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Neural localization of semantic context effects in electromagnetic and hemodynamic studies

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Abstract

Measures of electrical brain activity (event-related potentials, ERPs) have been useful in understanding language processing for several decades. Extant data suggest that the amplitude of the N400 component of the ERP is a general index of the ease or difficulty of retrieving stored conceptual knowledge associated with a word, which is dependent on both the stored representation itself, and the retrieval cues provided by the preceding context. Recordings from patients with brain damage, intracranial recordings, and magnetoencephalographic data implicate a (probably large portion of) the left temporal lobe as the largest source of the N400 semantic context effect, with a substantial but lesser contribution from the right temporal lobe. Event-related functional magnetic resonance (fMRI) studies using semantic context manipulations are dominated by observations of greater hemodynamic activity for incongruent sentence completions or semantically unrelated words than congruent or related words, consistent with the direction of the ERP effect. The locations of the hemodynamic effects show some variability across studies, but one commonly identified region is the left superior temporal gyrus, which is compatible with the electrophysiological results. A second commonly identified region in the fMRI studies is the left inferior frontal gyrus, which does not appear to make a substantial contribution to the N400 effect.

Keywords: Event-related potential; N400; Magnetoencephalography; Functional magnetic resonance imaging; Brain damage; Aphasia; Semantic context

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1. Introduction

Event-related brain potentials (ERPs) are small fluctuations in voltage, typically recorded noninvasively from the scalp, as participants process external stimuli and/or make overt motor responses. ERPs are the summation of synaptic potentials that are time-locked (synchronized) with stimulus presentation or motor responses. These synaptic potentials are almost exclusively cortical in origin, and are likely to arise primarily from the principal cell type of the cerebral cortex, pyramidal cells (Allison, Wood, & McCarthy, 1986; Regan, 1989; Nunez, 1981). In cognitive ERP research, the continuously varying waveform of voltage across time is conventionally carved up into "components" defined by their polarity (positive- or negative-going), latency, spatial distribution across the scalp, and functional sensitivity to experimental manipulation.

Many distinct components of the ERP have proven useful for understanding different aspects of language processing (see Kutas, Van Petten, & Kluender, in preparation for a more extensive review). For instance, components reflecting motor programming and response inhibition have been applied to speech production (the Lateralized Readiness Potential and no-go N2; Schmitt, Schlitz, Zaake, Kutas, & Münte, 2001; van Turennout, Hagoort, & Brown, 1998). A component that indexes the perceptual familiarity of auditory patterns (Mismatch Negativity) has been useful in understanding how the processing of phonemes from one's native language differs from processing phonemes of an unknown language, and in tracking the acquisition of the phonological patterns of a first or second language (Cheour et al., 1998; Näätänen et al., 1997). Distinct ERP components that may or may not be specific to morpholog-

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ical and syntactic processing (P600, left anterior negativity) have been productively applied to basic psycholinguistic questions about parsing, second-language acquisition, and the relationship between natural and artificial grammars (Friederici, Steinhauer, & Pfeifer, 2002; Hahne & Friederici, 2001; Osterhout, Holcomb, & Swinney, 1994).

Of the large number of ERP components showing sensitivity to language processes, the N400 has been the most commonly utilized, to date. The label "N400" refers to a negative-going voltage in the averaged ERP that reaches its peak amplitude around 400 ms after stimulus onset. This component was first noted by Kutas and Hillyard in the late 1970's (Kutas & Hillyard, 1980a, 1980b, 1980c) in a comparison of sentence-final words that formed predictable completions and those that were semantically incongruent. While predictable endings elicited a broad positive waveform from 200 to 600 ms, the incongruent words elicited a large negative wave in this time range. Shortly thereafter, it became clear that neither anomalous endings nor even sentences were required to observe contextual modulation of N400 amplitude. The second words of semantically related pairs also elicited smaller N400s than the second words of unrelated pairs (Bentin, McCarthy, & Wood, 1985; Boddy, 1981; Rugg, 1985). Moreover, examination of the ERPs elicited by the intermediate words of sentences presented one word at a time showed large N400s for the first open-class words, which grew progressively smaller as the sentence context accrued and provided semantic constraints for subsequent words (Van Petten, 1993; Van Petten & Kutas, 1990, 1991). The semantic context effect is evident in printed, spoken, and signed language (Holcomb & Neville, 1990, 1991; Kutas, Neville, & Holcomb, 1987; Neville, Mills, & Lawson, 1992; see Fig. 1).

Perhaps less well known is that N400 amplitude is also sensitive to several lexical characteristics in addition to contextual factors. Low frequency (less commonly used) words elicit larger N400s than high frequency words. The N400 word frequency effect is likely to have a semantic basis, because the effect disappears when words are placed in a supportive semantic context (Van Petten, 1993; Van Petten & Kutas, 1990, 1991). In large part, low frequency words are uncommonly used because the concepts they express are less commonly invoked in text or conversation (see King & Kutas, 1998 for description of a frequency-sensitive ERP component that precedes the N400, which may index a processing difference that is more perceptual in origin). In reading, words with more orthographic neighbors (other words than can be formed by changing one letter) elicit larger N400s than words with fewer neighbors (Holcomb, Grainger, & O'Rourke, 2002). Holcomb and colleagues attributed this latter effect to greater global semantic activation when a word from a dense neighborhood is encountered, because of partial activation of numerous other words that form near-matches (activation that must ultimately be suppressed to isolate and interpret the meaning of the current word). Finally, concrete words elicit larger N400s than abstract words, although concrete words are typically associated with faster reaction times in behavioral measures (West & Holcomb, 2000). The concreteness effect on N400 amplitude may reflect a process similar to the neighborhood effect—retrieval of more information for concrete than abstract words, because of greater visual or other sensory detail included in the meaning representation of concrete words. Overall, the extant data suggest that

