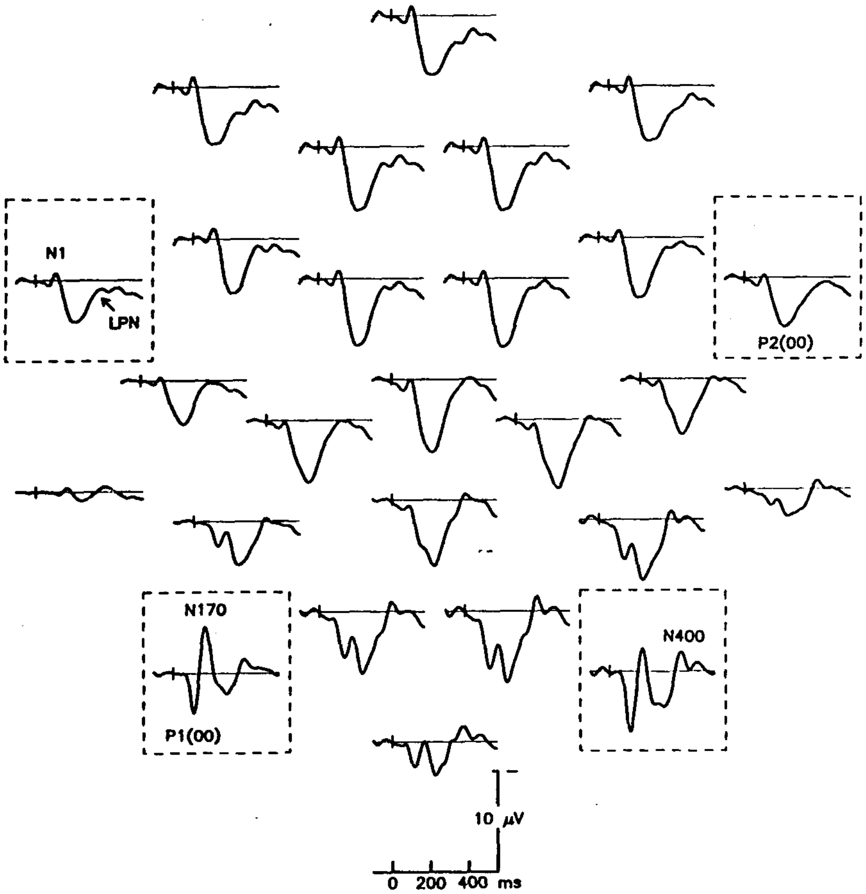

FIG. 8.1 Grand average (N = 21) ERPs to sentence intermediate content or open-class words at 26 locations on a geodesic grid. Recordings were referenced to an off-line average of activity at the left and right mastoid processes. Data were sampled at 250 Hz and bandpass filtered (.O1-100 Hz). Negativity is up on this and all subsequent figures.

THE EFFECT OF SUBJECT VARIABLES ON OBSERVED LATERALITY PATTERNS

In almost any kind of psychological investigation, one can attempt to control some combination of subject, stimulus, or task variables. In the ERP literature on hemispheric differences in language, stimulus variables have been most widely varied, task variables less so, and subject variables least of all.[1] This last omission is somewhat surprising because variability in lateralization seems to be an important part of the natural variability in human brains. Gender, handedness, and familial sinistrality are but some of the factors that correlate with degree of hemispheric lateralization to some extent. The relationship between handedness and asymmetric organization for language has received considerable attention in anatomical and behavioral studies, with the general conclusion that some 60-80% of left-handers show a left hemisphere dominance equivalent to that of right-handers, but a substantial minority show a reversed asymmetry or a greater degree of bilaterality (for reviews see Bradshaw & Nettleton, 1981; Kolb & Whishaw, 1990; Perecman, 1983). Relatively few ERP studies with words or sentences have contrasted left- and right-handed subjects to see if they yield opposing patterns of asymmetry. Barrett and Rugg (1989) examined handedness and phonological priming and observed no reliable group differences. Somewhat more frequently studied has been the effect of the presence of one or more left-handed relatives in a person's immediate family. The logic of this approach is that the presumably genetic component of left-handedness may affect the cerebral organization of language not only in left-handers, but in non-left handers with similar genetic makeup. See, for example, theories that posit that right-handedness is caused by one or more "shift" genes, and that only about 50% of those who lack such a shift gene will be phenotypically left-handed (e.g., Annett, 1985). In investigations of both healthy and brain-damaged individuals, family history of left-handedness has sometimes proven as important as the handedness of the participants themselves; specifically, right-handers with left-handed family members appear to have a more bilateral language representation than those without (Bever, Carrithers, Cowart, & Townsend, 1989; Bradshaw & Nettleton, 1983; Hardyck & Petrinovich, 1977; but see also Orsini, Satz, Soper, & Light, 1985).

We found somewhat different patterns of ERP lateralization during reading in right-handed individuals who have no left-handed relatives and those who have one or more left-handed family members. Specifically, the usual right-greater-than-left asymmetry in the N400 activity (between 300 and 700 msec)

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[1] There are, of course, studies that have examined individuals differing in handedness and familial history of handedness, individuals who do not have an intact corpus callosum, and individuals with lateralized brain damage, but they are far less common than one might expect.

elicited by ordinary, noninitial content words in sentences is largest in those who have no left-handed first-order relatives, but essentially absent in those who have sinistrals in their immediate families (e.g., Kutas, Van Petten, & Besson, 1988). We should emphasize that it is the asymmetry that we know to be diminished in individuals with sinistral relatives; the degree to which this also includes a reduction in N400 amplitude per se is uncertain. Whether the laterality of the N400 in speech and sign language is also sensitive to familial left-handedness is also an open question.

