

ERP Manifestations of Processing Printed Words at Different Psycholinguistic Levels: Time Course and Scalp Distribution

S. Bentin

Hebrew University

Y. Mouchetant-Rostaing, M. H. Giard, J. F. Echallier, and J. Pernier

INSERM-U280, Lyon, France.

Abstract

■ The aim of the present study was to examine the time course and scalp distribution of electrophysiological manifestations of the visual word recognition mechanism. Event-related potentials (ERPs) elicited by visually presented lists of words were recorded while subjects were involved in a series of oddball tasks. The distinction between the designated target and nontarget stimuli was manipulated to induce a different level of processing in each session (visual, phonological/phonetic, phonological/lexical, and semantic). The ERPs of main interest in this study were those elicited by nontarget stimuli. In the visual task the targets were twice as big as the nontargets. Words, pseudowords, strings of consonants, strings of alphanumeric symbols, and strings of forms elicited a sharp negative peak at 170 msec (N170); their distribution was limited to the occipito-temporal sites. For the left hemisphere electrode sites, the N170 was larger for orthographic than for nonorthographic stimuli and vice versa for the right hemisphere. The ERPs elicited by all orthographic stimuli formed a clearly distinct cluster that was different from the ERPs elicited by nonorthographic stimuli. In the phonological/phonetic decision task the targets were words and pseudowords rhyming with the French word *vitrail*, whereas the nontargets were words, pseudowords, and strings of consonants that did not rhyme with *vitrail*. The most conspicuous potential was a negative peak at 320 msec, which was similarly elicited by pronounceable stimuli but not by nonpronounceable stimuli. The N320 was bilaterally distributed over the middle temporal

lobe and was significantly larger over the left than over the right hemisphere. In the phonological/lexical processing task we compared the ERPs elicited by strings of consonants (among which words were selected), pseudowords (among which words were selected), and by words (among which pseudowords were selected). The most conspicuous potential in these tasks was a negative potential peaking at 350 msec (N350) elicited by phonologically legal but not by phonologically illegal stimuli. The distribution of the N350 was similar to that of the N320, but it was broader and including temporo-parietal areas that were not activated in the "rhyme" task. Finally, in the semantic task the targets were abstract words, and the nontargets were concrete words, pseudowords, and strings of consonants. The negative potential in this task peaked at 450 msec. Unlike the lexical decision, the negative peak in this task significantly distinguished not only between phonologically legal and illegal words but also between meaningful (words) and meaningless (pseudowords) phonologically legal structures. The distribution of the N450 included the areas activated in the lexical decision task but also areas in the fronto-central regions. The present data corroborated the functional neuroanatomy of word recognition systems suggested by other neuroimaging methods and described their timecourse, supporting a cascade-type process that involves different but interconnected neural modules, each responsible for a different level of processing word-related information. ■

INTRODUCTION

Levels of Processing in Visual Word Recognition

Visual word recognition is a complex process that involves several cognitive operations, such as visual encoding of letters, translation of the letters' shapes into a sequence of graphemes and orthographic patterns, and activation of lexical/phonological structures and their meanings. All these processes have been shown to be involved in reading words through many experiments

with normal subjects as well as by neuropsychological investigations of patients with different types of dyslexia. For example, the importance of visual processing for word recognition was highlighted by patients with neglect dyslexia, who have difficulty identifying letters while keeping track of their order in the word (e.g., Ellis, Flude, & Young, 1987) and by patients with attentional dyslexia who correctly identify the letters while misplacing them within or across words (e.g., Shallice & Warrington, 1977). The need for efficient orthographic

integration is demonstrated by patients with simultagnosia who are letter-by-letter readers (e.g., Patterson & Kay, 1982). The phonological dyslexia syndrome indicates that reading without phonology is deficient and, in conjunction with surface dyslexia and deep dyslexia, demonstrates the importance of the lexical access for normal reading. (For a detailed discussion of these syndromes, see Coltheart, Patterson, & Marshall, 1980, and Patterson, Marshall, & Coltheart, 1985.) On the basis of such evidence, the model used as a framework for the present study posits that visual word recognition involves different levels at which printed information is processed. These levels are (1) an orthographic level at which visual features are integrated to represent orthographic patterns, (2) a lexical level at which the phonological (and possibly the whole-word orthographic) representation of the printed word is activated, and (3) a semantic level at which the meaning of the word is accessed. In addition, tasks in which attention is directed to the phonetic features of the words (such as rhyming judgments) may induce phonetic activity that may or may not be involved in the word recognition process.

Although the exact nature of the processes involved in visual word recognition is still a matter of debate, the notion of levels (either of processing or of representation) is accepted and incorporated into most theories (e.g., Ellis & Young, 1996, ch. 8; McClelland & Rumelhart, 1981; Seidenberg & McClelland, 1989). Moreover, there is evidence that the level at which a word is processed is task-dependent and can be controlled. For example, several studies did not find semantic priming when the prime was processed at a letter level, at least if the stimulus onset asynchrony (SOA) between the prime and the target was longer than a few hundred milliseconds (e.g., Henik, Friedrich, & Kellogg, 1983; Smith, Theodor, & Franklin, 1983). In fact, semantic priming was absent even at a short SOA (200 msec) if the prime task was letter-search (Henik, Friedrich, Tzelgov, & Tramer, 1994). This result suggests that it is possible to control the putatively automatic activation of the semantic system by directing subjects' attention to the letter level. Other studies, however, challenged this interpretation, suggesting that the absence of priming in the Henik et al. (1994) experiment was an epiphenomenon caused by the difficulty of the task, which prevented the activation of the prime's semantic representation within the short SOA time range. When easier letter-level tasks were used, semantic priming was obtained, suggesting that the activation of meaning, although not resource-free, is the default in visual word perception (Smith, Bentin, & Spalek, submitted). It appears, therefore, that the questions of whether the processing of printed words may be restricted to a shallow level and whether the cognitive system involved in visual word recognition can be influenced and shaped by the purpose of reading the words are still open. A related question addresses the

word-related information that is processed at each level. For example, although traditional models of word recognition assume the existence of a mental lexicon in which word-related information is represented (but see Hinton & Shallice, 1991, and Seidenberg & McClelland, 1989, for alternative views), there is no consensus regarding the characteristics of this representation. According to some models, the lexicon contains only structural word-related information (phonologic and orthographic), whereas others see no evidence requiring separation between the structure of the word and its meaning.

An additional, major question concerning the levels of processing printed words is how the level-specific processes interact among themselves. One traditional view suggested a series of stages. Accordingly, the printed word should be processed first at the orthographic level. The output of this stage addresses a visual lexicon activating a word pattern and, subsequently, its semantic representation (e.g., Morton, 1969). Other models suggested that the various visual word perception operations are exerted in "cascade;" that is, a processing stage can begin before the previous stage is finished (McClelland, 1979). More recent models of reading suggest parallel, interactive processes by which the visual stimulus is processed in parallel at all levels and different words are represented by different patterns of activity in a neural network (Carr & Pollatsek, 1985; Coltheart, 1985; McClelland & Rumelhart, 1981; Seidenberg & McClelland, 1989; see also Jared & Seidenberg, 1991). Investigating the dynamics of visual word recognition has been partly hampered by the difficulty of disentangling processes by the use of discrete measures of performance such as the reaction time (RT). Some of these impediments can be overcome by studying the neurophysiological mechanisms that subserve this cognitive function. In addition to providing ways to distinguish between cognitive mechanisms by relating them to the neuroanatomically distinct structures that mediate them, some neurophysiological measures (such as ERPs) provide an on-line and time-continuous index of processing.

Neuroimaging and Electrophysiology of Word Recognition

Using positron emission tomography (PET), several studies have identified a number of brain structures activated during language processing (Beauregard et al., 1997; Demonet et al., 1992; Frith, Friston, Liddle, & Frackowiak, 1991; Frith, Kapur, Friston, Liddle, & Frackowiak, 1995; Petersen & Fiez, 1993; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Petersen, Fox, Snyder, & Raichle, 1990; Wise et al., 1991; Zatorre, Meyer, Gjedde, & Evans, 1996). The tasks typically used in those studies required either visual processing of words and wordlike stimuli during silent reading or "phonetic" processing of words, synthetic syllables, pure tones, and clicks while listening to speech. The activity elicited in these "low-level" process-

ing stages was subtracted from that elicited when subjects were instructed to perform higher-level processing such as phonologic (e.g., reading aloud) or semantic (e.g., generating the verbs associated with presented nouns). Similar tasks were also used in functional magnetic resonance imaging (fMRI) studies (e.g., McCarthy, Blamire, Rothman, Gruetter, & Shulman, 1993). These neuroimaging studies have contributed to locating brain areas involved in different aspects of processing words and wordlike stimuli, but they do not reveal the time course of the different types of brain activation. The recording of the on-line electrophysiological manifestations of the different levels of visual word processing may provide information about the time course of those processes. Moreover, topographic analyses of the scalp potentials and of the current densities may provide converging information about brain regions activated at the different processing levels.

Several main families of ERP components associated with language processing have been described in the electrophysiological literature. These families are represented by the N200, the N400, and the P600 components. In the following brief review of the literature, we will only address the first two of the above components, those elicited by the processing of single words.

An N200 specific to orthographic stimuli was revealed in a study in which ERPs were recorded using intracranial implanted electrodes (Nobre, Allison, & McCarthy, 1994). In this study the authors compared the ERPs elicited by strings of letters with those elicited by other complex visual stimuli such as human faces. They found that although all the visual stimuli elicited negative components peaking around 200 msec from stimulus onset, the intracranial distribution of the N200 elicited by letter strings (pronounceable words and pseudowords, and unpronounceable nonwords) was distinct from the distribution of N200 elicited by nonorthographic stimuli. Both letter strings and faces elicited activity in the posterior fusiform gyrus, but the regions activated by the two types of stimuli never overlapped within a subject (Allison, McCarthy, Nobre, Puce, & Belger, 1994). Furthermore, the potentials elicited by words were more negative in the left than in the right hemisphere, whereas those elicited by faces were either similar across hemispheres or were more negative in the right than in the left. The fact that the intracranial N200 did not distinguish between pronounceable and nonpronounceable letter strings indicates that this component is elicited by a shallow-level process, one that is not affected by phonology. On the other hand, the distinction between the N200 distribution elicited by letter strings compared to that elicited by other visual complex stimuli suggests that this component may be associated with a mechanism of processing letters. Thus there are data suggesting the existence of a visual mechanism tuned to process orthographic stimuli whose activ-

ity is reflected by a negative component peaking around 200 msec.

Higher-level analysis of words seems to be associated with negative potentials peaking later than 200 msec (see reviews by Bentin, 1989; Hillyard & Kutas, 1983; Kutas & Van Petten, 1988). Among those, the most extensively investigated potential is the N400 component, first described by Kutas and Hillyard (1980). Initially, the N400 was linked with the processing of semantically anomalous words placed in final sentence position either in reading (Kutas & Hillyard, 1980) or in speech perception (McCallum, Farmer, & Pocock, 1984). It was found that its amplitude can be modulated by the degree of expectancy (cloze probability) as well as by the amount of overlap between the semantic characteristics of the expected and the actually presented words (Kutas, Lindamood, & Hillyard, 1984; see also Kutas & Hillyard, 1989). Therefore, it was assumed to reflect a postlexical process of semantic integration and to be modulated by the difficulty of integrating the word into its sentential context (e.g., Rugg, 1990). Other studies, however, revealed that the N400 can also be elicited by isolated printed or spoken words and pseudowords presented in sequential lists and modulated by semantic priming outside the sentential context (Bentin, Kutas, & Hillyard, 1993; Bentin, McCarthy, & Wood, 1985; Holcomb, 1986; Holcomb & Neville, 1990). Consequently, the semantic integration process that may modulate the N400 has been extended to include semantic priming between single words. It is unlikely, however, that simple lexical activation is a major factor eliciting or modulating the N400 because closed-class words, although represented in the lexicon, neither elicit nor modulate this component (Nobre & McCarthy, 1994). Furthermore, unlike the letter-processing-specific N200, the N400 is not elicited by letter strings that do not obey the rules of phonology and cannot be pronounced (i.e., illegal nonwords).

This pattern of results suggests that the N400 is not associated with a visual mechanism dedicated to processing of letters, but rather with a higher-level word-processing system. In particular, the absence of an N400 in response to illegal nonwords suggests that it is sensitive to the phonologic structure of the stimulus. However, it is probably not elicited by phonological processing per se because negative waveforms peaking at about 400 msec were modulated by the immediate repetition of unfamiliar faces (Bentin & McCarthy, 1994) and other pictorial stimuli (Barrett & Rugg, 1989, 1990). Hence, the currently existing evidence indicates that the N400 is elicited only by stimuli that allow deep (semantic) processing and that its amplitude is enhanced by semantic incongruity and attenuated by semantic priming and repetition. This pattern is consistent with the assumption that the N400 reflects a link search process between a stimulus and its semantic representation. It is possible, however, that different aspects of semantic activity in general, and language comprehen-

sion processes in particular, are associated with different negativities elicited during the same time epoch. The scalp distribution of the N400 may support this suggestion.

The description of the N400 scalp distribution seems to vary according to the task. Elicited by semantic incongruities in sentences, the N400 is largest over the centro-parietal regions and slightly larger over the right hemisphere than over the left (Kutas & Hillyard, 1982; Kutas, Hillyard, & Gazzaniga, 1988). In contrast, when elicited by single words, the N400 has a more anterior distribution, with maxima over frontal or central sites (Bentin, 1987; Bentin, McCarthy, & Wood, 1985; McCarthy & Nobre, 1993) and a larger amplitude over the left than over the right hemisphere (Nobre & McCarthy, 1994). In a recent study, using intracranial ERP recordings, McCarthy, Nobre, Bentin, and Spencer (1995) found large medio- and antero-temporal distributions of the N400, suggesting the existence of one, or several, deep neural generators bilaterally distributed in the anterior medial temporal lobe and associated with semantic processing.

The Current Study: Goals, Rationale, and Working Hypotheses

The above review suggests that different components of scalp-recorded ERP, which are generated in different brain structures, may be differently sensitive to the level at which words are processed. Previous research of levels-of-processing effects on ERPs focused primarily on the N400, providing inconclusive results. On the one hand, several studies reported that the N400 was not elicited or not modulated under shallow-processing conditions (Bentin, Kutas, & Hillyard, 1993; Chwilla, Brown, & Hagoort, 1995; Deacon, Breton, Ritter, & Vaughan, 1991). Other studies, however, reported N400 priming effects with shallow-processing tasks (Besson, Fischler, Boaz, & Raney, 1992; Kutas & Hillyard, 1989). Therefore, a more systematic, within-subject manipulation of levels of processing is required, in which the task effects on different ERP components are assessed. To the best of our knowledge, no such studies have been published. A major goal of the present study was to bridge this gap. In particular we sought (1) to investigate the neurophysiological manifestations of processing words at different levels (2) to assess the time course of processing within each of those levels, and (3) to test the hypothesis that lexical processes can be temporally and functionally dissociated from semantic processes.