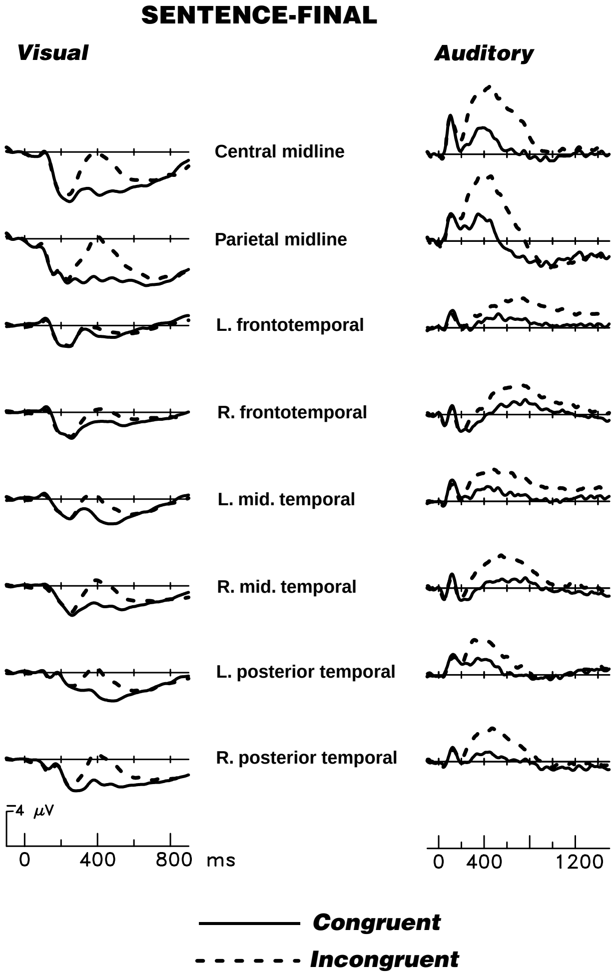

Fig. 1. Grand average ERPs to the final words of printed and spoken sentences, from 28 participants for the visual experiment and 21 for the auditory experiment (with different materials in the two experiments). In both experiments, participants performed a delayed word recognition task (decide if a word presented a few seconds later occurred in the sentence), so that decision-related potentials were postponed beyond the epoch shown here. The general morphology of the waveforms is distinct for the two modalities: note the negative peak at about 100 ms for spoken words (the auditory N100) that is absent in the visual modality, and that the auditory ERPs are predominantly negative with respect to the prestimulus baseline (the zero voltage line for the average) whereas the visual ERPs are predominantly positive with respect to the prestimulus baseline. The sentential semantic context effect is, however, broadly similar across modalities. Some of the differences in the semantic context effect between these particular examples are fairly typical of other published studies. Note that the context effect is somewhat larger over right than left scalp sites in the visual modality, but that this asymmetry is less evident in the auditory modality. Also note the earlier onset and longer duration of the context effect for spoken than printed words. Left column: data from Van Petten (1993). Right column: data from Van Petten et al. (1999).

N400 amplitude is a general index of the ease or difficulty of retrieving stored conceptual knowledge associated with a word, which is dependent on both the stored representation itself, and the retrieval cues provided by the preceding context (see also Kutas & Federmeier, 2000).

It is important to note that access to semantic memory need not depend on a verbal prompt. N400-like potentials are also evident in response to other meaningful stimuli—line drawings, photos, and environmental sounds—and also reduced in amplitude when these nonverbal stimuli are preceded by conceptually related stimuli (Ganis, Kutas, & Sereno, 1996; Holcomb & McPherson, 1994; Plante, Van Petten, & Senkfor, 2000; Van Petten & Rheinfelder, 1995; for recent review, see Kutas et al., in preparation). We refer to these potentials as "N400-like" because they closely resemble the verbal N400 in waveshape and timing, but have slightly different spatial distributions across the scalp. The conceptual context effect for pictorial materials has shown a more anterior maximum than the analogous effect for printed words, and the effect for meaningful nonlinguistic sounds has a small lateral asymmetry that is opposite that for spoken words (left-greater-than-right for sounds, right-greater-than-left for words, see below for more discussion of scalp asymmetries). These data suggest that verbal and nonverbal N400s reflect similar cortical computations occurring in different, but overlapping, populations of neurons.

One of the appeals of using ERPs to study language processing is the exquisite temporal resolution of brain electrical activity, which can be used to evaluate the sequence of cognitive operations intervening between the arrival of a sensory signal to the cortex and comprehension of its meaning, syntactic role in a current sentence, or motor program required to say its name (see e.g., Hahne & Friederici, 1999; Van Petten, 1995; Van Petten, Coulson, Rubin, Plante, & Parks, 1999; van Turennout et al., 1998). ERPs have been somewhat less informative about the anatomical substrates of the cognitive processes they reflect, due to their coarser spatial resolution. When recorded noninvasively from the scalp, the spatial pattern of electrical activity in the cortex undergoes some blurring imposed by the poor electrical conductivity of the skull. A second obstacle to inferring the neural generators of scalp-recorded activity is produced not by coarse spatial resolution per se, but by the complex shape of the cortex. The spatial pattern of electrical activity outside the head is determined not only by the location of intracranial currents around active synapses, but also the geometrical orientation of current flow along the long axes of pyramidal neurons (see Kutas & Dale, 1997; Kutas, Federmeier, & Sereno, 1999 for description and discussion). The cortical convolutions ensure that current flow can be oriented perpendicular to the surface of the skull (toward or away), parallel (pointing anteriorally, posteriorally, inferiorally, or superiorally), and any angle in between. The so-called *inverse problem* of computing the intracranial pattern of activity from the spatial pattern recorded at the scalp is mathematically ill-defined (i.e., has multiple solutions) unless additional constraints are provided. Over the last decade, additional constraints that have proven useful have been knowledge of an individual subject's pattern of cortical convolutions derived from structural magnetic resonance (MR) images, as well as the use of locations of hemodynamic activity from positron emission tomography or functional MR to suggest candidate locations that can then be evaluated for their fit to the spatial pattern of electrical fields from the scalp (Dale & Sereno, 1993; Heinze et al., 1994).

As compared to other scalp-recorded components of the ERP, the amplitude of the N400 context effect is relatively large, and its distribution across the scalp is wide—observable at essentially all scalp locations, but largest at sites over the central and parietal midline, as seen in Fig. 2. At the outset, these simple observations suggest that a large region of cortex—substantially larger than a single Brodmann area—may contribute to the scalp effect. If indeed a large swath of cortex comprising more than a single gyrus or sulcus (or multiple nonadjacent regions) is responsible for the scalp-recorded N400, the application of modeling techniques based on the assumption of a single equivalent dipole may be less successful than for other ERP components with more focal scalp distributions. The initial attempt to model the cortical generators of the N400 context effect from its distribution on the scalp was unsuccessful (Curran, Tucker, Kutas, & Posner, 1993), and the second attempt suggested a broad collection of sources widely distributed across the cortex with substantial individual variability (Haan, Streb, Bien, & Rösler, 2000). Another recent study used a larger electrode array, and in particular, more sites located below the base of the brain—below the inion of the skull, and below the ear canals. Although they did not attempt to fit a dipole model, Johnson and Hamm (2000) observed polarity inversions (P400s rather than N400s) at these inferior sites, the pattern one would predict if the generating sources lay in the temporal lobes.

Other methods for inferring the neural generators of an ERP component include recordings from patients with well-characterized brain damage, recordings of ERPs from electrodes located on or in the cortex (inside the skull), and evoked magnetic fields that parallel their electrical counterparts in functional specificity. All of these have been applied to the neurogenesis of the N400, as reviewed below. Extant data converge to implicate a (probably large portion of) the left temporal lobe as the largest source of the scalp N400, with a substantial but lesser contribution from the right temporal lobe. It is important to keep in mind, however, that only a subset of the N400 manipulations noted above have yet been applied in the patient, intracranial, and magnetoencephalographic studies. It is quite possible, for instance, that repeating some of the experiments below in a different modality, or using pictorial material or nonliteral language, would produce a slightly different description of the set of relevant cortical areas within the broad network identified thus far, and/or a different balance of activity between the two cerebral hemispheres.