ERP Data From Commissurotomy and Stroke Patients

Much of the evidence for the linguistic capabilities of the right hemisphere has come from investigations of individuals afflicted with epilepsy treated with a drug regime following a partial or complete separation of the corpus callosum. We conducted a series of electrophysiological investigations of five different commissurotimized patients (J.W., L.B., V.P., P.S., and N.G.) to get a better idea of the language capabilities of each hemisphere. We attempted to determine the extent to which each hemisphere could appreciate semantic congruity versus incongruity for words presented in meaningful contexts (Kutas, Hillyard, & Gazzaniga, 1988). In this experiment, sentence fragments (missing only the final word) were spoken so that both hemispheres had access to the priming context. By contrast, the final words were presented over one degree lateral to fixation in the two visual half-fields so as to limit access of each word to a single hemisphere. Sentences were completed by a pair of words that were presented simultaneously (for 180 msec) to the right and left visual fields in one of four combinations:

1. Same word in each field, congruent with preceding fragment
2. Same word in each field, incongruent with preceding fragment
3. Two different words matched for length in each field, one congruent and one incongruent
4. Same as previous but reversed

The last two conditions provided the most interesting contrast in that in each case only one hemisphere, albeit a different one, received a semantically anomalous word. The question was whether or not the two hemispheres in isolation would yield identical ERP effects.

The five split-brain subjects studied all showed some degree of receptive language ability in both hemispheres. In a pretest, they were able to judge with greater than 70% accuracy whether or not a word presented to the LVF (right hemisphere) formed a sensible completion to the spoken context; they displayed significantly higher accuracies for the RVF. All five patients also produced N400s when the semantic violation was flashed to the left hemisphere. Only two of the patients (VP and RS.), however, also showed N400s when the anomaly was flashed to the right hemisphere. The critical distinction between the two groups of patients seemed to be right hemisphere control of expressive language. At the time of testing, PS. could control overt speech with the right hemisphere, whereas V .P. showed a high degree of generative capacity with respect to written output.[2] These data suggest that both hemispheres are capable of maintaining a lexicon for semantic integration of sorts, but that the functional organization of our mental lexicons may have evolved primarily for the purposes of subserving speech rather than comprehension. On this view, priming during receptive language tasks may simply be a by-product of the brain's organization for speech, which is generally but not exclusively subserved by the left hemisphere.

Another approach to hemispheric specialization for language is to study individuals with lateralized brain lesions. Swaab, Brown, and Hagoort (1994) examined N400s to the final words of naturally spoken sentences (in Dutch) that were either semantically congruent or anomalous with respect to the preceding sentence context. Several groups were investigated including age-matched controls, patients with a lesion in the right hemisphere (RHD), and aphasic patients with left hemisphere lesions (LHD). The age-matched controls showed the expected congruity effect (e.g., Holcomb & Neville 1991). Although the nonaphasic RHD patients also showed a clear N400 congruity effect at the normal latency, it was reduced in size relative to normal controls; they also showed a larger N400 effect over the left than the right hemisphere (i.e., the opposite of the usual pattern). The ERP data from the LHD patients systematically varied with the severity of their comprehension deficit. Those patients with a mild comprehension deficit showed essentially normal amplitude and latency N400 effects; by contrast, the patients with moderate-to-severe comprehension deficits showed delayed N400 congruity effects. This pattern of results suggests that there may be a close connection between the generation of the N400 and speech comprehension and generation (e.g., the delayed N400 in LHD patients). By the same token, data from the RHD patients suggest that the right hemisphere also may play an important role in the generation of N400 activity, and that this is especially true when sentences provide context rich enough to be violated at a deeper level. Although suggestive, the ERP studies done to date on language processing in both split-brain patients and stroke victims have been few and far between, so that much of our knowledge of the contribution of the right hemisphere to language processing must come from studies using non-brain-damaged individuals.

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[2] Furthermore, 6 months after the ERP experiment, V .P. began to show a right hemisphere speech capability which was fully developed 2 years later.

HEMISPHERICITY AND THE SINGLE WORD

Both pictures and written words are visual and have referents in the external world and in memory. Although much has been said about differences in the way meanings of pictures and words are accessed, much less has been said about the very real structural and perceptual differences between them. For example, in many languages, written words are linear arrays of a small set of possible characters (i.e., an alphabet). By contrast, most objects do not have this array-like property, in the sense that they do not necessarily consist of units drawn from a fixed and limited repertoire (although see Biederman, 1987, for an alternative viewpoint). The investigation of hemispheric asymmetries for words and faces, for example, is complicated because hemifield asymmetries related to simple visual features such as contrast and spatio-temporal frequency have frequently been observed, usually in behavioral visual half-field studies (see Hellige, 1995, for a recent review). ERPs to checkerboard and simple sinusoidal gratings are likewise characterized by asymmetries (e.g., Onofrj, Bazzano, Malatesta, & Fulgente, 1991; Pike & Polich, 1988; Rebai, Bagot, & Viggiano, 1993; Spinelli & Mecacci, 1990). Realistically complex visual stimuli contain information in a wide range of spatial frequencies, however, leaving open the possibility that the observed hemispheric asymmetries are due in part to purely visual aspects of the stimuli that covary with stimulus type but are not necessary features for the categorical difference between, for example, words and faces. Further difficulties can arise from the fact that the distribution of "meaningful elements" is not uniform across most visual objects in either the pictorial or frequency domain; this also may be the case for English words at both the perceptual (Solomon & Pelli, 1994) and syllabic or "morphographic" levels (Taft, 1987).

A number of scalp ERP studies have addressed the issue of hemispheric asymmetries specific to the processing of verbal as opposed to nonverbal visual stimuli in isolation (e.g. Butler, Glass, & Heffner, 1981; MacKay, & Ludwig, 1986; Ornstein, Johnstone, Herron, & Swencionis, 1980; Sobotka & Grodzicka, 1989). The results of these studies were not wholly conclusive, perhaps in part because the verbal-nonverbal distinction is not a pure dichotomy; pictures can be named, words can be imaged or rotated; both can and do carry verbal meaning.