To achieve our goals we have asked participants to perform several tasks, each designed to promote activity at each of the levels of processing implied by the word-recognition model we adopted. The activity associated with the visual/orthographic analysis of the stimulus was assessed comparing the ERPs elicited by letter strings to those elicited by strings of alphanumeric symbols and nonorthographic ASCII forms, in a "font-size" discrimina-

tion task. We hypothesized that orthographic analysis is automatically induced by letter strings but not by nonorthographic stimuli. The possibility that phonological or semantic activity would account for the differences between ERPs elicited by orthographic versus nonorthographic stimuli was controlled by comparing words, pseudowords, and unpronounceable strings of consonants (hereafter labeled "nonwords"). Words and pseudowords are distinct from nonwords by being phonologically legal and differ from each other in their semantic value. We assumed that the onset of orthographic processing would precede the onset of any other activity related to the recognition of printed stimuli. The second and third levels would be phonological/phonetic and phonological/lexical. We had no a priori predictions regarding the relative timing of these two levels. Phonetic processing was promoted by a rhyme-detection task, whereas the lexical processing was induced using a series of lexical decision tasks. Phonology is probably involved in both rhyme detection and lexical decision for letter strings. However, in the former task it mediates the activation of phonetic structures that are necessary for detecting the rhyme, whereas in the latter we presumed that phonetic structures are not needed and probably not generated. Therefore, the phonology in the lexical decision task leads to word recognition and may entail other linguistic processes than the "shallower" rhyme-detection task. Finally, the fourth level of processing words was semantic. Semantic processing was induced by asking the participants to distinguish abstract from concrete words. It is important to realize that none of these tasks could separately provide evidence for a particular level (or kind) of processing. Obviously, words can be (and probably were) processed at all levels, regardless of task. We hoped, however, that the demand characteristics of each task would intensify the activity at the respective levels and that across-task comparisons in the timing and scalp distribution of the ERPs might help disentangle one process from another.

To avoid speeded response-related processes, we did not measure RTs. Rather, we used an "oddball" paradigm in which the distinction among the targets and the distractors was based on processing the words at the above described levels. Thus, in the font-size task the subjects were instructed to keep a silent count of "targets" that were characterized as being twice the size of the "distractors." The type of stimulus (words, pseudowords, illegal nonwords, alphanumeric symbols, or forms) was irrelevant to the task. In the rhyme task, subjects were instructed to keep a silent count of stimuli (words and pseudowords) that rhymed with a pre-designated French word, while disregarding other words, pseudowords, and nonwords. In the lexical decision tasks, subjects were instructed to keep a silent count of words either presented among nonwords (a relatively shallow discrimination) or among pseudowords (a

deeper discrimination). In a third lexical decision condition, the subjects were instructed to keep a silent count of pseudowords interspersed among words. Finally, in the semantic decision task, subjects were instructed to keep a silent count of abstract words, disregarding concrete words, pseudowords, or nonwords that were present in the same list. Table 1 describes the experimental paradigm. Note that, both within and across lists, our relevant comparisons were among the distractors. The targets were expected to elicit a late positive component (P300), whose latency and amplitude were presumed to reflect the different levels of discrimination difficulty between targets and distractors in each task.

RESULTS

ERPs Elicited by Nontarget Stimuli

As is common in ERP studies in which the electroencephalogram (EEG) is recorded from more than a few scalp sites, the entire data set was used to describe spatial scalp distributions, whereas statistical analyses were performed on selected sets of scalp sites. The analyzed sites were chosen to cover the distribution of each component as observed in the topographic maps, as well as to cover an area sufficiently large to allow a distribution-based distinction among components and comparisons across tasks. With slight variations among tasks (specified where relevant), the dependent variables were (1) mean amplitudes calculated for time ranges during which the ERPs elicited by different stimulus types were distinct by visual observation, (2) mean amplitudes calculated for more restricted time ranges that encompassed the relevant component in each task, (3) the peak latency (defined as the latency of the most

negative point within the same time range), and (4) the latency to the onset of these components. The onset was defined as the first latency at which the distinction between conditions was significant, determined by point-by-point *t* tests. On the basis of the observed distributions, the statistical analysis of ERPs elicited in the visual task were limited to posterior and posterior temporal areas (OM1/2, O1/2, PO3/4, and T5/6), whereas in all other tasks the sites of interest covered the middle and anterior temporal lobes as well as lateral aspects of the precentral and frontal areas (TP7/8, T3/4, C3/4, FC1/2, FC5/6, F3/4, and F7/8).

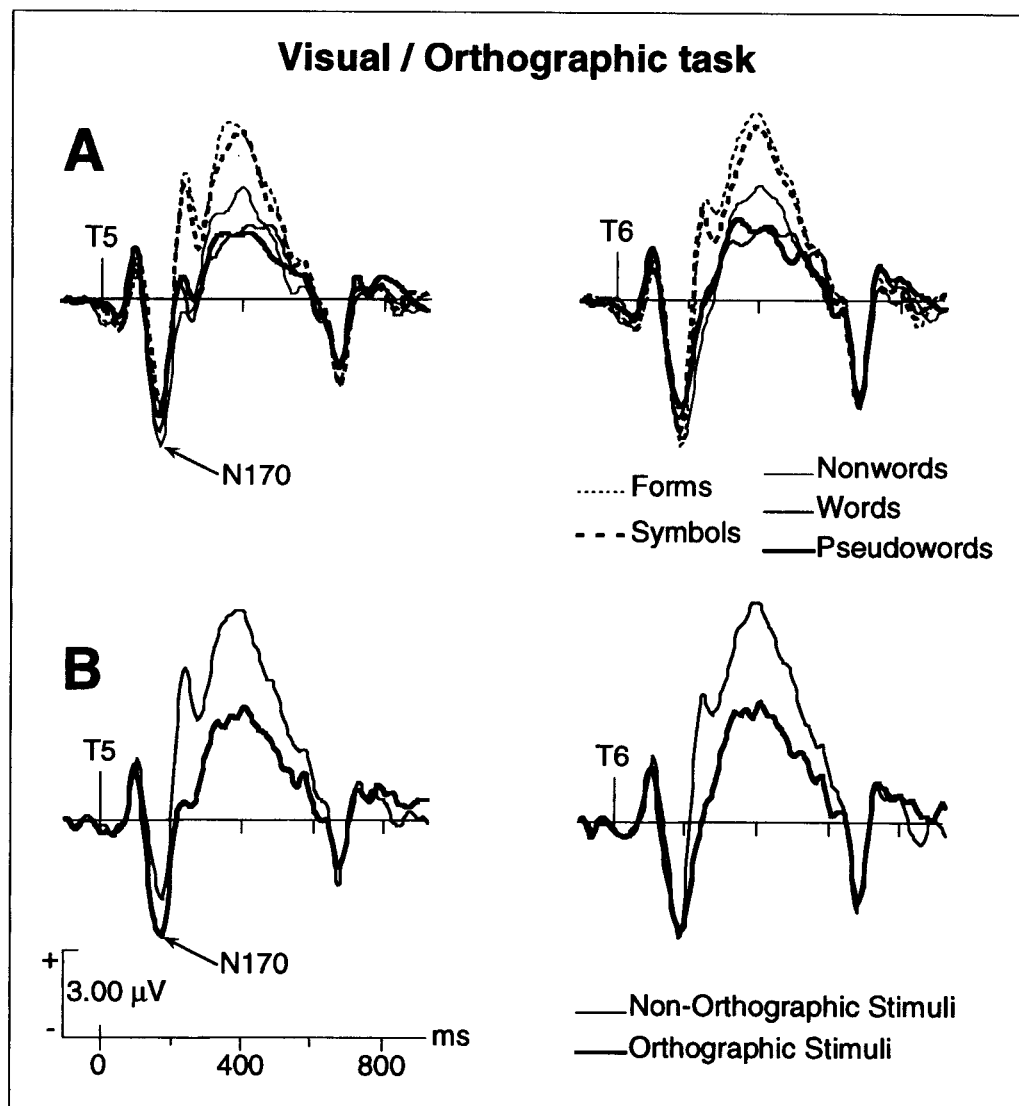
Visual Processing (Size) Task

The ERPs elicited by the five stimulus types in the size discrimination task revealed two distinct categories of responses. One included all the three types of orthographic stimuli (words, pseudowords, and nonwords); the other included the two types of nonorthographic stimuli (symbols and forms) (Figure 1). This difference began in the latency range of a negative wave peaking at T5 and T6 around 170 msec (N170) and lasted for about 600 msec, throughout the stimulus exposure time (Figure 1A). The initial statistical evaluation of this pattern compared the mean amplitude elicited between 140 and 600 msec by each Stimulus Type (words, pseudowords, nonwords, symbols, forms) at four posterior sites (OM1/2, O1/2, PO3/4, T5/6) on each Hemisphere (left, right). The analysis of variance (ANOVA) showed that the stimulus type and the site effects were significant ($F(4, 92) = 29.3$, $MSE = 6.6$, $p < 0.0001$, GG epsilon = 0.87, and $F(3, 69) = 28.3$, $MSE = 6.2$, $p < 0.0001$, GG epsilon = 0.53, respectively), whereas the hemisphere effect was not ($F(1, 23) < 1.00$). Post hoc

Table 1. Summary of the Experimental Design

<i>Level of Processing</i>	<i>Task</i>	<i>Nontarget Stimulus Type (N)</i>	<i>Target Stimuli (N)</i>
Visual/orthographic processing	Size decision	Concrete words (84) Pseudowords (84) Illegal nonwords (84) Alphanumeric symbols (84) Forms (84)	Double-sized stimuli (16 of each type)
Phonetic processing	Rhyme decision	Concrete words (84) Pseudowords (84) Illegal nonwords (84)	Stimuli rhyming with <i>vitrail</i> Concrete words (16) Pseudowords (16)
Lexical/phonological processing	Lexical decision LD-1 LD-2 LD-3	Illegal nonwords (84) Pseudowords (84) Concrete words (84)	Concrete words (16) Concrete words (16) Pseudowords (16)
Semantic processing	Semantic decision	Concrete words (84) Pseudowords (84) Illegal nonwords (84)	Abstract words (32)

Figure 1. ERPs in the visual/orthographic task. (A) ERPs elicited by nontarget stimuli (strings of forms, strings of alphanumeric symbols, words, pseudowords, and nonwords) at lateral posterior sites (T5, T6). (B) ERPs collapsed across orthographic stimuli (words, pseudowords, and nonwords) and nonorthographic stimuli (strings of alphanumeric symbols and strings of forms) in the visual/orthographic task. The N170 wave was largest at the lateral posterior sites T5 and T6 and peaked around 170-msec latency. The negative peak at about 600 msec is probably the "off" response of the stimuli (which lasted on the screen for 500 msec).



univariate ANOVAs revealed that the mean amplitudes elicited by words, pseudowords, and nonwords did not differ among themselves ($F(2, 46) < 1.00$), nor did the mean amplitude elicited by symbols differ from that elicited by forms ($F(1, 23) < 1.00$). The average mean amplitude of the three orthographic stimuli was significantly less positive than the average of the mean amplitude of the two nonorthographic stimuli ($F(1, 23) = 81.1, MSE = 0.5, p < 0.0001$) (Table 2). As revealed by significant interactions, the difference between orthographic and nonorthographic stimuli was larger at the left than the right hemisphere sites (2.01 and 1.65 μV , respectively) ($F(4, 92) = 7.69, MSE = 0.37, p < 0.001, GG \text{ epsilon} = 0.56$) and larger at the PO (2.26 μV) and O (1.91 μV) sites than at the T (1.73 μV) and OM (1.43 μV) sites ($F(12, 276) = 14.3, MSE = 0.21, p < 0.0001, GG \text{ epsilon} = 0.37$). No other interactions were significant. Because no differences were found among the three orthographic stimulus types or between the two nonorthographic stimulus types, for the subsequent statistical

analyses the responses to the five stimulus types were grouped into two distinct categories: *orthographic* stimuli including words, pseudowords, and nonwords (252 stimuli) and *nonorthographic* stimuli including strings of alphanumeric symbols and strings of forms (168 stimuli) (Figure 1B).

A series of point-by-point *t* tests comparing the waveforms elicited by orthographic and nonorthographic stimuli showed that the difference between the two categories became significant ($p < 0.01$) at 140 msec at T5 (left hemisphere) and at 210 msec at T6 (right hemisphere). Because the latency range of the N170 wave (140 to 200 msec) was the earliest time window where the responses to orthographic and nonorthographic stimuli differed (Figure 1B), and because previous studies suggested that the N170 is the earliest information-specific ERP component elicited by visual stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996), we focused the analysis on the influence of stimu-

Table 2. Mean Amplitudes (OM1, OM2, O1, O2, PO3, PO4, T5 and T6) between 140 and 600 msec, for Each Stimulus in the Size-Decision Task

	Words	Pseudowords	Nonwords	Symbols	Forms
Mean Amplitude	0.30	0.35	0.38	2.16	2.20
SEm ^a	0.37	0.37	0.42	0.40	0.40

^a (SEm = standard error of the mean).

lus-type category on N170 latency, amplitude, and topography.

N170 Amplitude and Scalp Distribution

Figure 2A shows the scalp potential (SP) and scalp-current-density (SCD) distributions of the responses to orthographic and nonorthographic stimuli 170 msec poststimulus. For both stimulus categories, the N170 shows bilateral activation centered between PO3, T5, O1, and OM1 over the left hemisphere and PO4, T6, O2, and OM2 on the right hemisphere (Figure 2B).

The mean amplitude of the N170 calculated between 140 and 200 msec, on the left and right hemispheres was compared by a three-way ANOVA with the Stimulus Category (orthographic, nonorthographic), Site (OM, O, PO, T), and Hemisphere (left right) as within-subject factors. This analysis showed no significant main effect for either Stimulus Category or Hemisphere (for both, $F(1, 23) < 1.0$) but a significant effect of Site ($F(3, 69) = 15.6$, $MSE = 4.2$, $p < 0.0001$, GG epsilon = 0.59). However, the interaction between Stimulus Category and Hemisphere effect was significant ($F(1, 23) = 11.2$, $MSE = 1.1$, $p < 0.005$), as was the interaction between Stimulus Category and Site ($F(3, 69) = 2.9$, $MSE = 0.4$, $p < 0.5$, GG epsilon = 0.45). Posthoc univariate ANOVAs showed that the mean amplitude of the N170 was larger at the temporal sites ($-3.22 \mu\text{V}$) and at OM ($-3.13 \mu\text{V}$) than at the parietooccipital ($-1.46 \mu\text{V}$) and occipital ($-2.25 \mu\text{V}$) sites. The Stimulus Category \times Hemisphere interaction was due to the fact that, at all sites, the N170 elicited by orthographic stimuli was larger over the left than over the right hemisphere sites, whereas the N170 elicited by nonorthographic stimuli was larger over the right than over the left hemisphere. However, the difference between the N170 elicited by orthographic and nonorthographic stimuli was not significant, except at T5 (left hemisphere), where the N170 elicited by orthographic stimuli ($-3.53 \mu\text{V}$) was significantly larger than that elicited by nonorthographic stimuli ($-2.67 \mu\text{V}$) ($F(1, 23) = 6.86$ $MSE = 2.55$, $p < 0.02$).