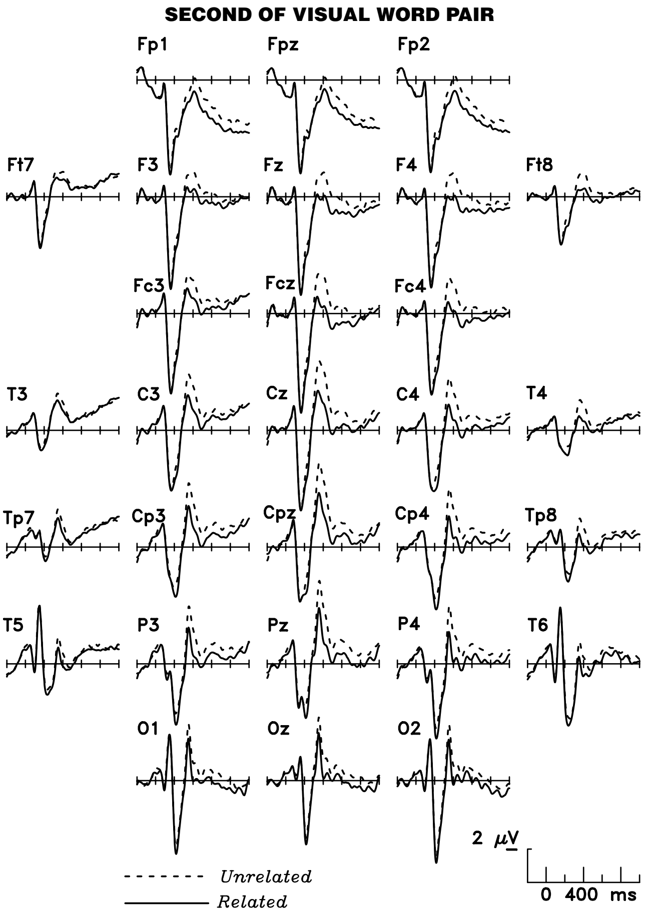

Fig. 2. Grand average ERPs to the second words of semantically related and unrelated visual word pairs, from 30 participants. Participants performed a delayed letter search task (decide if a letter presented after the second word was present in either word of the pair), so that decision-related potentials were postponed beyond the epoch shown here. Scalp sites are arrayed from anterior at the top to posterior at the bottom, and from left (on the left) to right (on the right). In contrast to completely predictable sentence completions, even related words elicit substantial N400s in this (and published) examples. Note the right-greater-than-left asymmetry of the context effect, particularly apparent when comparing sites over the right temporal lobe (Ft8, T4, Tp8, and T6) to those over the left temporal lobe (Ft7, T3, TP7, and T5). Electrode site nomenclature: "z" for zenith or midline, odd numbers on the left, even numbers on the right, larger numbers indicate greater distance from the midline; Fp for prefrontal, F for frontal, Ft for frontotemporal, Fc for frontocentral, C for central, P for parietal, O for occipital, T for temporal, and Tp for temporoparietal. Unpublished data from Luka and Van Petten.

2. Hemispheric asymmetry

2.1. Lateral asymmetry at the scalp

In the auditory modality, the scalp distribution of the N400 semantic context effect for both sentences and word pairs appears to be bilaterally symmetric, on average. Only a small minority of auditory studies include statistically significant asymmetries and these are not consistent (right-greater-than-left: Van Petten & Rheinfelder, 1995; van den Brink, Brown, & Hagoort, 2001; left-greater-than-right: Hahne & Friederici, 2002; Holcomb & Neville, 1990). Inspection of figures and tables for auditory experiments with statistically nonsignificant asymmetries shows both left-larger and right-larger effects (Balconi & Pozzoli, 2004; Connolly & Phillips, 1994; Connolly, Phillips, & Forbes, 1994; Federmeier, McLennan, de Ochoa, & Kutas, 2002; Hagoort & Brown, 2000; Röder, Rösler, & Neville, 2000; van den Brink & Hagoort, 2004; Van Petten et al., 1999). In the visual modality, the scalp distribution of the N400 semantic context effect has a small but persistent rightward asymmetry for both word pairs and sentences (Coulson, Federmeier, Van Petten, & Kutas, 2005; Holcomb & Neville, 1990; Kutas, 1993; Kutas & Hillyard, 1982; Kutas, Van Petten, & Besson, 1988b; Olichney et al., 2000; see Figs. 1 and 2 for examples). This asymmetry is not statistically significant in every report, perhaps because it is most reliable in right-handed subjects lacking left-handed family members, but when significant asymmetries are reported, there are essentially always in the direction of right-greater-than-left.

When subjects perform rhyme judgments on visually presented words, nonrhyming words elicit a larger negative potential with a striking resemblance to the semantic N400 effect, but with a larger rightward asymmetry (Barrett & Rugg, 1989; Kramer & Donchin, 1987; Rugg, 1984a, 1984b). The direction of this latter asymmetry is surprising, as the conversion of orthography to phonology is generally considered to be a strongly lateralized ability, but lateralized to the left hemisphere (Levy & Trevarthan, 1977; Patterson & Besner, 1984; Rodel, Dudley, & Bourdeau, 1983). Based on these and other considerations, Van Petten and Rheinfelder (1995) argued that the rightward scalp asymmetry of the N400 is a case of "paradoxical lateralization" arising from a slight tilt in some of the left hemisphere tissue that gives rise to the scalp field, such that the summed electrical dipole points slightly toward the right. The greater bilateral symmetry of auditory than visual results suggests that slightly different cortical regions contribute to the semantic context effect in the two modalities.

2.2. Hemispheric contributions to the N400 in commissurotomy patients

One of the considerations leading to our suggestion that the rightward scalp asymmetry of the N400 reflects a stronger contribution from the left than right hemisphere comes from a study in "split-brain" patients whose corpus callosi had been severed for the relief of severe epilepsy (Kutas, Hillyard, & Gazzaniga, 1988a). In these individuals, stimuli presented to the right visual hemifield are largely[1] restricted to the left hemisphere and vice-versa. Sentence frames were spoken so that both hemispheres had access to the semantic

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[1] Visual information from the ipsilateral field can reach the cerebral cortex via subcortical commissures that are not sectioned in this operation, in addition to the anterior commissure that is variably included in the standard surgery. However, the large majority of cortico–cortico connections between occipital and posterior temporal visual cortical regions travel in the corpus callosum.

context. These were completed by a pair of words presented to each hemifield in four conditions: the same congruent completion in both hemifields, the same incongruent completion, or mixed pairs such that one hemisphere received a congruent and one an incongruent word. Right visual field (left hemisphere) completions resulted in N400 context effects for all five patients. Left visual field (right hemisphere) completions resulted in N400 context effects for only those patients whose right hemispheres also had productive language capability (i.e., patients who could read aloud words appearing in the LVF). Words presented to a "speaking hemisphere" resulted in N400 context effects over both the right and left scalp, while words presented to a mute right hemisphere resulted in no context effect. Bilateral control of speech production is an unusual state of affairs, one that often takes years to develop in commissurotomy patients post-surgery. In most neurologically intact individuals, it is generally thought that the "speaking hemisphere" is the language-dominant or left hemisphere. These data thus suggest that in the majority of normal individuals, the N400 is more dependent on the left than right hemisphere.