Our approach to detailing the differences between verbal and nonverbal materials has been to compare the ERPs to various visual stimuli that are closely matched in size, contrast, and spatial frequency content. For the moment, we focus on the earliest ERP effects that may help define the role of early right hemisphere processing; the data are described elsewhere in detail (e.g., Schendan, Ganis, & Kutas, 1995).

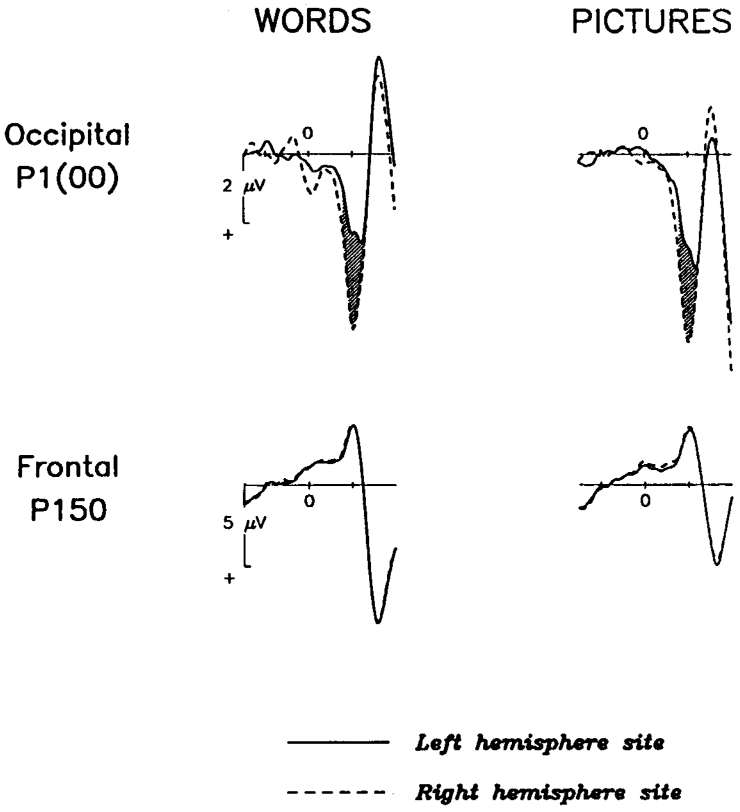

FIG. 8.2 Grand average ERPs (N = 12) to words (left column) and pictures (right column). The task involved detection of immediate stimulus repetitions. The occipital P1(00), and the frontal P150 components are shown in the top and bottom rows, respectively. Overlapped are the ERPs recorded from left (solid) and right (dashed) hemisphere sites.

As can be seen in Fig. 8.2, one of the earliest components is the occipital P100. It is larger over the right than left hemisphere for words and pictures, alike. Note that prior to this point the ERPs are nearly indistinguishable. This lateral asymmetry of the P100 is a robust finding for both words (e.g., Compton, Grossenbacher, Posner, & Tucker, 1991; Neville, Kutas, & Schmidt, 1982) and pictures (Holcomb & McPherson, 1994). Based on its timing and relative insensitivity to certain manipulations, it has been suggested that the P100 reflects early visual processing in extrastriate cortex. Consistent with this interpretation, it has been localized via current source modeling to the posterior fusiform gyrus (Heinze et al., 1994).

Thus, up to about 100 msec, verbal and nonverbal visual stimuli appear to be processed by largely overlapping, if not identical, neural systems.

Differences between verbal and nonverbal materials emerge at around 150 msec poststimulus onset as evidenced in the P150 component (Fig. 8.2). This difference is bilaterally symmetric, although its scalp distribution suggests a deep generator, which, if it were the case, could blur fine distinctions in the component's laterality. Hereafter, we see not only a divergence in the ERPs to verbal versus nonverbal stimuli, but also among the different kinds of verbal (and nonverbal) stimuli as a function of both the stimuli and the task requirements.

The pattern of asymmetries one might expect starting around 150 msec to 200 msec is dependent on one's view of the nature and laterality of the long-term memory representations that these types of visual input are beginning to contact of this point. One of the more influential theories on the differential representation of verbal and nonverbal stimuli is Paivio's (1991) dual coding hypothesis. In this theory, nonverbal information is encoded in a pictorial system located in the right hemisphere and linguistic information is encoded in a verbal system located in the left hemisphere. This predicts that abstract words will be encoded only in the left hemisphere, whereas concrete ones will be encoded bilaterally to the extent that they are imageable.

Limitations to the inferences that can be drawn on this issue from scalp ERPs notwithstanding, Kounios and Holcomb (1994) conducted a study that bears directly on this hypothesis. In their experiment, subjects saw the same list of concrete and abstract words matched for length and frequency presented one word at a time. The subject's task was to categorize the words as concrete or abstract. Concrete words were associated with greater negativity between 300 msec and 500 msec than were abstract words; this "concreteness effect" was larger over the right than left hemisphere, and apparently attributable to the response to concrete words as the response to abstract words in this time was was not asymmetric. Moreover, although both concrete and abstract words showed the typical reduction in the amplitude of this negativity on repetition, the laterality of the repetition effect differed for the two word types; it was bilateral for concrete words, but larger over the left than right hemisphere for abstract words. Let us assume, for the moment, that differences in scalp negativity index processing involvement and take the laterality of the repetition effects at face value. Then the pattern of data suggests that concrete words typically engage regions in the right hemisphere to a greater degree than in the left but that the "priming" of these regions is equivalent in the two hemispheres. By contrast, the pattern for abstract words suggests that although the two hemispheres are equally engaged initially, this processing (or some post-processing not visible in the ERP during this time frame) results in an additional priming of left hemisphere regions. These results are consistent with the idea that concrete and abstract words are processed by partially nonoverlapping neural systems, but are not completely consistent with the present form of the dual coding theory, which does not speak to the consequences of stimulus repetition.