Similar analyses performed on the SCD waveforms led to similar results: There was no effect of Stimulus Category or Hemisphere on the mean current amplitude of the N170 (averaged across the four sites), but a significant interaction between the two factors ($F(1, 23) = 11.96$, $p < 0.01$). The mean current amplitude of N170 tended to be larger over the left occipito-temporal areas

for orthographic stimuli ($-0.73 \mu\text{A}/\text{m}^3$) than for nonorthographic stimuli ($-0.61 \mu\text{A}/\text{m}^3$) ($p < 0.10$) and was larger over the right occipito-temporal areas for nonorthographic stimuli ($-0.78 \mu\text{A}/\text{m}^3$) than for orthographic stimuli ($-0.54 \mu\text{A}/\text{m}^3$) ($p < 0.05$).

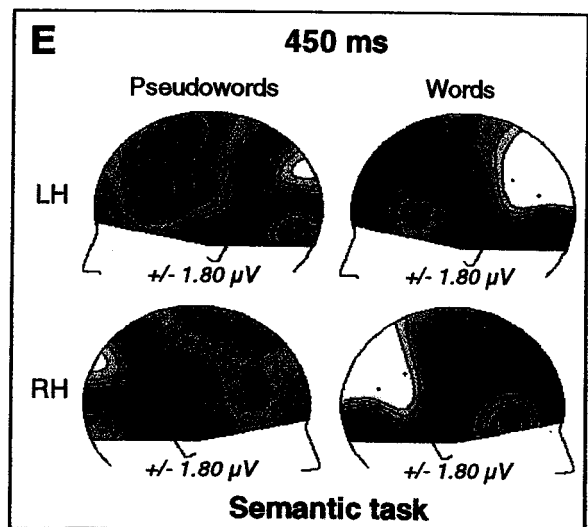
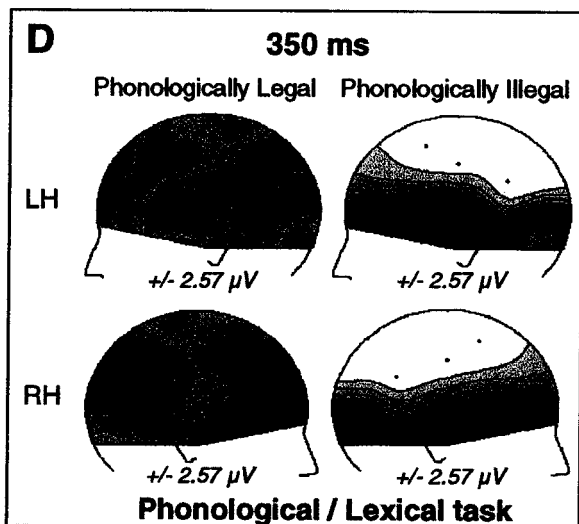
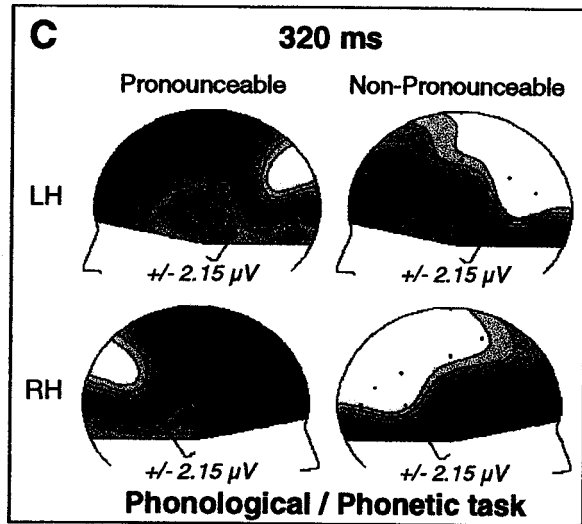
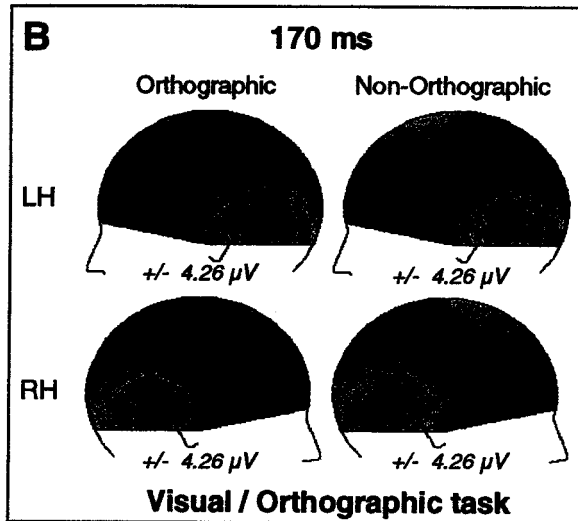
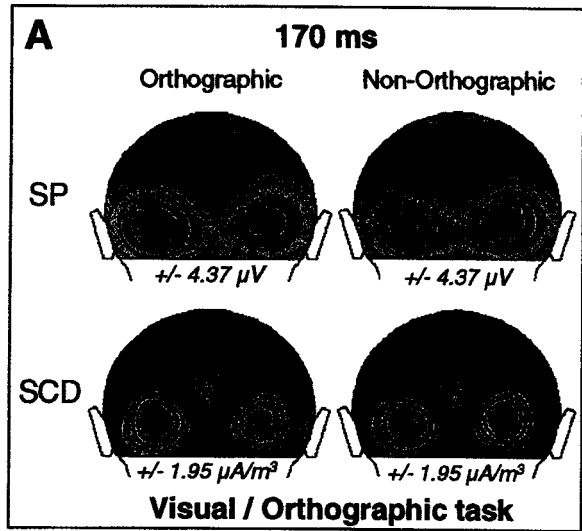
These results thus show a double dissociation between the interhemispheric distribution of orthographic and nonorthographic stimuli. Orthographic stimuli elicited the largest N170 at posterior left hemisphere sites, whereas the N170 elicited by nonorthographic stimuli was largest at posterior right hemisphere sites. However, only at the left posterior temporal site (T5) was the difference between the N170 elicited by orthographic and nonorthographic stimuli significant.

Although only 8 out of the 24 subjects were males, given the interhemispheric asymmetrical distribution of the N170 on the one hand, and the recent controversy regarding gender differences in the interhemispheric asymmetry for language processing (Pugh et al., 1996; Shaywitz et al., 1995; but see Frost et al., 1997), on the other, we compared the pattern of the interhemispheric asymmetry of the N170 amplitude between the male and the female participants. This comparison was based on a mixed model ANOVA with Gender as the between-subject factor and Stimulus Category and Hemisphere as the within-subject factor. This analysis revealed that, although the pattern of interhemispheric asymmetry tended to be different for men and women,¹ neither the interaction between Gender and Hemisphere nor the interaction between all three factors were statistically significant ($F(1, 22) < 1.0$ for both interactions).

N170 Latency

A two-way ANOVA was performed on the N170 peak latency measured between 140 and 200 msec at T5 and T6 (where the N170 was most conspicuous), with Stimulus Category (orthographic, nonorthographic) and Hemisphere (left, right) as within-subject factors. This analysis showed that the N170 latency was similar for orthographic and nonorthographic categories ($F(1, 23) < 1.00$) and significantly shorter at T5 (168 msec) than at T6 (175 msec) ($F(1, 23) = 5.96$, $p < 0.025$). The interaction between Stimulus Category and Hemisphere was not significant ($F(1, 23) = 0.05$).

Figure 2. Scalp distribution of the negative potentials elicited in each task. Pink-purple hues represent negative voltages, yellow-green hues represent positive voltages. (A) Back view of the scalp potential (first row) and current density (second row) distributions of the N170s to orthographic (left) and nonorthographic (right) stimuli in the size task. (B) Lateral view of the N170s scalp potential distributions to orthographic and nonorthographic stimuli in the size task. (C) Scalp potential distributions of the N320s to pronounceable and nonpronounceable stimuli in the rhyme task. (D) Scalp potential distributions of the N350s to phonologically legal and phonological illegal stimuli in the lexical decision task. (E) Scalp potential distributions of the N450s to pseudowords and words stimuli in the semantic decision task.



Phonological/Phonetic (Rhyme) Task

The ERPs elicited by the three stimulus types in the rhyme discrimination task displayed two distinct categories of responses. One included the pronounceable stimuli (words and pseudowords); the other included the nonpronounceable stimuli (nonwords). This distinction started at about 290 msec from stimulus onset and lasted for about 330 msec (Figure 3). During that period, a negative potential peaking at about 320 msec after stimulus onset (N320) was most evident over the temporal and temporo-parietal regions, particularly in the ERP elicited by pronounceable stimuli; the ERPs elicited by nonpronounceable stimuli during that period were dominated by a positive potential that was interrupted by a "shoulder" in the region of the N200 (see Figures 2C and 3). An initial ANOVA comparing the mean amplitude of the ERPs elicited by each stimulus type at all seven lateral electrodes over each hemisphere between 270 and 500 msec supported the categorization between pronounceable and nonpronounceable stimuli. This analysis showed a significant main effect of stimulus type ($F(2, 46) = 20.0$, $MSE = 0.44$, $p < 0.001$, GG epsilon = 0.98) that, as revealed by post hoc univariate contrasts, reflected only the fact that the mean amplitude elicited by the nonwords (1.43 μV) was significantly more positive than that elicited by either words (0.45 μV) or pseudowords (0.33 μV), which did not differ one

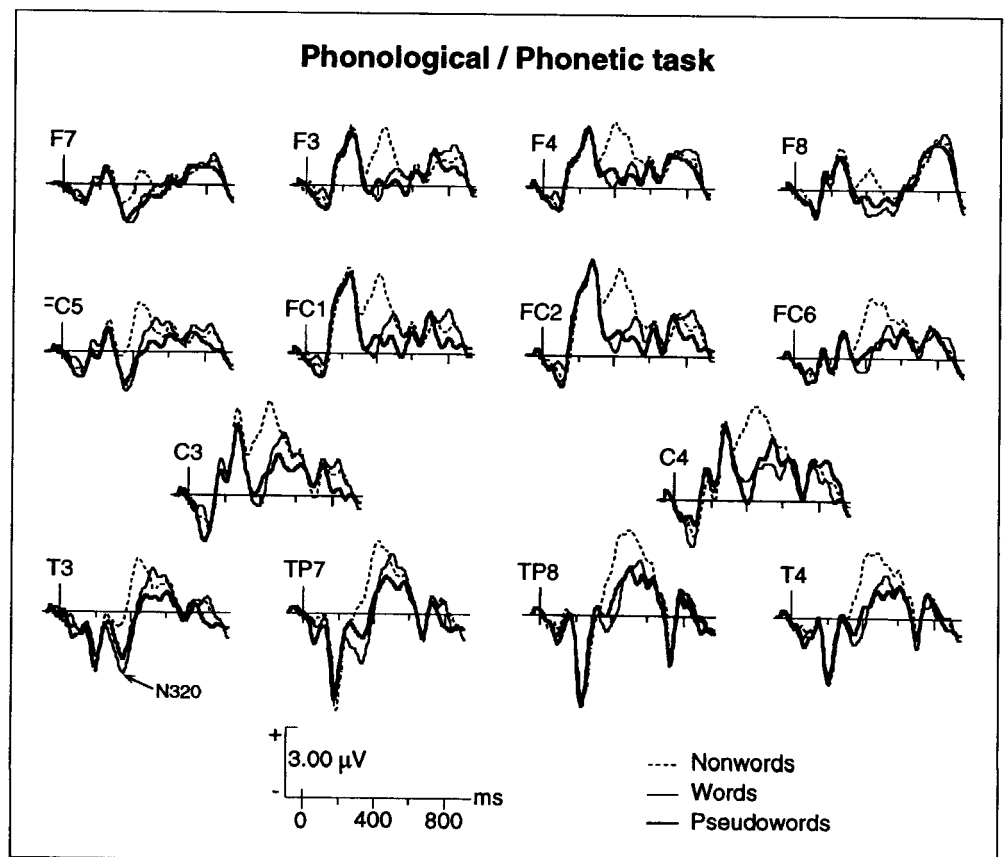
from another ($F(1, 23) < 1.0$). Therefore, for the subsequent analyses, the responses to the three stimulus types were grouped into two distinct categories: *pronounceable* stimuli including words and pseudowords (168 stimuli) and *nonpronounceable* stimuli, which were the nonwords (84 stimuli). A series of point-by-point *t* test analyses revealed that the difference between these two categories was significant ($p < 0.01$), starting at 295 msec at T3 (left hemisphere) and at 305 msec at T4 (right hemisphere).

Because the latency range of the N320 wave (270 to 370 msec) was the earliest time window where pronounceable and nonpronounceable stimuli elicited different ERPs, we focused the analysis of the influence of stimulus category on the N320 latency, amplitude, and scalp distribution.

N320 Amplitude and Scalp Distribution

Figure 2C shows the scalp potential distribution of the responses to pronounceable and nonpronounceable stimuli at 320 msec poststimulus onset on the left and right hemispheres. A wide positive field on the occipito-central areas characterized the responses to nonpronounceable stimuli. The potential distribution to pronounceable stimuli displayed two voltage patterns: a negative potential field over the temporal areas and a

Figure 3. ERPs to nontarget stimuli (words, pseudowords, and nonwords) at the sites of interest in the phonological/phonetic task. The N320 wave was largest at T3—on the left temporal hemisphere—and was much smaller for nonwords than for pseudowords and words.



negative/positive pattern over the occipito-parietal region, slightly larger at the left than at the right hemisphere sites. N320 shows a larger amplitude over the left temporal areas (around T3) than over the right temporal areas (around T4) and larger for pronounceable stimuli than for nonpronounceable ones.