2.3. N400 effects in patients with right hemisphere lesions

Only a small number of studies have examined semantic context manipulations in patients with right hemisphere (RH) lesions, who have typically been included as controls for aphasic patients. Hagoort, Brown, and Swaab (1996) presented spoken word pairs to eight nonaphasic stroke patients with RH lesions in variable locations, but centered around the Sylvian fissure. In the comparison between strongly associated and unrelated words, the RH patients generated N400 context effects that were very similar to healthy controls. For weakly associated versus unrelated words, the RH patients generated a visible N400 effect, but one that was considerably smaller than in the controls; the group comparison was marginally significant ($p = .06$). In a brief conference proceedings paper, Kotz, Friederici, and von Cramon (1999) and Kotz and Friederici (2003) also described normal N400 context effects in seven RH patients for strongly related word pairs, but reduced effects for weakly related pairs, although no statistical analyses were reported. Swaab, Brown, and Hagoort (1997) presented auditory sentences with congruent or incongruent final words to six nonaphasic patients with strokes centered around the right temporoparietal area. These patients showed an N400 context effect with the same onset and peak latency as in healthy age-matched controls, but only some two-thirds of the amplitude. This apparent amplitude reduction due to right-hemisphere lesions was, however, not statistically significant. Overall, it appears that right hemisphere lesions do reduce the N400 semantic context effect, but only moderately, so that small subject numbers have made it difficult to quantify this impact in a rigorous way.

3. Anterior versus posterior lesions in neurological patients

Numerous studies have examined N400 effects in neurodegenerative disorders such as Alzheimer's disease, Parkinson's disease, schizophrenia, and temporal lobe epilepsy (e.g., Ford et al., 1996; Friederici, Kotz, Werheid, Hein, & von Cramon, 2003; Kumar & Debruille, 2004; Miyamoto, Katayama, Kohsaka, & Koyama, 2000; Schwartz, Federmeier, Van Petten, Salmon, & Kutas, 2003; Schwartz, Kutas, Butters, Paulesn, & Salmon, 1996). Here, we consider only brain damage associated with more discrete lesions that can be more readily linked to the anatomical basis of the N400 in the normal brain. Lesions that spare comprehension of word meaning—although they may produce other cognitive deficits—are generally associated with preserved N400 effects. For instance, patients with episodic memory deficits due to medial temporal or diencephalic damage show normal modulation of the N400 by semantic context, and by word repetition with lags less than a minute (Olichney et al., 2000).

Large amplitude reductions and delayed latencies of the N400 semantic context effect are observed in patients who have suffered strokes in the left temporal lobe or temporoparietal junction—broadly, the same regions leading to an aphasic syndrome marked by a semantic comprehension deficit (Friederici, Hahne, & von Cramon, 1998; Hagoort et al., 1996; Swaab et al., 1997). Indeed, there is a close correspondence between the magnitude of the N400 effect and standardized comprehension tests in these aphasic patients (Kojima & Kaga, 2003; Marchand, D'Arcy, & Connolly, 2002).

In contrast to the severe impact of left temporal and inferior parietal damage[2] on the scalp-recorded N400, patients with damage restricted to the frontal lobe have typically shown normal semantic context effects. Neuropsychologically, these are patients who may have difficulty in the comprehension of syntactically complex sentences, or word-finding problems (anomia) in production, but who show spared comprehension of isolated words and simple sentences. In a group of patients with lesions confined to the inferior frontal gyrus, anterior insula, and basal ganglia, Friederici, von Cramon, and Kotz (1999) observed normal N400 differences between semantically congruent and incongruent sentence completions. However, the patients with inferior frontal or insular damage lacked a different ERP effect in response to a phrase structure violation (early left anterior negativity triggered by an illegal preposition–verb sequence). Hagoort, Wassenaar, and Brown (2003) divided a group of patients with large lesions that included the frontal lobe into those with "agrammatic" comprehension versus others with a "remaining capacity for processing syntax." These investigators examined two types of syntactic sentence errors (word order and agreement

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[2] The impact of damage to the left temporal versus inferior parietal regions has not been experimentally separated, as strokes influencing one region tend to affect the other as well.

violations) that produced large positive potentials in normal control subjects, rather than N400 differences. The less-impaired aphasic group showed reduced, but qualitatively normal ERP responses to both error types. The agrammatic patients lacked any ERP difference between correct and incorrect verb number. However, the word order violations (as in "…the expensive very clock…") elicited an N400 effect in the agrammatic group, attributed to their increased reliance on semantic processing strategies in the absence of an ability to use syntactic cues. These results suggest that although the frontal lobe is critical for many aspects of language processing, it makes little direct contribution to the N400.

A third study confirms that damage to prefrontal cortex can result in abnormal ERPs during language comprehension, but that these abnormalities are in components other than the N400. Swick and colleagues examined 11 stroke patients with damage to dorsolateral prefrontal cortex, a brain region associated with a variety of cognitive processes that can be loosely characterized as executive function (8 had left hemisphere damage, 3 right hemisphere damage). The damage extended ventrally into the left inferior frontal gyrus in some of these patients, who also showed anomia and/or apraxia in production, but little comprehension deficit. The group of frontal patients exhibited N400 context effects that were indistinguishable from age-matched controls in the comparison between simple sentences ending with congruent or incongruent words (Swick, Kutas, & Knight, 1998; see also Swick, 2004). However, Swick et al. (1998) did report an abnormality in the ERPs of the frontal patients. In the control group, the larger N400 elicited by incongruent sentence completions was followed by a prominent positive component that was also larger than that elicited by congruent sentence completions, which we will label the *post-N400 positivity* for lack of a better term. This late positive effect was absent in the frontal patients.