Moving from the processing of single stimuli to the processing of pairs of stimuli presented in succession requires that we consider the relationship between the two. Generally, the N400-like response to the second item in a pair decreases to the extent that the two are related to each other. One could speculate that the laterality of the relatedness effects might implicate one or the other hemisphere in the processing of specific types of stimuli. On the whole, no clear asymmetries have been observed in the ERP relatedness effect in semantic priming paradigms using written word pairs (e.g., Kutas, 1993), which contrasts with behavioral asymmetries obtained following lateralized presentations (reviewed by, e.g., Beeman, chapter 10, this volume). Laterally asymmetric ERPs have been observed, however, in a semantic priming paradigm with line drawings of real objects. Specifically, Holcomb and McPherson (1994) used pairs of pictures in which the first (prime) always depicted a real object to which the second was either semantically related or unrelated; these were intermixed with "pseudo-object" targets as the subject's task was to decide whether each target was or was not a real object. The results showed an ERP relatedness effect between 300 msec and 500 msec that was larger over the left than the right hemisphere. This might not be expected from some conventional models of hemispheric processing, but could have resulted from covert verbal recoding of the objects, for example, or the fact that the task required relating two events.

One potential drawback common to all of the studies just reviewed is that they involved the processing of isolated stimuli in situations that required verbal judgments of some stimulus property. Perhaps different effects would have obtained if the tasks required the rapid integration of stimuli into a larger, ongoing context instead. Potter et al. (1986) pioneered the use of the so-called rebus paradigm comparing the ease of integration of words and pictures into specific sentence contexts with a variety of behavioral measurements. We used this paradigm in an ERP investigation of words and pictures in sentence contexts (Ganis, Kutas, & Sereno, 1996). Twenty-eight undergraduates read a series of sentences presented one word at a time for comprehension. Each sentence ended with either a written word or a line drawing; half were semantically congruent with the sentential context and half were incongruent. For half the subjects, sentences ended by words and pictures were randomly intermixed (mixed condition), whereas for the remaining half the two sentence types appeared in separate blocks (blocked condition).

Our aim was to use the similarity or difference in the scalp distributions of the N400 congruity effects for words and pictures to assess whether or not the two are encoded in identical neural systems. As shown in Fig. 8.3, we found clear differences in the distribution of the N400 congruity effect

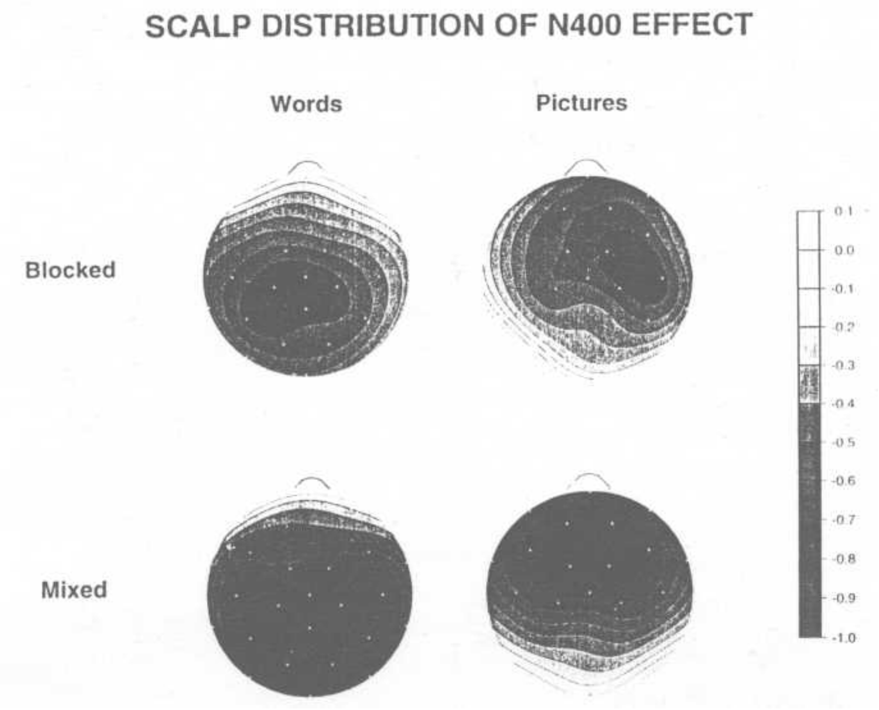

FIG. 8.3 Normalized scalp distributions of the grand average (N = 12) N400 congruity effect for words and pictures in the blocked and mixed conditions. The N400 effects were measured as mean amplitude between 325 and 475 msec relative to 150 msec prestimulus baseline and normalized for words and pictures, separately.

for words and line drawings. Such differences were seen mainly along the antero-posterior axis, with the "word" N400 congruity effect having the usual parietal focus whereas the "picture" N400 effect had a more frontal focus. In the blocked condition, where the predictability of the final item's modality might induce specific strategic processes, the congruity effect was asymmetrical, but for pictures only. Here the N400 congruity effect was slightly larger over the right than over the left scalp, especially at temporo-occipital electrodes. A similar trend for blocked materials of this type was reported by Nigam, Hoffman, and Simons (1992). Overall, these data suggest that although there is a family resemblance between the N400 effects to words and pictures in context, there are differences between them that may reflect the quantity and type of information in pictures and words.

PROBING MORE DEEPLY INTO WORD REPRESENTATIONS WITH DEPTH RECORDINGS

Although intracranial ERP recordings may be somewhat better suited than scalp recordings for localizing the source(s) of brain potentials, there are certain caveats to bear in mind when interpreting intracranial data, especially with regard to hemispheric asymmetry. First, because the electrodes are implanted for clinical purposes, usually in patients with medically intractable epilepsy, it is likely that the brain may have undergone some reorganization. Second, the spatial coverage of intracranial electrodes is quite limited relative to what is possible with scalp electrodes. Moreover, most crucial for present purposes, electrodes are often not placed symmetrically in the two hemispheres, at least within a single patient. For these reasons, conclusions about hemispheric asymmetries in processing based on intracranial ERPs are usually not based on within-subject comparisons (but see Grunwald et al., 1995, for an exception).