The statistical analysis of these differences was based on a three-way ANOVA with Stimulus Category (pronounceable, nonpronounceable), Site (TP7/8, T3/4, C3/4, FC1/2, FC5/5, F3/4, F7/8), and Hemisphere (left, right) as within-subject factors. The dependent variable was the mean amplitude of the N320 between 270 and 370 msec from stimulus onset. This analysis revealed that the N320 was larger (i.e., more negative) for pronounceable ($-0.18 \mu\text{V}$) than for nonpronounceable stimuli (which in fact elicited a positive waveform in the same latency range, $0.99 \mu\text{V}$) ($F(1, 23) = 15.7$, $MSE = 14.66$, $p < 0.001$) and at the left ($0.04 \mu\text{V}$) than at the right hemisphere sites ($0.77 \mu\text{V}$) ($F(1, 23) = 19.92$, $MSE = 4.53$, $p < 0.001$). The main effect of site was also significant ($F(6, 138) = 16.92$, $MSE = 3.57$, $p < 0.001$). The interaction between the Stimulus Category and the Site effects was significant, suggesting that the difference between the pronounceable and the nonpronounceable stimuli was larger at some sites than at others ($F(6, 138) = 8.82$, $MSE = 0.37$, $p < 0.001$). No other interactions were significant. The scalp distribution of the N320 was analyzed by a one-way ANOVA in which the dependent variable was the

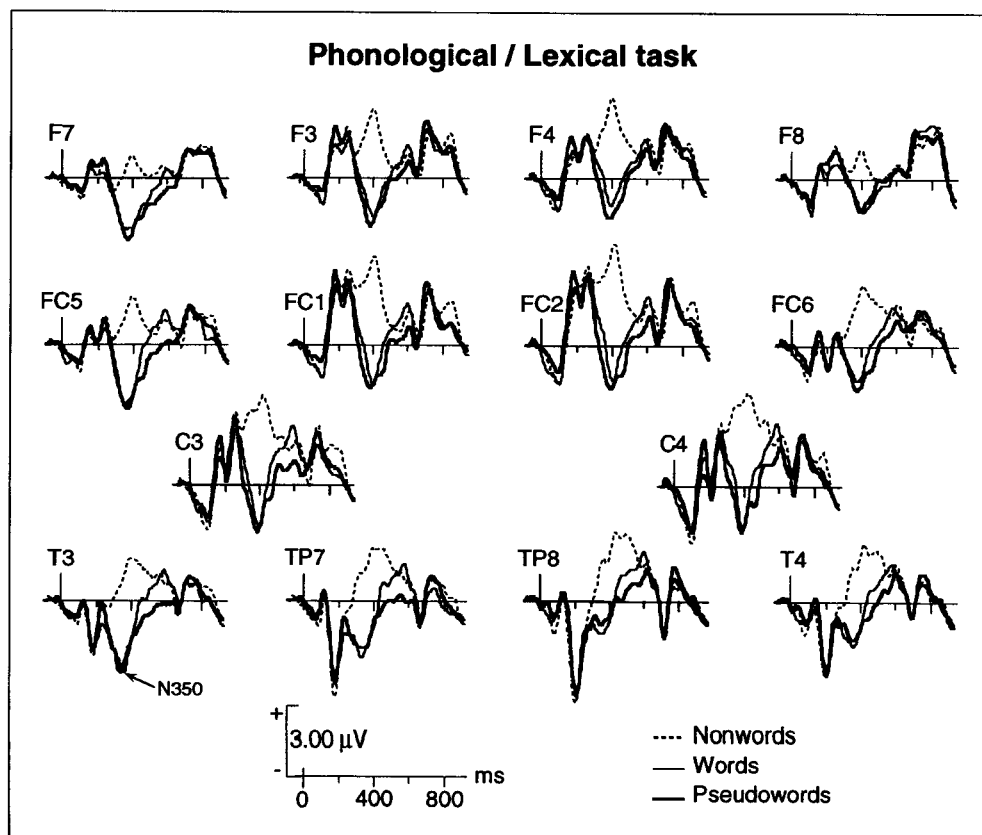
amplitude of N320 elicited by pronounceable stimuli averaged across hemispheres. This analysis showed that the N320 varied significantly with site ($F(6, 138) = 13.4$, $p < 0.001$, $GG \text{ epsilon} = 0.35$). Post hoc univariate contrasts revealed that the amplitude of the N320 was significantly larger at T3/4 ($-1.1 \mu\text{V}$) than at any other location and that it was negative at F7/8, TP, and FC56 (-0.68 , -0.65 , and $-0.53 \mu\text{V}$, respectively) and positive at the more central and frontal electrodes, C, FC1/2, and F3/4 (0.59 , 0.76 , and $0.31 \mu\text{V}$, respectively). This distribution statistically validates the lower midtemporal distribution of the N320. A post hoc analysis of the interaction between the stimulus category and the site showed that the difference between pronounceable and nonpronounceable stimuli was largest at F7/8 ($1.85 \mu\text{V}$).

The possible interaction of the hemispheric differences with gender was examined for the N320 as for the N170 potential. This analysis showed that neither the Gender \times Hemisphere nor the Gender \times Stimulus Type by Hemisphere interactions were significant (for both $F(1, 22) < 1$).

N320 Latency

A Stimulus Category by Hemisphere ANOVA was performed on the N320 peak latency measured at T3 and T4 (where the amplitude of the N320 elicited by pronounceable stimuli was maximal). This analysis showed

Figure 4. ERPs elicited by nontarget stimuli (words, pseudowords, and nonwords) at the sites in the lexical decision task. The N350 wave was largest at T3—on the left temporal hemisphere—and was elicited only by words and pseudowords. Unlike legal phonological stimuli, nonwords elicited a large positive deflection.



that N320 latency was significantly shorter for nonpronounceable stimuli (303 msec) than for pronounceable stimuli (326 msec) ($F(1, 23) = 16.55, p < 0.001$), without a significant main effect of hemisphere ($(F(1, 23) < 1.00)$). The interaction between Stimulus Category and Hemisphere, however, was significant ($F(1, 23) = 5.68, p < 0.025$), revealing that in response to pronounceable stimuli the N320 peaked earlier at T3 (321 msec) than at T4 (331 msec), whereas in response to nonpronounceable stimuli it peaked earlier at T4 (297 msec) than at T3 (309 msec). Hence, the left hemisphere responded faster to pronounceable than to nonpronounceable stimuli, whereas the opposite pattern was found for the right hemisphere.

Phonological/Lexical Task

As in the phonological/phonetic task, the ERPs elicited by the three stimulus types in the lexical decision tasks revealed two distinct categories of responses. One included the words and the pseudowords and the other included the nonwords. This distinction was evident starting at about 270 msec from stimulus onset and lasting for about 250 msec, an epoch that encompassed a negative positive deflection for the words and pseudowords, but a positive peak for the nonwords (Figure 4). An initial ANOVA compared the mean amplitude of the ERPs elicited between 270 and 500 msec by each Stimulus Type (words, pseudowords, nonwords) at the midtemporal and anterior-temporal Sites (T3/4, C3/4, FC5/6, F7/8, see Figure 2D) and over each Hemisphere (left, right). This ANOVA showed that the main effects of Stimulus Type and Site were significant ($F(2, 46) = 47.1, p < 0.001, GG \text{ epsilon} = 0.84$ and $F(3, 69) = 14.7, p < 0.001, GG \text{ epsilon} = 0.58$, respectively) and that, across all condition and sites, the ERPs elicited at the left hemisphere sites were more negative ($-0.33 \mu\text{V}$) than at the right hemisphere sites, which were actually positive ($0.17 \mu\text{V}$) ($F(1, 23) = 9.9, p < 0.005$). The interaction between Stimulus Type and Site was also significant, suggesting that the effect of Stimulus Type was different at different scalp locations² ($F(6, 138) = 14.5, p < 0.001, GG \text{ epsilon} = 0.54$). Post hoc univariate contrasts showed that the mean amplitude of the ERP elicited by words ($-0.63 \mu\text{V}$) and by pseudowords ($-1.00 \mu\text{V}$) during this period did not differ significantly ($F(1, 23) = 3.2, p = 0.085$), both being significantly more negative than the mean amplitude of the ERP elicited by the nonwords at this time ($1.38 \mu\text{V}$) ($F(1, 23) = 62.6, p < 0.001$ and $F(1, 23) = 52.2, p < 0.001$ for pseudowords and words, respectively). Consequently, the words and pseudowords (168 stimuli) were collapsed to form one category of phonologically legal stimuli to be compared with the nonwords, which were phonologically illegal stimuli (84 stimuli). A series of point-by-point *t* tests between the waveforms elicited by the pronounceable and the nonpronounceable stimuli showed that this difference be-

came significant ($p < 0.01$) at 270 msec over the left hemisphere (T3) and at 300 msec over the right hemisphere (T4).

The difference between the two stimulus categories was most evident about 350 msec from stimulus onset, at the peak of the negative deflection elicited primarily by the phonologically legal stimuli (N350). Around that latency, the increase in the positivity elicited by nonwords was interrupted by a "shoulder" (i.e., a decrease in the magnitude of the positive derivative of the waveform) and even a short-lasting change in its direction at some locations. Hence, it appears that phonologically legal and illegal stimuli were processed significantly differently, at least as these processes were reflected by ERPs. Because the present task was designed to examine the difference between the deeper, lexical processes that may be required to distinguish between words and pseudowords, and the more superficial processes that are probably sufficient to distinguish nonwords (Balota & Chumbley, 1984), our analyses focused on the N350, which was most conspicuous at the temporal and fronto-central sites.

N350 Amplitude and Scalp Distribution

Figure 2D shows the scalp-potential distribution of the responses to phonologically legal and illegal stimuli, 350 msec poststimulus over the left and right hemispheres, respectively. Although the scalp distribution of the N350 was apparently more anterior and central than that of the N320, for the purpose of intertask comparisons we have analyzed the same subset of scalp sites as in the phonological/phonetic task. Hence, the mean amplitude of the N350 was calculated between 300 and 400 msec separately for legal and illegal stimuli at TP7, T3, C3, FC5, FC1, F3, and F7 over the left hemisphere and the corresponding sites over the right hemisphere. These data were analyzed using a Stimulus Category \times Site \times Hemisphere within-subject ANOVA. The analysis showed that all three main effects were significant ($F(1, 23) = 85.6, p < 0.001, F(6, 138) = 12.8, p < 0.001, GG \text{ epsilon} = 0.41$ and $F(1, 23) = 7.1, p < 0.015$ for the Stimulus Category, Site, and Hemisphere, respectively). The interaction between Stimulus Type and Site and that between Stimulus Type and Hemisphere and the three-way interaction between Stimulus Type, Site, and Hemisphere were also significant ($F(6, 138) = 16.5, p < 0.001, GG \text{ epsilon} = 0.37, F(1, 23) = 8.5, p < 0.01$, and $F(6, 138) = 8.5, p < 0.025, GG \text{ epsilon} = 0.38$, respectively). The distribution of the N350 was examined with a Site \times Hemisphere ANOVA. This analysis showed that the N350 was larger (i.e., more negative) at left ($-1.58 \mu\text{V}$) than at right ($-0.91 \mu\text{V}$) hemisphere sites ($F(91, 23) = 15.6, p < 0.005$). Across hemispheres, its amplitude varied significantly ($F(6, 138) = 2.9, p < 0.01, GG \text{ epsilon} = 0.4$). Post hoc univariate contrasts revealed that, like the N320, the N350 was largest at T3/4 ($-1.75 \mu\text{V}$). However,

in contrast to the N320, its amplitude was not significantly smaller at FC5/6 ($-1.6 \mu\text{V}$) than at T3/4, and it was only slightly reduced at F7/8 ($-1.34 \mu\text{V}$). The difference between the amplitude of the N350 at these three sites was not significant. In contrast, the amplitude of the N350 at the TP5/6 ($-1.24 \mu\text{V}$) sites, which were immediately posterior to the T3/4, was significantly smaller than at T3/4 ($F(1, 23) = 12.9, p < 0.01$). These results confirmed a midtemporal and dorsotemporal scalp distribution of the N350, with ramifications in the anterior temporal lobes. This distribution is different from that of the N320. Yet, given the spatial and temporal proximity of the N320 and the N350, we cannot exclude the possibility that the topography observed in Figure 3D was influenced by an overlap of N320 and N350. As previously, none of the interactions with the participant's gender were significant.

N350 Latency

The N350 latency for the phonologically legal category did not differ significantly between the T3 (340 msec) and the T4 (345 msec) electrode sites ($F(1, 23) = 0.22$).

Semantic Task

In the semantic task, all the stimulus types elicited distinguishable ERPs. In particular, the semantic task differed from the phonological tasks in that the responses to words and pseudowords were also distinct. However, at most sites, the period during which the ERPs elicited by words seem to be different from those elicited by pseudowords began later and was shorter than the period during which the ERPs elicited by nonwords were distinct from the other two categories. Therefore, for the initial analysis of the differences among stimuli types we divided the entire period during which differences were noticeable (270 to 600 msec) into two epochs. The first was from 270 to 350 msec and the second was from 350 to 600 msec. The differential activity was distributed at the fronto-central and anterior-temporal sites (Figure 2E). Consequently, the initial ANOVA compared the mean amplitude of the ERPs elicited by each stimulus type, during each epoch, at T3, FC5, FC1, F3, F7, and at the correspondent sites over the right hemisphere. This analysis showed significant main effects of Stimulus Type ($F(2, 46) = 16.9, p, GG \text{ epsilon} = 0.90$), Site ($F(4, 92) = 15.0, p < 0.001, GG \text{ epsilon} = 0.50$), and Hemisphere ($F(1, 23) = 29.6, p < 0.001$). There was no significant main effect of the epoch ($F(1, 23) < 1.00$). The interaction between the Stimulus Type effect and the epoch was significant ($F(2, 46) = 15.7, p < 0.001, GG \text{ epsilon} = 0.69$). The source of this interaction was revealed by separate analyses for each epoch. These analyses, followed by univariate contrasts, revealed that during the first epoch the ERPs elicited by words and pseudowords were not significantly different ($F(1, 23) = 2.35, p =$

0.14), both being more negative than those elicited by nonwords ($F(1, 23) = 5.0, p < 0.05$, for words versus nonwords). During the second epoch, however, the three stimulus conditions differed significantly from one another ($F(1, 23) = 4.9, p < 0.05$ for pseudowords vs. words and $F(1, 23) = 45.6$, for words vs. nonwords).