The elimination of the post-N400 positivity by frontal damage in Swick et al.'s (1998) study leads to an unusual state of affairs in cognitive ERP research—good knowledge about the neural generator of a scalp-recorded potential, accompanied by little knowledge about the functional process it indexes. Across published studies, larger late positivities sometimes accompany the N400 elicited by incongruent sentence completions, and sometimes not (see Ford et al., 1996; Gunter, Jackson, & Mulder, 1992; Schwartz et al., 1996; Woodward, Ford, & Hammett, 1993 for examples of this late positive response, and Chwilla & Kolk, 2003; Friederici, Pfeifer, & Hahne, 1993; Van Petten et al., 1999, Fig. 1 for cases where it is absent). To date, little research effort has been expended in describing the relevant difference(s) between the cases of a monophasic context effect (larger N400 only) and the cases of a biphasic effect (larger N400 followed by larger positivity; see Coulson & Van Petten, 2002). Based on a preliminary survey of published studies, it appears that post-N400 positivities are more frequently observed in sentence than in word-pair experiments, and may be more frequently observed in healthy older adults than in young adults. However, it is equally possible that the presence or absence of this effect is dependent on the exact nature of the stimulus materials, which are difficult to compare across published studies (see Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991 for a post-N400 positivity that was contingent on word frequency). Finally, it is not currently clear whether post-N400 positivities observed in different studies have similar topographic distributions across the scalp (suggesting a unitary effect) or distinct distributions that are more suggestive of diverse effects triggered by different causes in different experiments (so that we would expect no single functional correlate).

4. Intracranial ERPs

Electrodes placed directly on the cortical surface, or within the depths of the cortex, are used in patients being evaluated for possible surgical relief of seizures that are resistant to drug treatment. The potentials recorded from these electrodes have the same neurophysiological basis in synaptic activity as scalp-recorded ERPs, but can show large amplitude gradients within a distance of a few centimeters. Intracranially recorded ERPs can thus be very informative about the responsiveness of local cortical regions to specific experimental contrasts. The information available from intracranial ERPs is, however, limited by the fact that electrode placement is governed by clinical considerations and does not provide whole-brain coverage in any patient. Across patients, the medial portion of the temporal lobe is more typically sampled than other cortical regions because this part of the brain is more seizure-prone than most.

A potential recorded in the anterior medial part of the temporal lobe (anterior to the hippocampus, in the vicinity of the collateral sulcus dividing the fusiform gyrus from the parahippocampal gyrus) has the same timecourse as the scalp-recorded N400, and is sensitive to the same experimental manipulations. This *AMTL-N400* is larger for open-class words than for closed-class words and unpronounceable letter strings, larger for semantically unrelated than related words in word pairs, and larger for incongruent than congruent sentence completions (Nobre, Allison, & McCarthy, 1994; Nobre & McCarthy, 1995). Other research groups have reported that what appears to be the same ERP component, in the same location, is reduced by repetition of words and line drawings (Elger et al., 1997; Fernández et al., 2001; Guillem, N'Kaoua, Rougier, & Claverie, 1996; Smith, Stapleton, & Halgren, 1986).

The anterior medial part of the temporal lobe is the core brain region affected in a neurodegenerative disease known as *semantic dementia*, in which patients suffer a progressive loss of semantic knowledge with relative preservation of phonology, syntax, and recent episodic memory (Bozat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000; Garrard & Hodges, 1999; Mummery et al., 2000; Patterson & Hodges, 2000). In patients with nonprogressive lesions of the temporal pole, Damasio and colleagues report a specific deficit in accessing words for pictures of people and animals, even when the concept is known (e.g., a patient is not able to produce the word SKUNK, but responds "a common animal around here, black and white, smells bad, often seen squashed on the road"). These authors thus suggest that the anterior temporal lobe is not the repository of conceptual knowledge, but a critical intermediary between word forms and semantic memory (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996). Whatever the correct functional description of the anterior medial temporal region turns out to be, the convergence between the intracranial recordings and the neuropsychological data are a very strong indication that this brain region is critical for access to semantic memory, and almost certainly contributes to the scalp-recorded N400.

However, as noted above, the large amplitude and broad scalp distribution of the scalp-recorded N400 suggest a more extensive swath of generating cortex than the small and circumscribed region where AMTL-N400s are recorded. Additionally, the lesions that produce large N400 decrements in aphasic patients are located in more superior and lateral aspects of the temporal lobe, and rarely extend as far ventrally as the AMTL region. Intracranial recordings have been conducted outside the medial temporal lobe, but unfortunately not with a semantic context manipulation. Instead, a more typical contrast is between new and repeated words or line drawings during continuous recognition tasks. Repeating a meaningful item within a short interval (~3 min) reduces the amplitude of the scalp N400, but can also influence a variety of other ERP components, so that it is more difficult to link the results of these memory paradigms with the N400 per se. Nonetheless, repetition is reported to influence an intracranial potential in lateral temporal neocortex (superior and middle temporal gyri), in the same latency range as the scalp N400 (Elger et al., 1997; Guillem et al., 1996; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994).

5. Magnetoencephalography

Current flow in the brain produces small magnetic fields in addition to the voltage fields recorded as ERPs. Epochs of the magnetoencephalogram (MEG) following stimulus presentation can be averaged to derive the event-related magnetic field in much the same way that ERPs are formed from the electroencephalogram. Although both the raw MEG and the event-related fields resemble their electrical counterparts in many ways, some physical differences make the anatomical origins of the magnetic signals easier to localize (while preserving the same temporal resolution as electrical signals; for review see Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). One reason is that although the skull is a very good electrical insulator and thus imposes a spatial blurring between the brain and the scalp, bone is magnetically transparent. The magnetic fields recorded just outside the head are also much more strongly influenced by the geometrical orientation of intracranial current flow. The latter fact is a mixed blessing. On the one hand, the convoluted shape of the cortex ensures that current flow in different sulci and gyri will have distinctive orientations, and this is useful in modeling the location of tissue responsible for a magnetic field (particularly when combined with structural magnetic resonance scans showing the gyral/sulcal pattern of each subject). On the other hand, only current flow that is at least somewhat tangential to the surface of the head will produce detectable magnetic fields. This means that it is primarily the activity of cortex in sulci, rather than in gyri (where the pyramidal cells are oriented perpendicular to the skull) that can be detected. This limitation is not as severe as it sounds, as it is estimated that two-thirds of the cortical sheet lies in sulci (Armstrong, Schleicher, Omran, Curtis, & Zilles, 1995; Zilles, 1990). A final difference between electrical and magnetic recordings is that MEG may be less sensitive to cortical sources located far away from the surface of the head (such as medial temporal cortex). Overall, MEG presents perhaps the best combination of spatial and temporal resolution of noninvasive methods in common use. Unfortunately, MEG studies are not very common, because the recording devices (SQUID, superconducting quantum inference device) are expensive and, to date, not widely supported by routine clinical applications in the way that magnetic resonance scanners are.