Intracranial ERPs to verbal and nonverbal stimuli have been recorded from widespread areas in the human brain (reviewed by, e.g., Ojemann, Cawthon, & Lettich, 1990). Here we focus on recordings from recently discovered basal temporal language areas (Luders et al., 1986). The basal temporal language area is defined functionally as that region of cortex at the base of the temporal lobe where stimulation produces transient language deficits; these are mainly along the fusiform, inferotemporal, and parahippocampal gyri. However, the localization of the stimulating sites has been far from ideal given the nature of the procedure, making it difficult to compare stimulation and recording results directly. Indeed, due to the somewhat heroic measures required to record from these regions, the systematic investigation of these areas long known to be crucial in the processing of visual stimuli has just begun (e.g., Allison, et al., 1994; Allison, McCarthy, Nobre, Puce, & Belger, 1994; McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1995). Conveniently, these data were collected in paradigms similar enough to those described above with scalp recordings to permit useful comparisons.

Field ERPs peaking around 150 msec to 200 msec that seem selective to either letter strings or faces (N200) have been recorded from different focal sites in the posterior fusiform gyrus of both hemispheres. It was suggested that these ERPs index "presemantic" visual processing of letter strings and faces. Remarkably, both the morphology of these N200 potentials and the frequency with which they are recorded from the two hemispheres are virtually identical. The occasional reports of laterally asymmetric response to words and faces in these brain regions are based on a much smaller number of cases (e.g. Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Halgren, Baudena, Heit, Clarke, Marinkovic, & Chauvel, 1994). Although it is difficult to compare intracranial findings with other results, we are encouraged by the degree to which these depth recordings agree with our findings at the scalp surface. In particular, the previously described P150 to letter strings (Schendan et al., 1995) could be in part a reflection of the intracranial N200 response at the scalp. Its latency, polarity, and scalp distribution (in particular the absence of hemispheric asymmetry) all seem consistent with this hypothesis.[3] It should be noted, however, that subtle differences in presentation parameters may affect the patterns of asymmetry observed.

Intracranial recordings also have yielded new information about the likely generators of the scalp N400, and its pattern of laterality. Specifically, depth-recorded ERPs that are modulated by many of the same factors that affect the scalp N400 to written words have been observed in the anterior parts of the fusiform gyrus. This intracranial N400 appears to have a similar morphology in the two hemispheres and is recorded with equal frequency in the two hemispheres (McCarthy et al., 1995; Nobre et al., 1994; Nobre & McCarthy, 1995). Because these tend not to be within-subject comparisons, however, it is not possible to compare the amplitude of these N400s across the hemispheres in any meaningful way.

The reports of N400-like potentials in the depths that are sensitive to repetition generally have been less conclusive than reports of those related to semantic congruity and priming. For example, Smith, Stapleton, and Halgren (1986) noted a left hemisphere predominance for an N460 sensitive to repetition in the anterior temporal lobe, but Guillem, N'kaoua, Rougier, and Claverie (1995) found no clear laterality differences for an apparently identical component recorded in a similar paradigm.

The regions on the basal temporal cortical surface where many of these language-related potentials have been recorded are usually in and around the recently discovered basal temporal language area (Luders et al., 1986). The language abilities of this cortical region were first brought to light via its electrical stimulation during the performance of various language tasks (e.g., Luders et al., 1991; Schaffler, Luders, Morris, & Wyllie, 1994). Stimulation of basal temporal regions in the dominant hemisphere often produces various transient language impairments, including speech arrest, impaired naming of words and objects, and impaired comprehension of both written and spoken language. The language-related effects of stimulation in this primarily visual region of cortex (at least in nonhuman primates, as reviewed by, e.g., Felleman & Van Essen, 1991) were unexpected, but they are in fact consistent with theories of language processing that emphasize a leading role of speech generation in the organization of the semantic system and the split brain data that show a clear connection between the generation

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[3] Note that in general a local negativity recorded on the surface of the basal cortex would appear as a more widespread positivity on the scalp because the recording electrode(s) are effectively being placed on the opposite side of the current generator although the location of the reference does not change.

of the N400 and speech production. They are also consistent with a recent theory of the evolution of language via the appropriation of the cortical apparatus first developed for visual scene recognition (Sereno, 1991).

Although stimulation of the basal temporal regions in the nondominant (i.e., right) hemisphere has not been as systematic, Luders et al. (1991) have reported these generally do not produce speech arrest or slowing during a "reading aloud test". Somewhat surprisingly given the stimulation results described already, Luders and his group reported in the same paper that the excision of the basal temporal language area in the dominant hemisphere produces at most a transient language deficit, which resolves quickly. The compensatory mechanisms mediating this recovery are unclear. However, it is possible that the relative contribution of the nondominant (but apparently capable) right temporal lobe is increased, as has now been documented in the case of split-brain patients.

These data then seem to indicate far fewer language-related asymmetries in the inferior and basal temporal lobes than one might have expected from the study of other brain areas. It should be made clear, however, that a bilateral response does not rule out qualitatively different processing across the two hemispheres. Based on results from more posterior (and uncontroversially visual) areas, one might be tempted to argue that the right temporal lobe may be sensitive to the spatial organization of letters in a linear array, whereas the left temporal lobe may be sensitive to the identity of the letters per se (e.g., Robertson, 1995). Thus far, no intracranial ERP experiments have tried to dissociate the various visual aspects within the category of written language. However, it is possible that basal and inferior temporal lobe structures are characterized by a lesser degree of functional lateralization than are the more dorsal structures (which could include Broca's and Wernicke's areas). Although space does not permit a detailed description of this literature, there is evidence that there are (at least) two larger subsystems within the visual system that are specific in their processing to different aspects of visual stimuli (see, e.g., Ungerleider & Haxby, 1994, for a review). The dorsal visual pathways, the so-called "where" system, are far more sensitive to features that depend on location information or changes in location (i.e., motion), whereas the ventral visual pathways, the so-called "what" system, are more sensitive to local stimulus dimensions including color and small-scale form. Anatomically, the dorsal, "where" system has more extensive and more direct connections with motor and premotor areas in the frontal lobe-presumably those areas involved in the generation of speech and dextrous hand movements that are known to be strongly lateralized. The connections of the "what" system with motoric areas, although by no means unimportant, may differ in their exact function, if we can be guided in our speculations by results from the visual working memory system in monkeys (Wilson, O'Scalaidhe, & Goldman-Rakic, 1993).