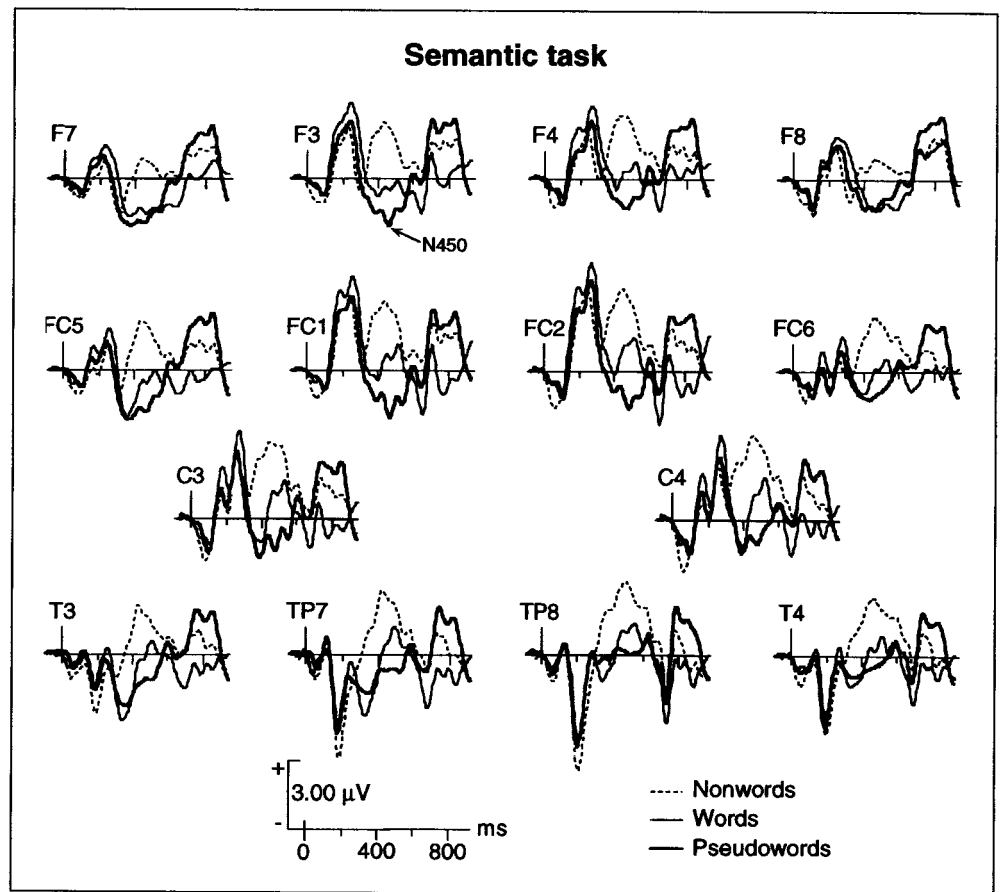
The most conspicuous event that distinguished words from pseudowords during the epoch of interest was a negative potential, that peaked at about 450 msec from stimulus onset. At that time the nonwords elicited a positive potential which resembled the potentials elicited by nonwords in the phonological discrimination tasks. Because no N450 was elicited by nonwords, and assuming that a superficial analysis was sufficient to decide that nonwords were not targets, we analyzed the characteristics and the scalp distribution of the N450, including only the ERPs elicited by pseudowords and words.

N450 Amplitude and Scalp Distribution

Figure 2E shows the scalp potential distribution of the responses to pseudowords and words at 450 msec post-stimulus onset, at the left and right hemisphere sites. Words elicited a well-circumscribed bilateral negativity peaking at more anterior sites than that elicited by words in the lexical decision task. Pseudowords display two negative maxima, more evident over the left than over the right hemisphere: one, centered between F7, FC5, and F3 had a topography that contained the areas activated by the N350 but also more anterior regions (Figure 2D and 2E). The second, centered around FC1, corresponds to the N450 shown in Figure 5 and was not observed in the lexical decision task. As in the previous experimental sessions, a negative activity was also observed above the occipital areas.

The scalp potential distribution of the N450 was assessed by a Stimulus Type (words, pseudowords) \times Site (TP, T, C, FC5/6, FC1/2, F3/4, and F7/8) \times Hemisphere (left, right) ANOVA. This analysis showed that the N450 elicited by pseudowords ($-1.0 \mu\text{V}$) was significantly more negative than that elicited by words, which, across sites, was positive ($0.15 \mu\text{V}$) ($F(1, 23) = 18.4, p < 0.001$); it was significantly more negative over the left hemisphere ($-0.60 \mu\text{V}$) than over the right hemisphere ($-0.22 \mu\text{V}$) ($F(1, 23) = 4.9, p < 0.05$) and differed significantly among scalp sites ($F(6, 138) = 9.5, p < 0.001, GG \text{ epsilon} = 0.42$). The interaction between Stimulus Type and Site effects was significant ($F(6, 138) = 13.2, p < 0.001, GG \text{ epsilon} = 0.33$), revealing that the Stimulus Type effect was not significant at the most anterior electrode sites (F7 and F8), whereas it was significant at all other sites, which did not differ among themselves. No other interactions were significant. Post hoc contrasts examining the site effect revealed that, across words and pseudowords, the N450 was significantly larger (more negative) at F7/8 ($-1.2 \mu\text{V}$) than at all other sites (the

Figure 5. ERPs elicited by nontarget stimuli (words, pseudowords, and nonwords) at sites of interest in the semantic decision task. The most salient event is the N450 wave, larger for pseudowords than for words at FC1—on the left fronto-central hemisphere, which was not elicited by nonwords.



difference between F7/8 and the second largest N450 at FC5/6 was significant, $F(1, 23) = 8.1, p < 0.01$, negative at the anterior supratemporal FC5/6 ($-0.68 \mu\text{V}$), F3/4 ($-0.65 \mu\text{V}$) FC1/2 ($-0.22 \mu\text{V}$) and midtemporal sites T3/4 ($-0.36 \mu\text{V}$) (which did not differ significantly among themselves), and positive at the centro-lateral C3/4 ($0.06 \mu\text{V}$) and posterior-temporal sites TP7/8 ($0.20 \mu\text{V}$). The difference between the N450 elicited at FC5/6 and F3/4 was significant ($F(1, 23) = 5.7, p < 0.05$). This distribution validates the anterior-temporal and anterior-supratemporal scalp distribution of the N450.³

N450 Latency

A Stimulus Type (words, pseudowords) by Hemisphere ANOVA performed on the N450 peak latency measured at FC1 and FC2 showed no significant main effects and no interaction (for the stimulus type effect $F(1, 23) = 2.0, p = 0.17$, and all other f values less than 1.00). The N450 latency for words and pseudowords at the left and right hemispheres was similar (448 msec).

Across-Task Comparisons

Because one of the aims of this study was to compare the processing of orthographic stimuli at different linguistic levels, we compared the ERPs elicited by words,

pseudowords, and nonwords across tasks. In particular, we focused on the comparison between the phonological/phonetic, phonological/lexical, and semantic decisions, testing the hypothesis that these processes are functionally and, as far as the scalp distribution of potentials and current densities reflect underlying brain mechanisms, neuroanatomically distinct. Overall, except for the N170 which was elicited at the posterior-temporal and occipital sites (Figure 6),⁴ the across-task comparison distinguished most clearly between the nonwords and the phonologically legal stimuli (words and pseudowords). Whereas the pattern of the ERP activity for words and pseudowords differed depending on whether the task required phonological/phonetic, lexical, or semantic analysis, the ERPs elicited by nonwords were about the same across tasks. Furthermore, the negative potentials elicited by phonologically legal stimuli in the phonological/phonetic, phonological/lexical, and semantic decision tasks were absent (or almost absent) in the ERPs elicited by nonwords (Figure 7).

The similarity of the ERPs elicited by nonwords across the three linguistic tasks (the two phonological and the semantic) was verified by an ANOVA of the mean amplitude of the potentials elicited by nonwords at the fronto-central and parietal electrode sites (F3, Fz, F4, FC1, FC2, C3, Cz, C4, P3, Pz, P4), where the positive peak was maximal. The mean amplitude was calculated for the

Figure 6. Back-view scalp potential distributions of the ERPs elicited by words, pseudowords, and nonwords in the visual/orthographic (first row), phonetic (second row), lexical/phonological (third row), and semantic (fourth row) tasks, at 170-msec latency. The N170 potential is elicited by all orthographic stimuli regardless of processing level, slightly bigger over the left than over the right hemisphere. White hue represents negative voltages, and black hue, positive voltages. Half of the scale (in μV) is presented below each map.

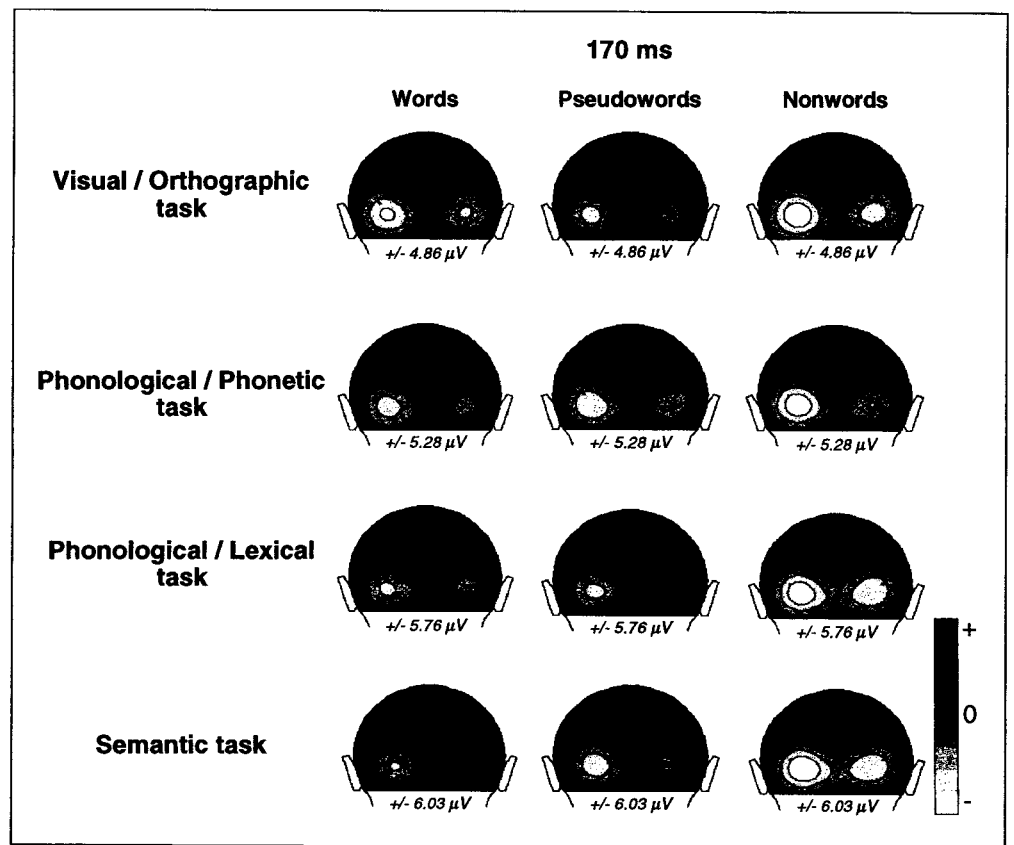
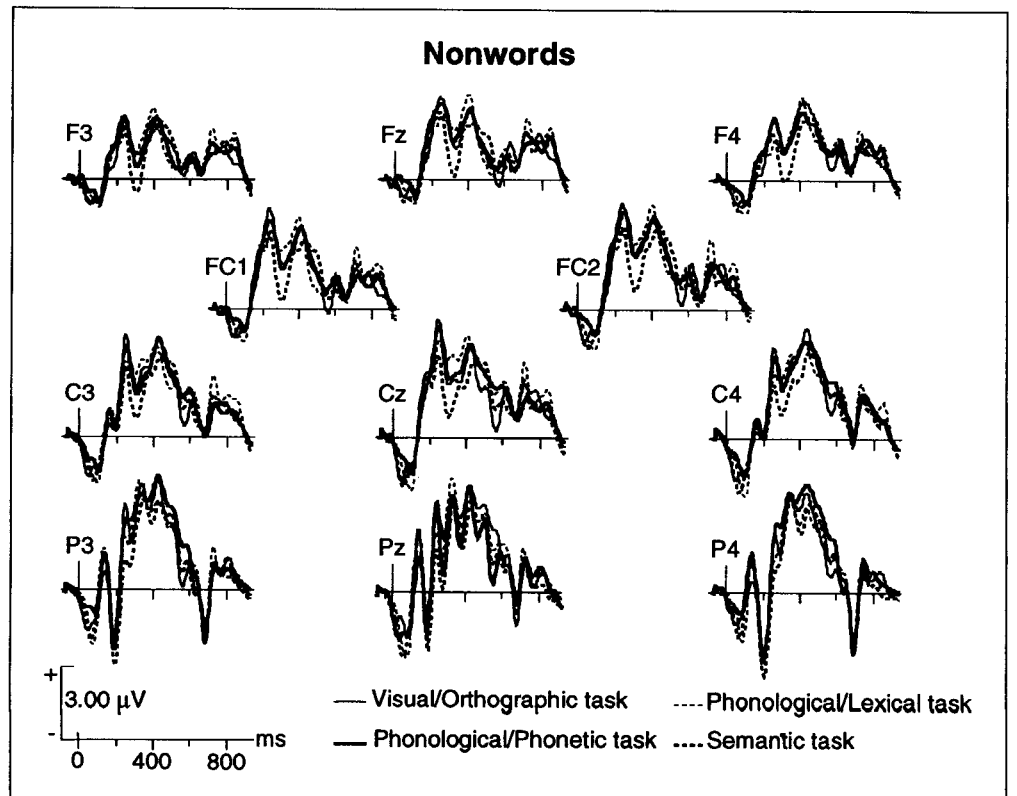


Figure 7. ERPs elicited by nonwords at the sites of interest in the four processing levels: visual/orthographic, phonetic, lexical/phonological, and semantic tasks.



epoch from 250 to 500 msec after stimulus onset, which includes the positive peak characteristic of the ERPs elicited by these stimuli. This analysis confirmed that the ERP elicited by nonwords was practically the same across the three tasks (0.23, 0.22 μV , and 0.18 μV for the rhyme, lexical decision, and semantic decision tasks, respectively; $F(2, 46) = 1.77, p = 0.18, GG \text{ epsilon} = 0.99$). The analysis of the positive peak latency (at Cz) similarly showed little difference across tasks (350, 359, and 388 msec for the phonological/phonetic, phonological/lexical, and semantic tasks, respectively; $F(2, 46) = 3.37, p = 0.05, GG \text{ epsilon} = 0.94$).

A separate analysis of each task showed that words and pseudowords elicited negative potentials that differed from the ERPs elicited by nonwords. These potentials peaked at about 320 msec in the phonetic task, 350 msec in the lexical task, and 450 msec in the semantic task (Figures 3 to 5, and 8). To verify the statistical reliability of these differences we analyzed the peak latency of the negative potentials elicited in each task by words and pseudowords at the sites where they were maximal (T3 for the phonetic and lexical tasks and F7 for the semantic task). The ANOVA showed that the latency of the negative potentials elicited by words and pseudowords was similar across tasks ($F(1, 23) = 1.6, p = 0.22$), whereas the main effect of task was highly significant ($F(2, 46) = 192.7, p < 0.001$). The interaction between the two factors was not significant ($F(2, 46) < 1.00$). Post hoc univariate comparisons revealed that the

latency of the negative peak in the semantic task (448 msec) was significantly longer than in the phonological/lexical task (358 msec; $F(1, 23) = 235.9, p < 0.001$), which in turn was longer than in the phonological/phonetic task (340 msec; $F(1, 23) = 10.9, p < 0.005$).