Four MEG comparisons between congruent and incongruent sentence completions have been published. Averaged waveforms of all studies show N400m semantic context effects with more focal spatial distributions than those seen in electrical recordings. Simos, Basile, and Papanicolaou (1997) placed detectors over the left side of the head only (because they used an older SQUID with few detectors), and modeled the spatial distribution of the event-related fields as dipoles for each subject, in conjunction with structural MR scans of each subject. This procedure indicated sources around the parietotemporal junction for five subjects reading English sentences, and sources in the medial temporal lobe in two subjects (perhaps near the AMTL region identified by Nobre et al., 1994 & Nobre & McCarthy, 1995). Kwon et al. (2005) similarly identified a superior temporal dipole in recordings over the left hemisphere only, for spoken Korean sentences. With printed Finnish sentences, Helenius, Salmelin, Service, and Connolly (1998) used a SQUID that allowed whole-head coverage, and a more sophisticated modeling technique that allowed the detection of multiple cortical dipoles. These investigators detected sources around the midpoint of the anterior–posterior extent of the left superior and/or middle temporal gyrus in eight of 10 subjects; three of these showed an additional source around the left temporoparietal junction. The two subjects who did not show a source near the center of the superior/middle temporal gyrus had the left tempoparietal source plus a source in the left frontal lobe (dorsolateral and ventral motor, rather than inferior frontal gyrus). Finally, five subjects showed a secondary source at the tempoparietal junction in the right hemisphere. A more recent study from the same research group (Helenius et al., 2002) using auditory materials found a source in left superior temporal gyrus for all the participants with normal language abilities (dyslexics were also included), and a source in the homologous region of the right hemisphere for the majority of these. The fairly broad distribution across the left superior and middle temporal gyri and inferior parietal lobe is in good agreement with the general description of the location of the lesions that produce language comprehension deficits in aphasic patients (Bogen & Bogen, 1976; Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004), together with the right-hemisphere homologue of "Wernicke's area."

Although comparisons between congruent and incongruent sentence completions yield the largest differences in N400 amplitude, the primary reason for research interest in the N400 is that this component is sensitive to a broader range of psycholinguistic manipulations. In addition to congruent and incongruent sentence completions, Halgren et al. (2002) thus examined other contrasts that influence the scalp-recorded N400: closed- versus open-class words in intermediate sentence positions, intermediate open class words appearing early in sentences versus later when they can benefit from the preceding context, and low- versus high-frequency open-class words. When modeled as a single dipole, all four contrasts produced a similar source centered in the left superior temporal gyrus, around the midpoint of its anterior–posterior extent.[3] The drawback to dipole modeling methods is that activity in a continuous region of cortex is represented as a single point at its center, which obscures the spatial extent of an active area. Halgren and colleagues thus applied a newer method of *distributed source modeling* (see also Dale et al., 2000; Darvas, Pantizis, Kucukaltun-Yildrim, & Leahy, 2004), and additionally subdivided the N400m latency range into briefer epochs to see how the sentence congruity effect evolved over time. The results showed an initial focus in the posterior half of the left superior temporal gyrus from 250 to 265 ms after final word onset, spreading forward and ventrally to occupy most of the left temporal lobe by 365 ms poststimulus onset. By the peak of the N400m response (370–500 ms), greater activity for incongruent words had spread to the frontal lobe bilaterally, and to the anterior temporal lobe in the right hemisphere. The contrast between open-class words occurring early in sentences (with little preceding context) versus later in the same sentence showed a similar spatial pattern, except for the near-absence of frontal activity. Because the sentence congruity and word position effects on N400 amplitude have appeared to be quite similar in electrical recordings (Van Petten, 1993), it is possible that the late frontal activity observed by Halgren et al. (2002) reflects not the N400, but the later positive component triggered by incongruent sentence completions in some studies, and eliminated by lesions of the frontal lobe (Swick et al., 1998).

Overall, the neuropsychological, intracranial, and MEG results converge to suggest that a large portion of the temporal lobes are responsible for the scalp-recorded N400 component, but that the left hemisphere makes a larger contribution than the right. Direct comparisons between language modalities (spoken, written, and signed), between literal and nonliteral language, and between conceptual relationships expressed by words versus nonverbal stimuli await further research.

6. Should we expect electromagnetic and hemodynamic studies to converge?

Currently, functional magnetic resonance imaging (fMRI) is the other most commonly used technique for studying language processing in neurologically intact individuals, so that comparisons of fMRI to ERP results are of some interest. Current knowledge from animal research suggests that the BOLD[4] response is closely correlated with intracranially recorded, low-frequency field potentials (i.e., those that produce scalp EEG) in several brain regions, at least at relatively slow stimulus presentation rates (see Lauritzen & Gold, 2003; Logothetis, 2003; Logothetis & Pfeuffer, 2004, for reviews). Indeed, there is general agreement that the BOLD response is more closely related to these field potentials produced by synaptic activity than to the average firing rate (action or spike potentials) of neurons. One study reports a linear correlation between the amplitudes of the BOLD signal and the very early components of the somatosensory ERP in humans (Arthurs, Williams, Carpenter, Pickard, & Boniface, 2000). These results suggest that ERPs and BOLD fMRI signals are produced by the same underlying cellular activity (although the BOLD signal follows with a substantial delay and is temporally prolonged), and can be readily compared. However, other considerations suggest some possible caveats to this conclusion, which reflect the incomplete state of our knowledge about both ERP and BOLD responses. Below, we note a not-completely resolved issue about the generation of the N400, and then a similarly unresolved issue about the localization of BOLD responses.

The N400 component, and its modulation by semantic context, are identified in **averaged** ERPs—extracted from the continuous electroencephalogram (EEG) by aligning time epochs at the moment of stimulus onset and then arithmetically averaging each post-stimulus time point across multiple trials. A standard assumption is that a larger amplitude at any given time point in the averaged signal reflects larger amplitudes at more or less that time in the individual trials that contribute to the average. How-

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[3] The estimated dipole for the word frequency effect was quite weak and not statistically significant. A likely reason for this is that larger amplitude N400s for low- than high-frequency words are observed only for the first one or two open-class words in congruent sentences (Van Petten, 1995), but the measure in Halgren et al. (2002) collapsed across the first several open-class words, which probably diluted the frequency effect.

[4] Blood oxygen level-dependent signal, the most typical measure in cognitive fMRI experiments.

ever, it has been pointed out that larger amplitude at Time X in an average could occur, not due to increased amplitudes at Time X in each individual trial, but to stronger phase locking between stimulus onset and ongoing oscillatory activity (Makeig et al., 2002; Makeig, Debener, Onton, & Delorme, 2004). Imagine, for instance, a continuous sine wave with both positive and negative peaks. If the phase of the sine wave were reset each time a stimulus occurred (so that, for instance, the phase was always negative at about 400 ms), averaging would result in a detectable response although the amplitude of the sine wave never varied. If indeed an ERP component were produced by phase-reset alone, without any net change in the number of active neurons and synapses, one would expect no corresponding BOLD signal.[5] The general idea that peaks in averaged ERPs are caused by event-related phase reset rather than absolute increases in the amount of neural activity is not universally accepted, and the analytic methods on which the argument rests have not gone unchallenged (Yeung, Bogacz, Holroyd, & Cohen, 2004). Even if some ERP components reflect primarily phase-reset, the contribution of this mechanism will have to be evaluated separately for each component of interest, because the neural dynamics underlying different components at different post-stimulus latencies could easily be distinct. Fell et al. (2004) have recently examined whether the intracranial AMTL-N400 is accompanied by greater phase coherence (indicative of phase reset) or greater absolute power (indicative of more neural activity) than a pre-stimulus period, and concluded that both mechanisms contributed to the AMTL-N400 (note, however that the analytic methods used were those whose logic was challenged by Yeung et al., 2004).