TO MAKE A SHORT STORY LONG: ERPS OF BASIC SENTENCE TYPES

In the 1960s and 1970s, it was expected that any "true" ERP marker of a language process would be asymmetric, so that the relative dearth of such asymmetries in the then-extant literature (reviewed by Donchin, McCarthy, & Kutas, 1977) relegated the ERP methodology to the role of a poor distant cousin in the grand play of functional brain imaging. However, very little of that research taxed the language system to any significant degree. Indeed, most of those were about language only by virtue of the stimulus materials; that is, they differed from nonlanguage studies primarily in the use of words (vs. nonverbal pictures, lights, tones, or sounds with speech as opposed to non-speech like characteristics). Moreover, there was a certain methodological premium placed on designing experiments wherein every aspect of the experiment (including the task) except the stimulus materials was held constant. Some very striking results showing that the same acoustic input can result in different perceptions (with different brain activations) depending on whether or not it is interpreted as speech attest to the strength of this sort of methodological purity. However, this approach ignores the possibility that language is unique in the sense that no other cognitive function serves the same purpose and does it in exactly the same way, so the best comparison may not always be linguistic input that is not treated as such.

The question really comes down to whether one is interested in knowing how language is subserved by the brain (and what the roles of the left and right hemispheres are in this) or in knowing what the specific anatomical and associated processing differences between the two hemispheres are and how these have been co-opted in the service of language reception and production. So what are some of the aspects of language that make it stand out among other cognitive processes? Certainly, one of the most persistent arguments for the uniqueness of language stems from its structure-its syntax. For example, although chimpanzees and gorillas have been observed to use symbols, it has nonetheless been argued they do not have language because they do not have syntax. That is, on the whole their use of symbols does not have an ordering or structure to it such that different orders of the same symbols mean something different. It is the hierarchical relations between words rather than their actual individual meanings that communicates "who did what to whom"-in other words, the subject, the verb, the object, and so forth. By many, this is considered the essence of language. Clearly no localization of language function is complete without data from sentence and discourse processing.

In fact, electrophysiological data from several laboratories indicate no dearth of asymmetries during sentence processing by neurologically intact children, young adult college students, and elderly individuals. To what extent each of these lateralized effects is language specific is a matter for further investigation, but nonetheless worth examining. We next describe a few of these lateralized ERP effects within the context of three sentence-processing studies from our laboratory. These data are useful for pinpointing lateralized ERP effects present not only at the word level but also at the sentence level. Indeed, one of the most startling observations we have made over the past few years is the striking differences in thecross-sentence ERPs at different regions of the scalp over both hemispheres. Depending on where on the scalp one looks, the pattern of ERPs even within a single condition is quite different across the courseof a sentence and in some cases across the hemispheres.

The simplest starting point for a study of sentence-level ERP effects is an investigation of syntactically identical simple transitive clauses such as "The secretary answered the phone" (Kutas & King, 1996). Although word-by-word examination of the average ERPs elicited during sentence processing is the prototypic type of analysis, we have found it equally informative to look at the average activity elicited across the course of entire sentences (as in Fig. 8.4). This way of looking at the data reveals electrophysiological properties that emerge across sentences that are more than the individual words lined up end to end; for example, in the presence of very slow effects that cumulate and fluctuate across the course of sentences. Fig. 8.4 contrasts the complete clause-length ERPs for these sentences with these data after the application of a low-pass digital filter, so that only the slow activity can be seen. Although the filtering simplifies the waveforms, the resulting data still exhibit a very rich temporal and spatial pattern of activity at different recording sites. This pattern shows notable differences in the responses from anterior and posterior sites on the scalp, and modulations in those differences as a function of the hemisphere they were recorded from.

As can be seen in Fig. 8.4A, at occipitotemporal sites there is a large, standing negativity that is relatively insensitive to any linguistic factor such as the difference between function and content words, clause beginning, or clause ending. Although the negativity is bilateral, it is significantly larger over the left hemisphere than over the right. We have suggested that this sustained potential reflects activity related to the continuous decoding of new words as they enter the visual system. The hemispheric asymmetry, then, could be due either to differences in the location of visual word forms (e.g., in the left hemisphere) or, alternatively, to hemispheric differences in the information processing of bilaterally represented word forms.

At lateral and more anterior sites (Fig. 8.413), we see additional asymmetries at and immediately following the time point where the verb appears in the clause. The first of these effects, a positivity that is best seen at a left anterior temporal site, we have tentatively linked with processes involved in the assignment of the thematic role to previously encountered subject noun phrases, which, like subsequent noun phrases, do not evoke such a positivity (Kutas & King, 1996). This positivity is immediately followed by a more widespread left hemisphere negativity that marks the end of the clause, and which we tentatively ascribed to processing that must be postponed until the clause boundary is reached. Both of these effects are phasic and of relatively small amplitude; they appear, and then disappear, as if they were just somewhat longer versions of the faster ERPs we have been discussing.

^{1}The ^{2}secretary ^{3}answered ^{4}the ^{5}phone ^{6}because...