The amplitudes of the negative peaks across the three tasks were compared using a Task (rhyme, lexical decision, semantic decision) \times Stimulus Type (word, pseudoword) ANOVA. The dependent variable was the mean amplitude of each peak as measured for the separate analyses for the rhyme and the lexical decision tasks at T3 and for the semantic decision task at F7. This analysis revealed a significant difference between tasks ($F(2, 46) = 16.4, p < 0.001$), whereas no difference was found across tasks between the potentials elicited by words and pseudowords ($F(1, 23) < 1.00$). The most interesting result, however, was a significant Stimulus Type \times Task interaction ($F(2, 46) = 5.1, p < 0.01$), suggesting that the difference between the responses to word and pseudowords varied across tasks. Post hoc univariate analyses revealed that the N320 was slightly larger for words ($-1.42 \mu\text{V}$) than for pseudowords ($-1.02 \mu\text{V}$) in the rhyme task ($F(1, 23) = 3.15, p < 0.09$), the two stimulus types elicited equally large N350 (-2.0 , and $-2.13 \mu\text{V}$ for words and pseudowords, respectively) in the lexical decision task ($F(1, 23) < 1.00$), whereas the N450 was larger for pseudowords ($-1.3 \mu\text{V}$) than for words ($0.54 \mu\text{V}$) in the semantic decision ($F(1, 23) = 24.4, p < 0.001$).

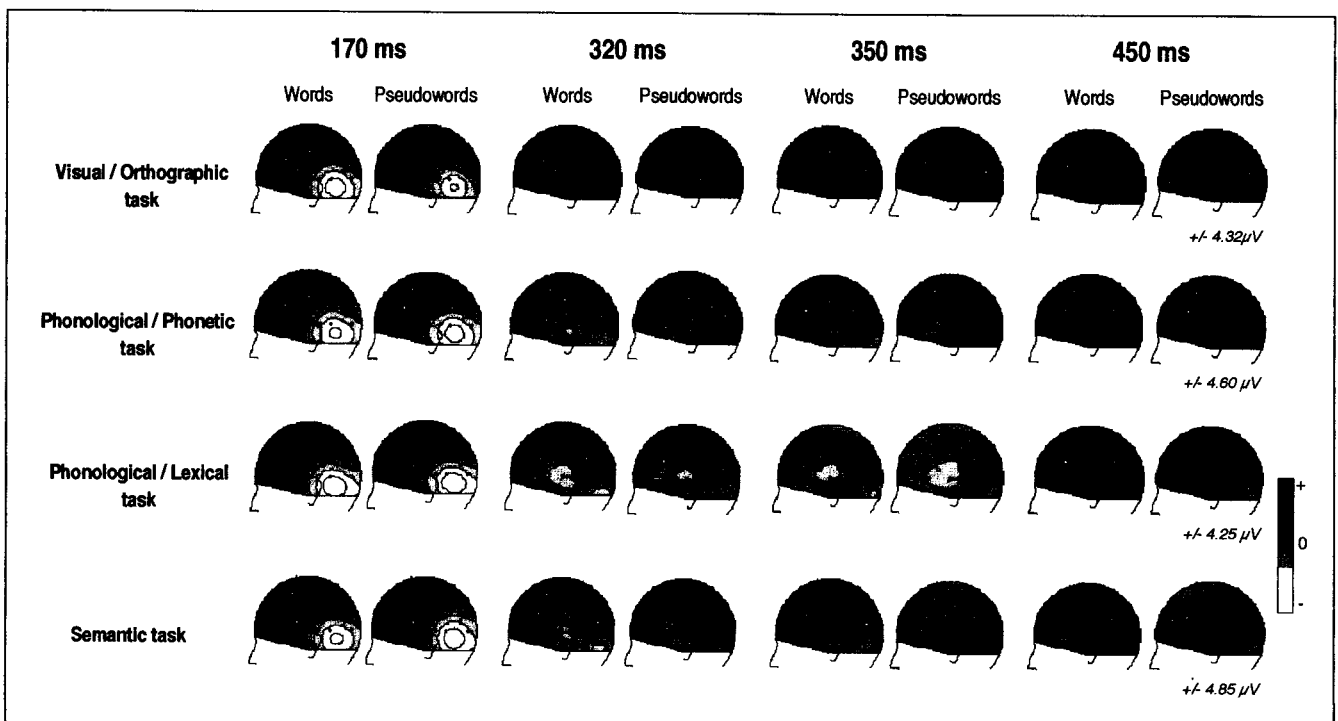


Figure 8. Left-hemisphere distribution of ERPs elicited by words and pseudowords at 170, 320, 350, and 450 msec, in each of the four experiments. White hue represents negative voltages, and black hue, positive voltages. Half of the scale (in μV) is presented below each map.

ERPs Elicited by Target Stimuli

In each task, the target stimuli elicited large P300 components that were maximally positive at the centroparietal site (Pz). Although the P300 elicited by target stimuli were not at the focus of this study, in the absence of any objective measure of task difficulty we analyzed the amplitude and peak latency of this component (Figure 9 and Table 3). Moreover, as will become clear in the general discussion, the comparison of the latency and the amplitude of the P300 across tasks enhanced our understanding of the cognitive processes involved in each task.

P300 Latency

The P300 latencies, measured as the most positive peak in the 350 to 650 msec window at Pz (Table 1), were significantly different among the six tasks ("size," "rhyme," lexical decision-1 (LD-1), lexical decision-2 (LD-2), lexical decision-3 (LD-3), and semantic ($F(5, 115) = 21.29, p < 0.001, GG \text{ epsilon} = 0.74$). Post hoc Tukey-A comparison tests revealed that P300 latency was significantly shorter for the visual task ("size" decision) than for all other tasks ($p < 0.01$), and shorter for the LD-1 and rhyme tasks than for the semantic, LD-2, and LD-3 tasks ($p < 0.05$). No other differences were significant.

P300 Amplitude

The P300 peak amplitudes, measured at Pz (Table 3), seem to be gradually reduced from the visual task to the semantic task ($F(5, 115) = 48.23, p < 0.001, GG \text{ epsilon}$

$= 0.76$). Post hoc Tukey-A analyses revealed, however, that the P300 amplitude was about the same in the two shallowest tasks (size and LD-1) and significantly larger in these two tasks than in all other tasks ($p < 0.01$). The P300 amplitude in the deepest (semantic) task was significantly smaller than in all other tasks ($p < 0.01$). Post hoc comparisons also showed that the differences between the rhyme, LD-2, and LD-3 tasks were statistically significant ($p < 0.01$).

Hence, the P300 data suggest that in the present study, as in other studies in which the level of processing has been manipulated, shallower tasks were performed faster than deeper tasks. Furthermore, assuming that the amplitude of the P300 is influenced by the amount of effort invested in the performance (e.g., Donchin, 1981) and the variance in the latency of the response in individual trials (jitter), the P300 amplitudes elicited by the targets suggest that the responses in the deeper tasks required more mental effort and were more variable than those in shallower tasks.

DISCUSSION

The present study was designed to explore the time course of processing visually presented words, as reflected by the neural electrical activity elicited while reading words at different task-induced levels of processing. An oddball paradigm was used in which the distinction between targets and nontargets was based on either visual, phonologic, or semantic processes. In addition we introduced a rhyme task in which we assumed the need for phonetic processing in task performance. We focused mainly on the ERPs elicited by nontargets for which the

Figure 9. Across-subjects average of P300 to target stimuli in the six tasks (size decision, lexical decision-1 (LD-1), rhyme decision, lexical decision-2 (LD-2), lexical decision-3 (LD-3), and semantic decision).

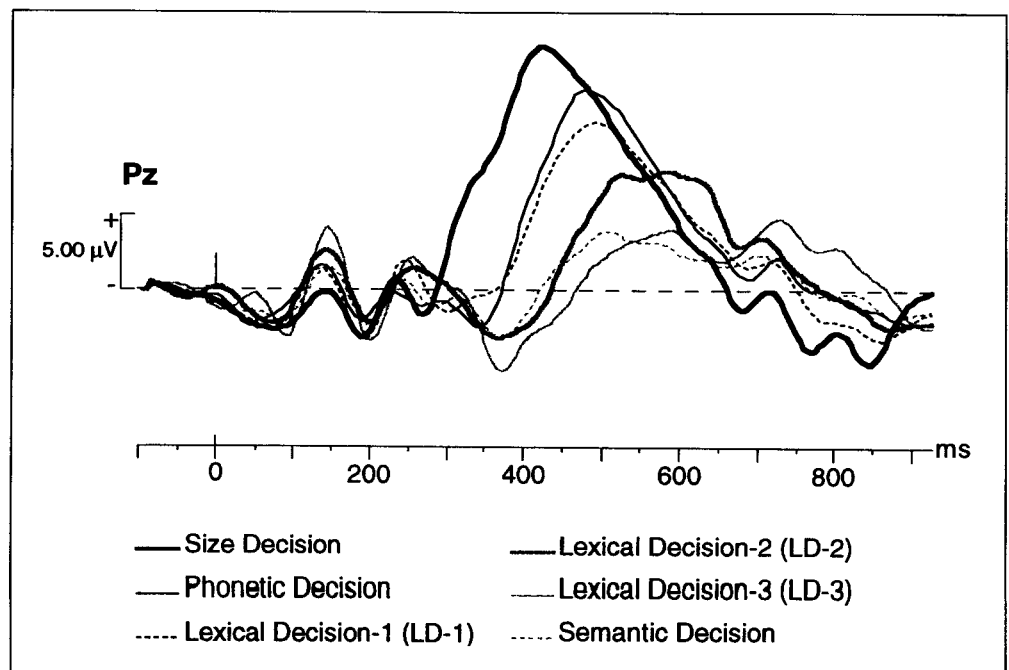


Table 3. Mean P300 Latencies and Amplitudes (\pm SEM) Elicited by the Targets in the Different Tasks. P300 was measured as the largest positive potential value at Pz between 350 and 650 msec (SEM = standard error of the mean).

<i>Task</i>	<i>Size</i>	<i>LD-1</i>	<i>Rhyme</i>	<i>LD-2</i>	<i>LD-3</i>	<i>Semantic</i>
Target stimuli	High-sized stimuli	Words among nonwords	Words and pseudowords rhyming with <i>vitrail</i>	Words among pseudowords	Pseudowords among words	Abstract words
Latency (msec)	429 \pm 30	485 \pm 50	499 \pm 46	554 \pm 56	548 \pm 69	530 \pm 70
Amplitude (μ V)	17.85 \pm 4.20	17.17 \pm 5.92	13.29 \pm 4.16	12.15 \pm 4.86	8.79 \pm 4.06	6.36 \pm 3.48

negative waveforms were relatively “unmasked” by the robust P300 that is typically observed in response to targets. Four negative potentials distinct in latency and scalp distribution were discerned, each associated with a different level of processing: (1) one peaked at a latency around 170 msec (N170) over the occipito-temporal areas and distinguished between orthographic and nonorthographic stimuli in the size-detection task; (2) the second peaked at a latency around 320 msec (N320) over midtemporal areas, was larger at left than at right hemisphere sites, and distinguished between pronounceable and nonpronounceable letter strings in the rhyme detection task; (3) the third peaked around 350 msec (N350) over left fronto-temporal regions and distinguished between phonologically legal and phonologically illegal orthographic patterns in a lexical decision task; (4) the fourth peaked around 450-msec latency (N450) over left fronto-central regions and distinguished between meaningful and meaningless phonologically legal orthographic patterns in a semantic decision task. A detailed examination of each of these negative potentials and their interpretation will be deferred until after discussing the late positive potential elicited by the target stimuli.

Modulation of P300

As is typical in oddball paradigms, all target stimuli in the present study elicited a late positive potential that was identified as P300 on the basis of task characteristics. Several studies have emphasized the distinction between a fronto-central (“P3a”) and a parietal (“P3b”) component of the P300. The P3a is believed to reflect the activation of brain reactions to unexpected events (“processing of surprise”) and P3b appears to be associated with the task-relevant categorization of oddball stimuli (Donchin, 1981; Verleger, Jaskowski, & Wauschkuhn, 1994). In the present study, the centro-parietal distribution of the P300 identified it as a P3b component. Many studies suggested that the P3b peak latency may be used as a temporal metric for stimulus evaluation (e.g., McCarthy & Donchin, 1981) and that it is sensitive to categorical decision strategies as well as the difficulty of discriminat-

ing targets from nontargets (e.g., Kutas, McCarthy, & Donchin, 1977). Its amplitude is determined by the task difficulty and the variance in the response latency in single trials, the amount of attention resources invested in the task, and design parameters such as the relative frequency of the target or its physical salience (Duncan-Johnson & Donchin, 1982). With this background in mind, we will examine the characteristics of our four tasks as reflected by the latency and amplitude of the P300 elicited by each target type.

Latency of P300: An Index of Task Complexity?

The P300 latency was significantly longer in the LD-1 and in the rhyme tasks than in the size-detection task and was longest for targets in the LD-2, LD-3, and semantic tasks. The latency did not differ significantly between the LD-1 and the rhyme tasks or among LD-2, LD-3, and the semantic tasks. Although, in general, the order in which the P300 in the different tasks peaked was congruent with the a priori determined level of processing, the correlation was not perfect. The significantly shorter latency to word-targets in LD-1 (where the nontargets were illegal nonwords) than in LD-2 (where the nontargets were pseudowords) supports Balota and Chumbley’s (1984) suggestion that the rejection of illegal nonwords (as well as the acceptance of high frequency words) is based on their orthographic familiarity rather than a deeper process of lexical search. Yet, the difference between the latency to word-targets in LD-1 and targets in the size task suggests that although the execution of both tasks was based on a shallow visual analysis, distinguishing words from illegal nonwords was more demanding than distinguishing targets on the basis of their size. Hence it appears that the P300 latency, like RTs, does not reflect the level of processing required to recognize the target but rather the complexity of the process and the decision time. This may also account for the absence of a significant difference between the P300 obtained in the semantic and the lexical decision tasks, which required distinguishing words from pseudowords (LD-2 and LD-3), that is, it could not be based on familiarity or pure phonological grounds, as was possible in

the LD-1 and the rhyme tasks. The level of processing seems to be better reflected in the amplitude of P300, to which we now turn.

The Amplitude of P300: An Index of Levels of Processing?