The ambiguity associated with the location of BOLD fMRI responses relative to the location of increased neural activity is simply that hemodynamic responses occur in blood vessels, not in neurons. Recent empirical work comparing the spatial distribution of neural and hemodynamic activity in animals indicates that a BOLD response can sometimes be observed in regions with no detectable neural response (Disbrow, Slutsky, Roberts, & Krubitzer, 2000), likely because the hemodynamic response can propagate both downstream (into draining venules) and upstream (to regulate incoming blood flow) from the capillaries surrounding active neurons (Harrison, Harel, Panesar, & Mount, 2002; see Lauritzen & Gold, 2003 for review). The magnitude of this spread might be detrimental for very fine-grain cortical mapping studies, but is probably of less concern for our current interest in determining the general cortical regions affected by semantic context manipulations. Much less clear is how regional differences in the density of capillaries, and in the distribution of blood-flow control points, might affect the ability to obtain a BOLD signal from different parts of the cortex. After demonstrating such differences (in the chinchilla brain), Harrison et al. (2002) conclude that "A worst-case scenario is that perhaps only certain high-activity regions of cortex are endowed with sufficient capillary network density/control to produce signals for functional imaging, and that some areas of association cortex, for example, may never generate such a response." This worst-case scenario of no hemodynamic response from some brain areas is almost certainly too pessimistic, but serves as a useful reminder that it may be easier (i.e., require fewer trials) to find BOLD responses in some areas than others.

Overall, existing knowledge about the neuro/hemo mechanisms underlying the generation of the N400 and the BOLD response suggest that it is reasonable to expect some degree of convergence about the brain areas sensitive to semantic context, but also that some discrepancies might be expected if, on the one hand, a portion of the N400 is produced by phase-reset rather than increased neural activity, and on the other hand, some brain regions generate weaker BOLD signals than others.

7. Comparing electromagnetic and hemodynamic imaging results

A large number of studies using positron emission tomography and functional magnetic resonance imaging (fMRI) have examined semantic processing, and a full listing is outside the scope of the current review. However, only a small number of fMRI experiments have used experimental designs typical of psycholinguistic studies with behavioral and ERP measures—event-related designs that avoid the effects of predictability, arousal, and strategy variability that may influence comparisons with blocked presentation of different stimulus conditions. Across published studies comparing semantically related and unrelated word pairs, or sentences ending with congruent and incongruent words, the unrelated or incongruent items invariably elicit a larger hemodynamic signal than the related or congruent items, with only a few scattered reports of brain regions showing a greater response in the related/congruent condition. This aspect of the fMRI results is like the ERP result of larger amplitude N400s for unrelated/incongruent items. Table 1 summarizes the results of the 12 event-related fMRI experiments published to date. There is no obvious division between the results of studies using different tasks (listed in Table 1), between word pairs and sentences, or between auditory and visual presentation.[6] A fair amount of variability is evident, in that no region is identified by more than two-thirds of the experiments. However, some

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[5] One reviewer of the current paper suggested that this scenario was itself arguable, in that phase-reset might require some quantitative change in neural activity that would, in turn, produce a BOLD response. This is an empirical question about which almost nothing is known, beginning with the nature of the hypothesized phase-reset signal, continuing with the magnitude of neural change needed to stimulate a hemodynamic change, and ending with the sensitivity of fMRI methods for detecting what might be very small changes in hemodynamic state.

[6] No fMRI experiment has directly compared semantic context effects in word pairs versus sentences, or auditory versus visual presentation, and the gyral description of brain regions in Table 1 may conceal subtle differences that depend on these factors.

Table 1
Semantic context results from event-related functional magnetic resonance imaging

Study	Stimuli	Modality	STG/PT	MTG	IFG	Fusi.	Temporal pole/PhG	Frontal	Insula	Parietal
Greater activity in the unrelated condition										
Copland et al. (2003)	Word pairs	Visual	L mid.	—	—	—	—	L IFG	—	—
Kotz et al. (2002)	Word pairs	Auditory	B mid.	—	—	—	—	L IFG B MFG	B	—
Matsumoto et al. (2005)	Word pairs	Visual	L	—	—	—	—	L IFG Ant. cingulate	—	—
Rissman et al. (2003)	Word pairs	Auditory	L mid.	—	—	—	—	B MFG L precentral	—	—
Rossell et al. (2003)	Word pairs	Visual	—	—	—	—	L	—	—	—
Baumgaertner et al. (2002)	Sentences	Visual	—	L post.	—	—	—	L IFG	—	—
Cardillo et al. (2004)	Sentences	Auditory	—	—	—	—	—	L IFG	—	—
Friederici, Rüscshemeyer, et al. (2003)	Sentences	Auditory	B mid.	—	—	—	—	—	B	—
Kiehl et al. (2002)	Sentences	Visual	—	—	—	L post.	B	B precentral	—	—
Kuperberg et al. (2003)	Sentences	Visual	L post.	—	—	—	—	L IFG L MFG L orbital	—	—
Newman et al. (2001)	Sentences	Visual	—	R	—	—	L	L IFG L MFG L SFG Frontal pole Mid. cingulate	—	B angular
Ni et al. (2000, Experiment 2)	Sentences	Auditory	L post	—	—	—	—	L IFG B MFG Medial MFG Medial SFG	—	—

Note. L, left; R, right; B, bilateral; ant., anterior; mid., midway along anterior–posterior extent; post., posterior; STG/PT, superior temporal gyrus and/or planum temporale; MTG, middle temporal gyrus; ITG, inferior temporal gyrus; fusi., fusiform gyrus; PhG, parahippocampal gyrus; IFG, inferior frontal gyrus; MFG, middle frontal gyrus. All five of the word pair experiments used a lexical decision task (Copland et al., 2003; Kotz et al., 2002; Matsumoto et al., 2005; Rissman et al., 2003; Rossell et al., 2003). Four of the sentence experiments used an acceptability task (Friederici, kotz, et al., 2003; Kiehl et al., 2002; Kuperberg et al., 2003; Newman et al., 2001); two used lexical decision on the final word of the sentence (Baumgaertner et al., 2002; Cardillo et al., 2004); and one used an animacy judgment (Ni et al., 2000).

clear patterns are evident as well. The two most commonly reported regions are the left superior temporal gyrus in seven of the 12 experiments, and the left inferior frontal gyrus in eight of the twelve. These correspond, at least loosely, to the traditional locations of Wernicke's and Broca's areas, which is reassuring.