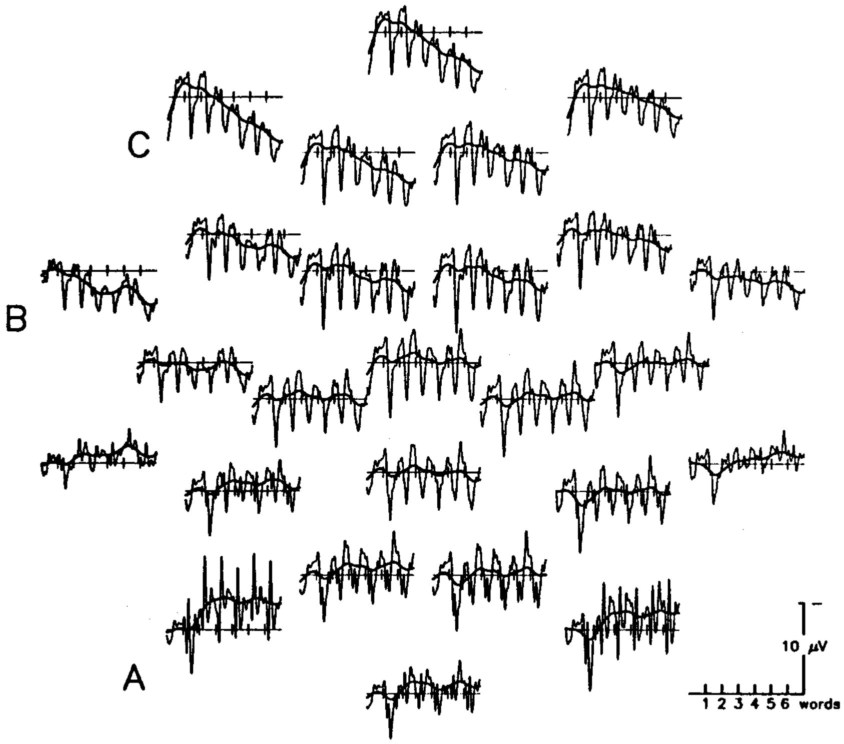

FIG 8.4 Grand average (N = 18) ERPs across the first six words of simple transitive clauses at 26 recording sites. Overlapped are the ERPs averaged with band pass .01-20 Hz (thinner line) and the same data after low-pass filtering (<.7 Hz.). (A) Note the slow negative shift at occipito-temporal sites; this is slightly larger over the left than right hemisphere. (B) Note the positivity coincident with the verb at left lateral temporal sites followed by the clause ending negativity. (C) Note the very slow positive drift that cumulates across the course of the sentence, most pronounced at left frontal sites.

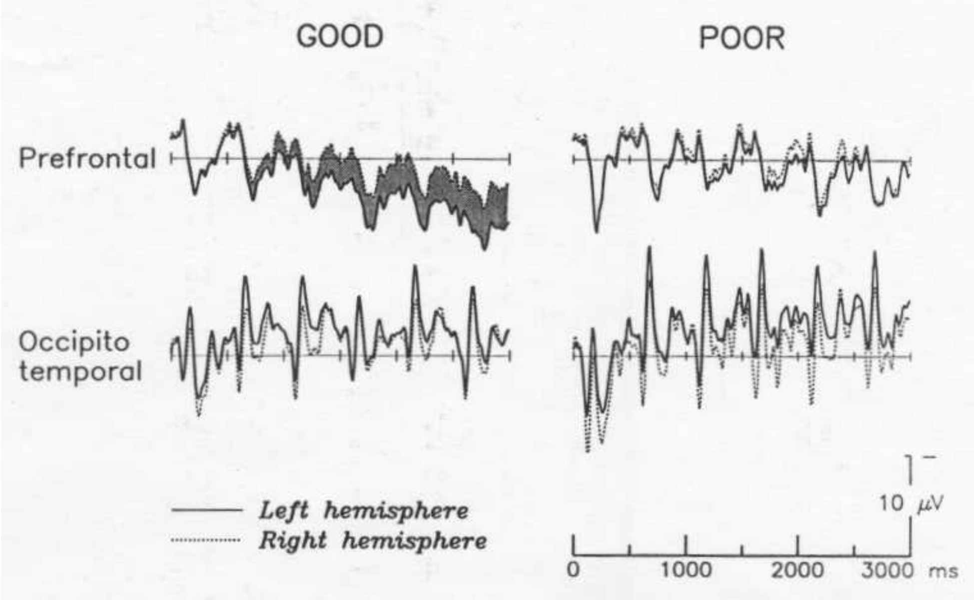

FIG 8.5 Grand mean simple transitive clause data at Prefrontal and Occipitotemporal electrode sites (C and A in Fig. 8.4) for Good (n = 12) and poor (n = 6) comprehenders. Note that the pronounced hemispheric asymmetry at frontal sites is large in good comprehenders and absent in poor comprehenders, whereas nearly the opposite trend can be seen at occipitotemporal sites.

The most prominent slow potential effect is the large positivity at frontal sites (Fig. 8.4C) that is neither phasic nor constant, but constantly growing throughout the sentence. The observed effect, although larger over the left hemisphere, is bilateral at these frontal sites, and could originate from a deep generator in either hemisphere. The cumulative nature of this effect, rather unusual in the slow potential literature, could index some process that builds over the course of the sentence, such as the construction of a discourse model.

Overall, Fig. 8.4 demonstrates a pattern over the back of the head best described as symmetric in terms of components but asymmetric in voltage levels, whereas the pattern over the front of the head suggests an actual asymmetry in the components. This view is consistent with the observation that the clause-length ERPs differ for good and poor (adult) comprehenders (see Fig. 8.5).[4] As can be seen in Fig. 8.5, poorer (but not good) comprehenders show a noticeable left-right asymmetry in the slower, nearly constant potential over occipito-temporal regions, which we have proposed as a reflection of the information-processing load posed by word recognition processes. By con-

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[4] Although average comprehension rates on these simple transitive sentences were over 95%, six subjects ("poor" comprehenders) showed lower comprehension rates in the 80-90% range; four of these had at least one left-hander in their immediate family.

trast, the slow, cumulative frontal positivity is much larger and left-lateralized for good than for poor comprehenders. The apparently reciprocal nature of these scalp effects could be the reflection of a more systematic trade-off in the processing styles of these two subject groups. One obvious possibility is that poor comprehenders expend greater effort on lower level processes such as word identification or lexical access that are dependent on posterior brain regions, whereas good comprehenders expend more effort on higher order processes that are dependent on frontal brain areas. This, of course, is making the tentative assumption that regional ERP differences index local activity in an obvious way, which may not be the case.