The P300 amplitude was equally high in the LD-1 and the size tasks, significantly higher than in all other tasks. Furthermore, it gradually decreased from the rhyme to the LD-2, LD-3, and semantic decision tasks. This variation in amplitude cannot be accounted for by the probability of the target because it was similar across tasks. It also cannot be explained by the nature of the target stimuli because the order of the amplitudes did not seem to reflect such factors. For example, although the frequency of the abstract-word targets was higher than that of concrete-word targets and of pseudowords, they elicited a lower P300 amplitude. Moreover, the amplitude of the P300 elicited by the physically outstanding targets in the size task (which were twice as large as all other stimuli) was equal to that in LD-1 where all the targets were words, equally in size with the nontarget stimuli. This suggests that the amplitude of the P300 may have captured the similarly shallow processes required to distinguish words from illegal nonwords or target stimuli that were physically larger than the nontargets. It may also have captured the increasingly deeper processes induced by the different tasks from the rhyme to the semantic decisions. Although this interpretation is tempting, it is obviously not the only one possible. A different factor that may account for the variation in the amplitude of the P300 in the different tasks is differential jitter in the latency of single trials. It is possible that for simple visual discriminations the decision time was about the same across the single trials. On the other hand, it is conceivable that in more difficult tasks the time required for discriminating between targets and primes varied across words. Consequently, the average decision-related ERP should have lower amplitude (and a larger duration) in the deeper than in the shallower tasks. For example, as is evident in Figure 9, the P300 was considerably broader in the semantic task than in the size or LD-1 tasks. This possibility is supported by the larger variance across subjects in the P300 latency for the LD-3 and semantic tasks than for the size and LD-1 tasks. Hence, the alternative interpretation is that the amplitude of the P300 in different tasks, like its latency, is (inversely) correlated with their complexity.

Whether the P300 variation across tasks reflected only task complexity or also, at least indirectly, the level of processing induced in each task, its pattern of variation supports our a priori distinction between the tasks. Consequently, we can now analyze the ERPs elicited by nontarget stimuli which, "unmasked" by the P300,⁵ may have better reflected the neural activity associated with each type of process.

Visual/Orthographic Processing

The most important outcome of the analysis of the ERPs elicited in the size-decision task was that orthographic and nonorthographic stimuli elicited significantly different responses without further distinction within each category. This pattern is similar to the results obtained intracranially by Nobre and colleagues (1994), suggesting that early in the course of visual processing, before phonological analysis occurs, the brain may distinguish between orthographic and nonorthographic visual information. Unlike the intracranial ERPs, however, in which the distinction between the two categories was limited to the N200, on the scalp the distinction between categories at the peak of N170 was followed by a longer lasting epoch during which the ERPs elicited by orthographic and nonorthographic stimuli were distinct. Furthermore, whereas intracranially orthographic and nonorthographic stimuli elicit N200 potentials in adjacent but not overlapping regions of the middle fusiform gyrus, this pattern may have been reflected at T5 and T6 as an interaction between the stimulus category and the hemispheric asymmetry: The N170 elicited by orthographic stimuli was larger than that elicited by nonorthographic stimuli in the left posterior-temporal/occipital regions of the scalp (T5) and smaller in the right posterior-temporal/occipital regions of the scalp (T6). Moreover, the difference between the two categories began considerably earlier at T5 (140-msec) rather than T6 (210-msec). This difference suggests that although both hemispheres probably respond to both orthographic and nonorthographic visual information, the well-documented superiority of the left hemisphere for processing language-related stimuli may affect early visual processing. In fact, the response of the right hemisphere may have been initiated by activity starting first on the left. Such a system could account, for example, for pure alexia resulting from lesions in the left occipital cortex that also include the splenium of the corpus callosum (e.g., Benton, 1975; Campbell & Regard, 1986; Damasio & Damasio, 1983; Henderson, 1986).

Assuming that, at least for orthography, processing specificity cannot be innate, the early distinction in the visual system between orthographic and nonorthographic information (as well as the demonstrated specificity of adjacent regions for human faces, Bentin et al., 1996; George et al., 1996) suggests that different parts of the visual system can learn to tune themselves to respond selectively to specific (probably ecologically important) visual information.

Although far-field recorded, in conjunction with intracranial recordings and neuroimaging data, the orthographic specificity observed in the present ERP results may also provide a better understanding of the functional neuroanatomy of the orthographic lexicon. They suggest the existence of a functionally specialized stream within the ventral visual pathway, specifically involved in

the perceptual processing of orthographic stimuli. Moreover, consistent with PET findings, the present results suggest that this process is particularly conspicuous in the left hemisphere. PET studies led some researchers to suggest that written word forms are processed (or at least initiated) in the occipital lobes (Petersen et al., 1989; Petersen et al., 1990; Posner & Petersen, 1990; Posner, Petersen, Fox, & Raichle, 1988; Posner & Raichle, 1994). Other researchers suggest that the extrastriate cortex responds to any complex visual stimulus whereas the specificity for visual word forms starts only in the midtemporal regions (Beauregard et al., 1997; Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995; Chertkow, Bub, Beauregard, Hosein, & Evans, in press; Howard et al., 1992; Price et al., 1994). The lateral-occipital scalp distribution of the ERPs and the SCD calculated on the basis of the ERPs elicited in the orthographic task supports a suggestion, based on intracranial recordings, that regions in the extrastriate cortex respond preferentially to orthographic information, and this process may be the first step toward the formation of a word visual pattern (e.g., Allison et al., 1994; Nobre et al., 1994). However, these regions do not distinguish between legal and illegal word forms and therefore cannot be the sole mechanism that subserves the orthographic lexicon. We will return to this issue when discussing the pattern of the ERPs elicited in the lexical decision stages of the present study.

Phonological/Phonetic Processing

Unlike decisions regarding stimulus size, which can be made just as well on orthographic and nonorthographic stimuli, rhyme decisions based on written stimuli usually require the transformation of orthographic patterns into phonological patterns from which phonetic codes can be discerned.⁶ Consequently, in the rhyme task we used only orthographic stimuli that, as expected, elicited an N170 evident particularly at the posterior temporal and occipital sites (see Figure 5, TP7 and TP8). As anticipated on the basis of the results in the size task, the ERPs elicited by the three orthographic stimulus types were not distinguishable at the level of the N170. One hundred milliseconds later, however, two categories of stimuli were evidently processed differently. One included the words and the pseudowords for which the formation of a phonological pattern was possible and on the basis of which the phonetic decision could have been made. The second category comprised the nonwords that could not be transformed into a coherent phonological structure and consequently allowed a negative decision based on shallow orthographic analysis. The difference between the ERPs elicited by pronounceable and nonpronounceable stimuli was probably associated with the difference in processing the two stimulus categories, as well as to a difference in decision-making strategies. Whereas, following the N170, the ERPs elicited by non-

words were dominated by a positive-going potential (possibly a P300 associated with the fast and easy reaching of a negative decision), the ERPs elicited by pronounceable stimuli were comprised first of a negative potential (N320), at the resolution of which the P300-like potential was observed.

Because the cognitive and linguistic processes required for making rhyme decisions are not evident in performance, it is impossible to unequivocally link the N320 to a particular cognitive event. For example, although the full activation of the lexicon is not necessary for generating phonetic codes,⁷ as revealed by the correct decisions made for pseudowords, phonology probably mediates between orthography and phonetics. Furthermore, it may be possible to decide whether two orthographic patterns rhyme on the basis of matching their abstract phonological realizations (i.e., without converting the phonemes to phones). Therefore, we cannot discard the possibility that the activity reflected by the ERPs in the rhyme-decision task was only phonological. Indeed, although the spatial distributions of the N320 and N350 did not completely overlap, both potentials were maximal at T3. Moreover, the *onset* of the difference between phonologically legal and illegal stimuli began slightly sooner in the lexical decision task (270 msec at T3) than in the phonetic decision task (295 msec at T3). This difference, however, was not significant, a fact that is hardly surprising if we assume that phonological processes were involved in both processes. Yet, compared with the N320, the distribution of the N350 is slightly more anterior in the left temporal lobe and clearly broader in circumference, including parietal and fronto-parietal areas that were not activated in the phonetic task. The difference in latency and scalp distribution between the N320 and the N350 that was observed in the lexical decision tasks suggests that the cognitive processes involved in these two tasks did not entirely overlap. It is possible that the N320 is associated with the phonetic transformation performed on pronounceable orthographic patterns, a process that began not earlier than 270 msec from stimulus onset, following the initiation of the orthographic analysis.

Assuming that ERPs are, at least partially, associated with cognitive events and reflect their time course and, to some extent, their underlying neural basis, the precedence of the N320 over the N350 and the partial overlap in scalp distribution suggests that while phonological units were activated in both tasks, the formation of phonetic codes is faster (concluded sooner) than the additional lexical (or postlexical) processes required to reach a lexical decision. The scalp distribution of the N320 was very different from that of the N170, being particularly conspicuous at midtemporal-parietal sites, predominantly over the left hemisphere. This pattern is inconsistent with the findings of Rugg (1984) (see also Praamstra, Meyer, & Levelt, 1994; Rugg & Barrett, 1987), who reported a right-hemisphere dominant N450 in a

rhyme-matching task. Yet, both the scalp distribution and the considerably shorter latency of the N320 relative to the N450 suggest that two different cognitive phenomena were tapped in the two studies. The N450 may be associated with a relatively late, postlexical phonological process, whereas the N320 could represent an early lexical or prelexical process of grapheme-to-phoneme-to-phone translation. This suggestion is supported by the distribution of the N320, which roughly corresponds to Wernicke's area. This distribution is consistent with the data reported in several PET studies in which temporoparietal activation was found when subjects performed rhyme-detection tasks on visually or auditory presented words (Petersen & Fiez, 1993; Petersen et al., 1989). Interestingly, these temporal/temporo-parietal regions were not activated by simple auditory stimuli, including tones, clicks, or rapidly presented synthetic syllables (Lauter, Herscovitch, Formby, & Raichle, 1985; Mazziotta, Phelps, Carson, & Kuhl, 1982). Moreover, clinical neuropsychological literature reported that lesions surrounding the left sylvian fissure (Wernicke's area, insular cortex, supramarginal gyrus) may cause a deficit in sound categorization and an inability to arrange sounds into coherent speech (Marshall, 1986). Hence, the ERP data in the present study concur with previous neuroimaging and neuropsychological evidence regarding the neuroanatomical distribution of areas associated with phonetic processing, suggesting that the phonetic analysis of written words starts at about 270 msec from stimulus onset, about 150 msec after the onset of orthographic analysis.

Lexical and Semantic Processing

Lexical decisions do not imply the processing of the word meaning; phonological patterns can be correctly recognized as words even if their meaning is not known. Yet, evidence for semantic priming at a short SOA following task-induced letter-level processing of the prime suggests that the access to the semantic network and the processing of the word's meaning is the default action of the word perception mechanism (see Smith, Bentin, & Spalek, submitted, for a comprehensive discussion). Consequently, using only performance measures, it is very difficult to disentangle lexical/phonological and semantic processes in single word recognition when only performance measures are used. It is not surprising, therefore, that influential models tend to devalue the role of phonological processing in word recognition, suggesting that following the orthographic analysis (on the basis of which, for example, a logogen is activated, Morton, 1969), the activation of the word's meaning in the cognitive/semantic system is a "direct" next step. One of the aims of the present study was to explore the possibility of distinguishing between lexical/phonological and semantic processing by taking advantage of the time continuous measure provided by ERPs. A comparison

between the ERPs elicited in the rhyme, lexical decision, and semantic decision experiments suggests that phonological and semantic processes are indeed distinct in time course and possibly also in their functional neuroanatomy.

Recall that lexical decision processes were examined in the present study in three separate oddball experiments that differed in the characteristics of the distinction between targets and nontarget stimuli. We assumed that the cognitive processes required for each distinction modulated the ERPs elicited by the nontargets in each experiment. As in the rhyme task, the ERPs in the lexical decision tasks distinguished mostly between the nonwords (which required only a shallow, orthographic process to be categorized) and the phonologically legal stimuli. Although the ERPs elicited by words and pseudowords were apparently distinguished better in the lexical decision task than in the rhyme task, this difference failed to reach statistical significance ($p = 0.085$). In contrast, a significant distinction was found between words and pseudowords in the semantic decision task. The difference between the effect of stimulus type in the lexical and semantic decision tasks might be explained by assuming that different cognitive processes were necessary for making each kind of decision. For example, whereas lexical decisions may be based primarily on activating phonological units in the lexicon, semantic decisions probably require a more extensive and deeper elaboration of the word's meaning. Consequently, although the activation of word meaning may start in parallel with phonological matching and may even help the lexical decision process, semantic decisions elicit cortical activation that should usually last longer. Indeed, in the present study, the onset of the difference between the ERPs elicited by each stimulus type in the lexical and semantic decision tasks were not very far apart, whereas the epoch during which different ERPs were elicited by each stimulus type was longer in the semantic than in the lexical decision task. Differences between the functional neuroanatomy of the semantic and lexical activity is suggested by the significantly different distribution of the N350 and N450, the two most prominent negative potentials that were elicited in the lexical decision and semantic tasks, respectively. Whereas the N350 was largest at T3 and was distributed over the midtemporal and supratemporal regions, the semantic decision seemed to involve, in addition, more anterior and superior areas of the temporal lobes and adjacent regions in the left frontal lobe. This distribution (particularly its left-hemisphere-dominant asymmetry) is different from that usually found for N400 potentials in sentences (Kutas & Hillyard, 1982) or lexical decision tasks (e.g., Holcomb, 1993). It is, however consistent with PET findings in tasks that require semantic activity (e.g., Demonet et al., 1992) and fMRI studies of word generation (McCarthy et al., 1994). At the very least, this distribution supports a dissociation between pure phonological and semantic

activity, consistent with neurological studies that have described a double dissociation between dyslexic patients who can read words without understanding their meaning (e.g., Schwartz, Saffran, & Marin, 1980), and patients who understand the meaning of spoken words but are unable to read them (for a recent review see Ellis & Young, 1996).

Comparing phonologically legal and illegal orthographic patterns across all tasks suggests that the linguistic-related ERP activity (in single-word processing) was reflected in negativities whose peak latency preceded the P3b. This finding is congruent with ample evidence that has been published since the discovery of the N400 (Kutas & Hillyard, 1980). In the present lexical decision task, the most prominent negativity peaked at 350 msec. As mentioned above, words and pseudowords elicited similar ERPs at this latency. This finding seems to contradict the well-established RT difference between words and pseudowords in lexical decision tasks. Our data, however, were derived from a lexical decision paradigm different from the ordinary word/nonword decision tasks. First, it required no speeded RTs, and therefore some of the factors influencing the RTs in lexical decision tasks were inconsequential in the present paradigm. Second, and more important, the ERPs measured for the present comparisons were not elicited by the target stimuli. Both the words and the pseudowords were equally irrelevant for the subject's task and were therefore members of the same task-related response category. Indeed, the amplitude of the P300 elicited by the words was significantly higher than that elicited by the pseudowords. In conclusion, we suggest that the N350 may be associated with the phonological analysis of the orthographic pattern applied to both words and pseudowords.