The degree of convergence between N400 and fMRI studies of semantic context effects is best described as moderate. The neuropsychological, MEG, and intracranial ERP evidence regarding the N400 suggest that a large portion of the left temporal lobe contributes to this potential, with two "hotspots" in the superior and anterior medial temporal lobes. Although the majority of the fMRI studies show superior temporal activity, it was a weak majority. Some studies lack any temporal lobe activations, and in most reports, the temporal lobe activations comprised small clusters of voxels. Compared to the robustness and replicability of N400 context effects across laboratories, this may indicate that fMRI (currently) has a lower signal-to-noise ratio than ERP recordings,[7] and that larger numbers of trials and/or subjects than typical may be required to visualize all of the active areas. Only three of the published studies report a differentiation between related/congruent and unrelated/incongruent conditions in anterior temporal cortex. The sparsity of significant context effects in this region may be artifactual: in at least some studies, this region was excluded from the field of view (Kotz, Cappa, von Cramon, & Friederici, 2002), and the most anterior part of the temporal lobe is particularly vulnerable to susceptibility artifacts causing signal loss.[8] As fMRI methods continue to improve, more anterior and medial temporal activations may be visible (see Devlin et al., 2000).

A point of divergence between electrophysiological and hemodynamic studies of semantic processing concerns the contribution of the left inferior frontal gyrus (IFG). As described above, lesions confined to the frontal lobe (including the IFG) appear to have little to no impact on the N400, but are the most commonly reported region in the event-related fMRI studies (8 of 12 experiments). Because it is generally accepted that frontal lesions also

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[7] See also Logothetis, Pauls, Augath, Trinath, and Oeltermann (2001) for reliability comparisons between intracranially recorded field potentials and the BOLD response, suggesting a better signal-to-noise ratio for the field potentials.

[8] In contrast, positron emission tomography (PET) studies comparing blocks of trials with semantic versus nonsemantic judgments have more frequently included hemodynamic activity in the temporal pole (Mummery, Patterson, Hodges, & Price, 1998; Price, Moore, Humphreys, & Wise, 1997; Vandenberghe, Nobre, & Price, 2002).

have little impact on the comprehension of word pairs or syntactically simple sentences, the authors of the hemodynamic studies have generally suggested that the observed activations reflect some aspect of strategic processing rather than comprehension per se. In future research, it may be of interest to determine whether left IFG activation can be reduced or eliminated if participants are assigned no overt task to perform, or if task-related activity can be confined to a time epoch separable from that of stimulus-related activity. ERP studies have generally shown little impact of the assigned task on the N400 sentence congruity effect,[9] and indeed large context effects when participants are instructed only to listen or read for comprehension (Connolly, Stewart, & Phillips, 1990; Kutas & Hillyard, 1980a, 1980b, 1980c), so that we would predict little change in temporal lobe activations contingent on task assignment, but it is possible that the IFG will prove more task-sensitive.

We have also speculated above that, in electromagnetic recordings, the frontal contribution to the semantic context effect manifests as a “post-N400 positivity” whose cognitive correlates are poorly understood (and may be diverse). If and when this ERP effect is brought under experimental control, so that it can be elicited and eliminated with some predictability, it will then be possible to determine whether or not hemodynamic IFG activity is sensitive to the same manipulations.

8. Summary

Manipulations of semantic context reliably produce modulations in the amplitude of the N400 component of the scalp-recorded ERP. When combined with the sensitivity of this component to lexical characteristics of the eliciting word (word frequency, concreteness), it is only a small inferential leap to associate the N400 with semantic processing per se, so that characterizing the neural tissue responsible for the N400 semantic context effect can clarify the brain regions critical for understanding the meanings of signs and symbols.

Although it is difficult to infer the neural generators of a scalp-recorded ERP component by visual inspection of data from healthy participants, likely anatomical locations can be indicated by intracranial recordings, magnetoencephalographic recordings, and scalp-recordings from patients with circumscribed brain damage. Damage to the left superior and/or middle temporal gyri leads to a severe reduction of the N400 semantic context effect, as expected from the fact that damage to this region also produces a behavioral deficit in comprehension. Lesion data alone are not sufficient to describe all of the neural tissue that generates a scalp-recorded potential, as damage to any portion of a neural circuit may preclude normal function of the remaining undamaged regions. Magnetoencephalographic studies of healthy individuals converge with the patient data in showing magnetic sources of the N400 semantic context effect in the left superior/middle temporal gyri, but also suggest involvement of a fairly broad swath of temporal neocortex that includes more anterior and ventral regions. The patient and MEG studies also converge to suggest a somewhat weaker contribution from homologous regions of the right temporal lobe, or perhaps a contribution that is more variable across individuals. The strength of the right hemisphere contribution for different sorts of stimulus materials has not yet been systematically investigated in neuropsychological or MEG studies, although recent work suggests that there are qualitative differences in the nature of the left and right hemisphere contributions to the scalp-recorded N400 in healthy participants (Coulson & Williams, 2005; Coulson & Wu, 2005; Federmeier & Kutas, 1999).

A second region of the temporal lobe has also been associated with semantic processing in neurological patients—the anterior medial temporal region. Intracranial recordings from patients prior to epilepsy surgery show locally generated N400s in the AMTL, although there has been little direct comparison of the two hemispheres because bilateral recordings are not often required for the clinical goal of localizing seizure activity. Overall, the three sources of evidence reviewed here—scalp recordings from neurological patients, intracranially recorded field potentials, and MEG data—are in good agreement in indicating that activity in a fairly large portion of the left temporal lobe is modulated by semantic context and contributes to the scalp-recorded N400, with a lesser contribution from the right temporal lobe.

The impact of semantic context on electrical brain activity was first documented in 1980, in contrast to a much shorter history in event-related hemodynamic measures (2000 onward). To date, fMRI studies with semantic context manipulations show a moderate degree of convergence with the electromagnetic evidence: all of the published reports show a larger hemodynamic response for semantically unrelated/incongruent stimuli than for semantically related/congruent items, but only a weak majority show activity in the superior or middle temporal gyri, and a smaller number show activity in the AMTL region. The absence of significant effects in some temporal lobe regions in some studies may only indicate that the signal to noise ratio of current imaging methods is such that more trials and/or more subjects may be required to visualize the full extent of cortical activation. The event-related fMRI studies have frequently found greater activity in the left inferior frontal gyrus for unrelated/incongruent items, although data from patients with frontal damage suggests that this region probably does not contribute to the scalp-recorded N400. Above, we discuss the possibility that IFG activity reflects processes that are distinct from those tapped by the electromagnetic N400, and suggest that it should be

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[9] ERP studies of word pairs have uniformly included an overt task assignment, largely due to the intuition that pairs are not very intrinsically interesting, so that an external task may be necessary to maintain participants’ attention at some minimal level.

possible to more closely link electromagnetic and hemodynamic results with further research.

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