Auditory Sentence Processing

One way of winnowing the possible explanations for the asymmetries seen during sentence reading is to compare them with those seen during auditory sentence processing. Although we have not yet examined the ERPs to spoken simple transitive sentences, we did replicate the effects we observed in another study involving the processing of sentences with relative clauses that differ in syntactic complexity (King & Kutas, 1995). It should be noted that auditory ERPs differ noticeably in character from visual ERPs due to differences in the time course of the visual versus the auditory recovery cycle, and to the fact that continuous speech does not contain the sharp onsets and offsets characteristic of visual stimuli. Nonetheless, data shown in Fig. 8.6 from Mueller, King and Kutas (1995, in press) demonstrate that the slow potential effects at both frontal and posterior parietal sites are remarkably similar in timing, and essentially identical over the left hemisphere. The primary difference between the reading and speech data is that the auditory data show more activity over right frontal electrode sites; the effect at right occipitotemporal sites is found in both modalities, although effects at such sites are frequently more prominent for visually presented materials.

We have ascribed the function of many of these slow potentials to the involvement of processes that depend on components of working memory. Clearly, working memory processes are integral to understanding a sentence and discourse, and could be more richly decomposed into subprocesses that could involve either of the hemispheres, as seems to be the case for many long-term memory processes. Work by Roesler and his colleagues has revealed a number of task-specific slow potentials whose amplitudes, timing, and distribution vary systematically with the nature of the information received (general vs. specific concepts, verbal vs. spatial materials, etc.) and the type of decision required (Roesler, Heil, & Glowalla, 1993; Roesler, Heil, & Hennighausen, 1995). For example, the largest negative slow potentials were observed over parietal sites when associations involved spatial

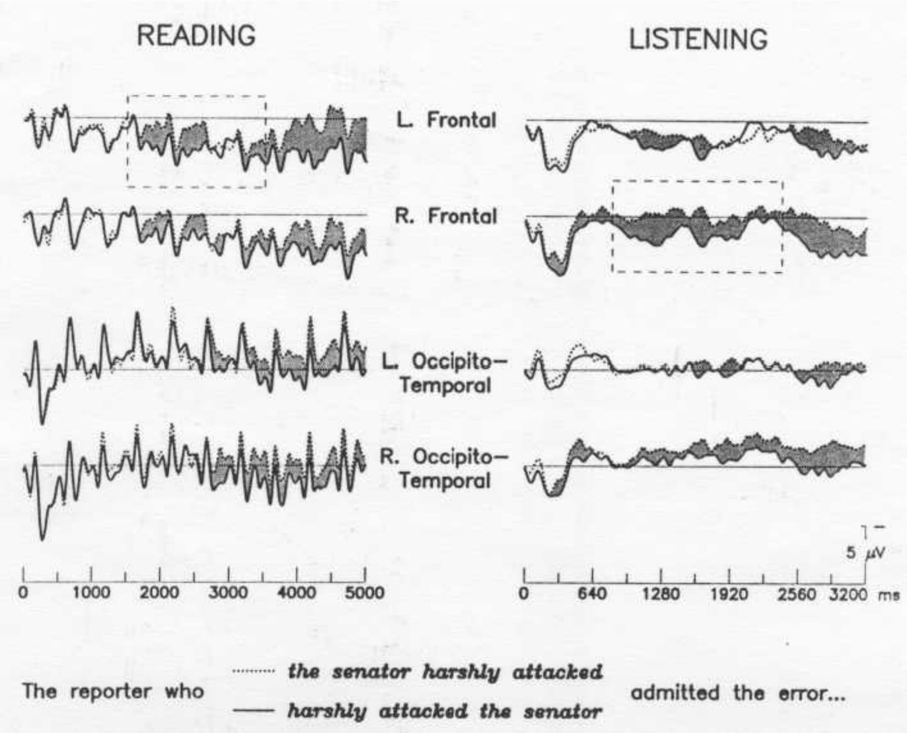

FIG. 8.6 Grand average ERPs elicited across the course of sentences with embedded relative clauses recorded as one group of subjects (N = 24) read and another group (N = 24) listened for comprehension. In the visual condition, sentences were presented one word at a time once every 500 msec whereas in the auditory condition the sentences were spoken naturally. Dashed boxes highlight ERPs to the material within the relative clauses at sites showing the largest ERP effects within the relative clause.

knowledge and over the occipital sites when associations involved color. Most importantly all these studies revealed a pronounced negativity whose time course was related to the process of retrieval, whose spatial topography reflected the type of material that was being retrieved, and whose amplitude varied systematically with the difficulty of the retrieval. These results generally fit with the notion that the brain areas involved in explicit memory are the same as those needed for encoding and perception; there is no single memory store for all memories, be they long-term or shorter term working memories.

In summary, we hope that we have shown that by recording the electrical activity during word processing, and across sentences in time and across the scalp in space, the ERP can help to describe the differential involvement of different brain regions (which can then be pinpointed with more sophisticated ERP analyses and other imaging techniques) and that this can be accomplished with the temporal continuity and precision that natural language processing requires. In the process, the functional roles of the various regions of the brain on the right and the left will not be left unrighted.

ACKNOWLEDGMENTS

Work reported in this chapter was supported by grants HD22614, AG08313, and MH52893 to M. Kutas. J. W. King was also supported in part by a McDonnell-Pew postdoctoral fellowship from the San Diego Center for Cognitive Neuroscience, funds from a grant to the Center for Human Information Processing (MH-14268), and funds from the Center for Research on Language (DC00041-01) at UCSD. G. Ganis also received support from a local McDonnell-Pew graduate training fellowship and the CRL training grant.

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