In the semantic task, the difference between words and pseudowords was apparently divided into two distinct epochs. The first ended at about 350 msec from stimulus onset (the peak latency of the negative potential in the lexical decision tasks). During this epoch the ERPs elicited by words and pseudowords did not significantly differ one from another. Therefore we suggest that the ERP activity elicited during this period is associated with phonological processes that are similar in the lexical decision and the semantic tasks. During the second epoch, words and pseudowords were clearly different. This difference started at about 350 msec and culminated at the peak of the N450, which is not seen in the lexical decision task (Figures 2E and 5). Surprisingly, the N450 elicited by pseudowords was significantly larger than that elicited by words. In general, we (as well as others) assume that larger negativities reflect more extensive processing that, in this experiment, was semantic (cf. the modulation of the N400 by semantic priming, Bentin et al., 1985, or by repetition, Rugg, 1985, in lexical decision). Because the task was

to distinguish between abstract and concrete words, one approach could have been to perform a lexical decision first and then continue the semantic processing only for words. Such an approach should have resulted in a larger N450 for words than for pseudowords. A second approach was also possible, however. In this approach the reader would attempt to decide directly whether a phonological legal orthographic pattern is an abstract word or not (i.e., without making a word/pseudoword distinction first). If this approach is taken, deciding that a (known) concrete word is not abstract may be easier (and faster) than deciding that a pseudoword is not an (infrequent) abstract word. Apparently our subjects chose the second decision strategy. Admittedly, this interpretation is post hoc. It is, however, consistent with the larger P300 observed for words (which might have been the source of the word/pseudoword difference) and not (a priori) implausible.

An Overview

The interpretation of the present results and their implications for the psycholinguistic and neural mechanisms involved in processing individual words are valid to the extent that (1) our tasks implicated, indeed, the presumed perceptual and linguistic processes and (2) the scalp-recorded ERPs were modulated by these processes. Although none of the above caveats can be easily overridden, we accepted both assumptions as working hypotheses. With these caveats in mind, we can continue our discussion and suggest some interpretations.

The ERPs elicited by the different stimuli across tasks displayed several important patterns. First, regardless of task and phonological values, orthographic patterns elicit fairly similar activity at the occipital and occipitotemporal scalp regions, predominantly in the left hemisphere (Figure 6). This pattern suggests that letters automatically activate visual modules that are tuned to detect orthographic material prior to any deeper linguistic process. Orthographic stimuli that allow phonological and/or phonetic processing activate language-processing-specific areas in the midtemporal and supratemporal regions, predominantly in the left hemisphere (Figure 8). These areas are probably involved in phonological and phonetic processing. In addition, semantic activity elicits ERPs that are distributed over the anterior-temporal fronto-central scalp areas. In the present study we used only orthographic patterns. Other studies, however, showed similar ERP distribution in response to visually presented objects (Barrett & Rugg, 1989) and even nonlinguistic stimuli such as unfamiliar human faces (Barrett & Rugg, 1989; Bentin & McCarthy, 1994). Hence, the fronto-central areas activated in the semantic decision task in the present study may be part of a conceptual semantic memory system that may include, but does not necessarily totally overlap with, the

words' meaning network. Interestingly, there seems to be a correlation between the site of activity on the anterior-posterior dimension, on the one hand, and the depth of processing in general and linguistic processing in particular, on the other (Figure 2B and 2E). Apparently deeper processing of the orthographic patterns is associated with activity in more anterior regions of the temporal lobe. A similar conclusion has been reached by McCarthy and his colleagues using intracranial recordings (McCarthy et al., 1995; Nobre & McCarthy, 1995), and it is congruent with the functional organization of the "ventral pathway" of the visual system described by several authors (e.g., Felleman & Van Essen, 1991; Maunsell & Newsome, 1987; Van Essen & DeYoe, 1995).

The scalp distribution of the ERP activity in the different tasks and their onset and time course is incongruent with either a unified brain mechanism for word perception or a serial model of processing. The scalp distribution of the negative peaks, although overlapping to some extent, was sufficiently distinct (across peaks) to suggest that different neural networks may be involved in each type of process. Overall, such a pattern may support a word-recognition mechanism based on a network of interrelated neural modules working in synchrony, each of which is responsible for a particular aspect of the word-recognition process. The peaks of the negative components associated with each level of processing were different, later in deeper processing tasks than in more shallow ones. Yet, the epochs during which the ERPs were modulated by each task overlapped in time to a great extent. Although the duration of an ERP does not necessarily equal the processing time, the two are probably connected. Therefore, the overlap between the ERPs elicited in different tasks suggests the onset of deeper levels of processing does not wait for the shallower process to conclude. Such a pattern should be more congruent with a cascade (McClelland, 1979) than with a serial-processing model of word recognition.

Although suggestive, this research is obviously not conclusive. It opens the door, however, for the investigation of the existence of separate functional "modules" involved in word recognition by providing converging evidence for their functional neuroanatomical dissociation and describing their relative time course of activation.

METHODS

Subjects

Twenty-four right-handed volunteers (eight males), aged 19 to 30 years, were paid for their participation in the experiment. They were all native French speakers with normal or corrected-to-normal vision and without any neurological or neuropsychological disorder.

Stimuli

The stimuli were 1368 words or wordlike four- to eight-character strings (mean = 5.8). The stimuli were divided into five types: (1) *words* in the French lexicon, (2) *pseudowords*, which were orthographic patterns that followed the rules of the French phonology and orthography (e.g., "lartuble"), (3) orthographically illegal *nonwords* that were unpronounceable consonant letter strings (e.g., "rtgdfs"), (4) strings of *alphanumeric symbols* such as "&@\$\$," and (5) strings of *forms* such as "llll." The pseudowords were constructed by substituting two letters in the selected words. Among the 432 words, 400 were concrete (e.g., placard) and 32 abstract (e.g., amour). The mean frequency of the concrete words was 1250, 1280, 1083, and 1720 (per 10 millions, Imbs, 1971) for the size, rhyme, lexical decision, and semantic decision tasks, respectively. A one-way ANOVA showed that the difference between the frequencies of these groups was not significant ($F(3, 336) < 1.00$). The mean frequency of the abstract words was 6228 per 10 million, higher than the mean frequency of the concrete words (1343 per 10 million). This difference, however, was irrelevant to the comparisons made in the present study because abstract words were only used as targets in the oddball task and never compared with other word types.

Tasks

The entire study was divided into four tasks, each of them inducing a different level of processing visual/orthographic (task 1), phonological/phonetic (task 2), phonological/lexical (task 3), and semantic (task 4). In each task, the experimental paradigm was a mental oddball task in which subjects had to mentally count the number of target stimuli delivered randomly among nontarget stimuli. In task 1 ("size" task), the targets were large-sized stimuli presented among standard-sized stimuli. The stimuli were words, pseudowords, nonwords, strings of alphanumeric symbols, and strings of forms. In task 2 ("rhyme" task), the targets were words or pseudowords rhyming with the word *vitrail*, with orthographically possible endings being "aille," "ail," "aye," or "ai." Nontarget stimuli were words, pseudowords, and nonwords. Task 3 included three lexical decision types: in LD-1 the targets were words interspersed among illegal nonwords; in LD-2 the targets were words interspersed among pseudowords; in LD-3 the targets were pseudowords interspersed among words. In task 4 (the semantic-decision task), subjects had to count abstract words interspersed among concrete words, pseudowords, and nonwords.

Procedure

Subjects sat on a reclining chair in an electrically and acoustically shielded room facing a computer monitor.

The screen was at a distance of approximately 100 cm from the subject's eyes. A rectangular blue window (11 × 3 cm) was always present at the center of the screen. Stimuli were foveally presented in this window for 500 msec, at a rate of one every 1250 msec (SOA). The subjects were instructed to avoid blinking while the stimuli were exposed. They were given one practice block before each of the four tasks, which were performed within one session lasting about 1.5 h (not including electrode placement procedures—see below).

The four experiments were presented in fixed order: size task, rhyme task, lexical tasks, and semantic decision. The fixed order was necessary to reduce the possible interference of a deeper-level process with a more superficial level. However, the order of the three lexical decision tasks was counterbalanced (using a Latin square design) between subjects. In each task, the stimuli were delivered randomly in blocks of 50 items each. The first task included 10 blocks (500 stimuli), and the second task included 6 blocks (284 stimuli); each of the three lexical decision types in the third task was composed of 2 blocks (100 stimuli), and the fourth task was composed of 6 blocks (284 stimuli) (Table 1). Subjects reported the number of target stimuli detected after each block.

ERP Recording

EEG was recorded by 32 Ag/AgCl scalp electrodes referred to the nose and positioned over symmetrical positions on the two hemispheres as illustrated in Figure 10. The montage was guided by a special-purpose computer-controlled system (Pastel) based on a three-dimensional digitization of the head (Echallier, Perrin, & Pernier, 1992). During recording the electrode impedance was kept below 2 k Ω .

Eye movement artifacts were controlled off-line by the two prefrontal electrodes (FP1 and FP2) and an electrode placed at the outer canthus of the right eye (YH). Trials in which the potential measured in any of those channels exceeded 150 μ V were rejected. Artifacts induced by amplifiers blocking were avoided, excluding trials in which amplitudes above 250 μ V were measured in any of the channels.

The EEG and electroculogram (EOG) were amplified with a bandpass of 0.03 to 320 Hz (sampling rate 1000 Hz) and stored on a computer disk for off-line analysis. The ERPs were averaged separately for each stimulus type in each experimental session over an analysis period of 1024 msec, including 100-msec prestimulus. After averaging, frequencies lower than 0.8 Hz and higher than 16 Hz (3 dB) were digitally filtered out.

Data Analysis

Scalp potential and current density topographic maps were generated on a color graphics terminal using a

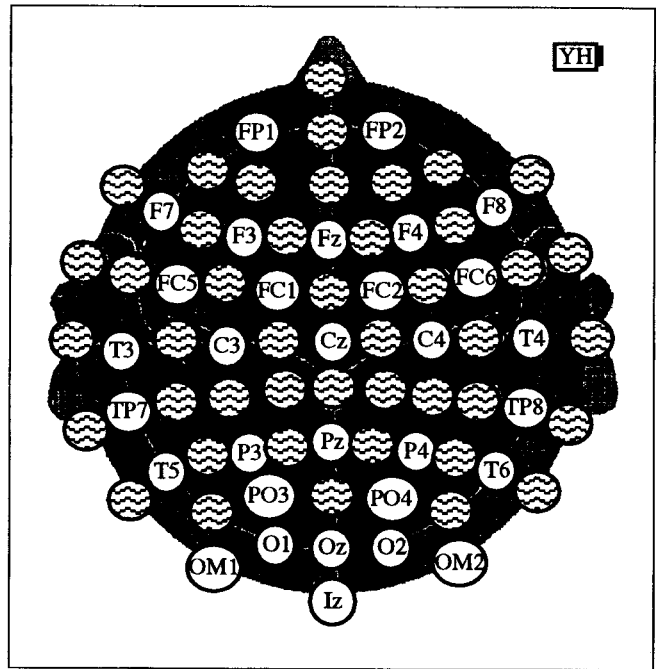


Figure 10. Thirty-two-channel electrode montage including all standard sites in the 10–20 system. The ground was located on the forehead between FP1 and FP2 and the nose was used as the reference.

two-dimensional spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989; Perrin, Pernier, Bertrand, & Giard, 1987) and a radial projection from Oz (back views) or from T3 or T4 (lateral views), along the length of the meridian arcs. The topographies were color coded and were normalized to the peak voltage value (positive or negative) of the recording montage. As described in detail at the beginning of the Results section, the electrophysiological manifestations at different levels of processing word were assessed by first calculating the statistical validity of the difference between the mean amplitude of the ERP elicited by each stimulus type in each decision task. The means were calculated for a visually determined epoch during which the waveforms seemed to be modulated by each task and for electrodes symmetrically located across the right and the left hemispheres. The onset of this difference was statistically determined as the first latency at which the difference between waveforms was significant using a series of point-by-point *t* tests. In addition, a series of negative potentials was associated with the different stimulus conditions in each task. The mean amplitude of each component was calculated for an epoch comprising 24 points (98-msec) 12 before and 12 after its visually determined peak. To allow the comparison of the scalp distributions of each component (and hence help distinguishing among them), these values were calculated at the same 14 electrodes that covered the temporal and superior temporal areas, symmetrically located over each hemi-

sphere. Finally, the latency of each peak was defined as the latency of the most negative point during the relevant epoch.

Statistical differences among the ERP components for different stimulus types in each experimental session (visual, phonetic, lexical, and semantic sessions) were tested with repeated-measures ANOVAs. For all repeated measures with more than 1° of freedom, the more conservative Greenhouse-Geisser adjusted df-values were used. ANOVAs were followed by post hoc Tukey-A tests or univariate *F* contrasts (Greenhouse & Geisser, 1959).

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Reprint requests should be sent either to Shlomo Bentin, Department of Psychology, Hebrew University, Jerusalem, 91905 Israel, or to Marie-Helene Giard, INSERM U280, 151, Albert Thomas, 69424 Lyon, Cedex 03, France.

Notes

1. Men were more asymmetric than women for orthographic stimuli (0.31 μ V vs. 0.18 μ V) and larger in the left than in the right occipito-parietal sites), whereas women were more asymmetric than men for nonorthographic stimuli (0.62 μ V vs. 0.24 μ V and larger in the right than in the left occipito-parietal sites).
2. We will analyze this interaction in more detail in our analysis of the distribution of the N350.
3. The significantly larger N450 at F7 and F8 may, however, reflect the absence of the stimulus type effect at these sites. Nonetheless, for pseudowords as well as for words, the largest N450 was found at F7 (-1.58 and -1.19 μ V for pseudowords and words, respectively).
4. An ANOVA comparing the N170 elicited at T5 and T6 in each task showed that there was indeed no significant main effect of task ($F(3, 69) = 1.9, p = 0.15$). A significant interaction between stimulus type and task, however, suggested that the difference between words, pseudowords, and nonwords was not the same across tasks. Separate analyses revealed that whereas the difference between words and pseudowords was not significant in any task, the nonwords elicited significantly larger N170 than the words in the lexical decision ($F(1, 23) = 59.3, p < 0.001$) and in the semantic decision ($F(1, 23) = 56.3, p < 0.001$) tasks. This interaction suggests that deeper tasks may have a top-down influence on the N170 recorded at the posterior-temporal lobes.
5. The positive amplitude elicited by nonwords in the phonological and semantic tasks may, however, be a P300 reflecting the faster decisions associated with these stimuli.
6. We chose a target that can rhyme with words ending in different spellings. Hence, subjects could not have performed this task by simply matching the orthographic patterns (see Methods).
7. Some models of word recognition, however, suggest that the phonological structures of pseudowords are derived by

activating lexical entries of analogous real words (e.g., Glushko, 1979).

REFERENCES

- Allison, T., McCarthy, G., Nobre, A. C., Puce, A., & Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cerebral Cortex*, *5*, 544-554.
- Balota, D., & Chumbley, J. I. (1984). Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 340-357.
- Barrett, S. E., & Rugg, M. D. (1989). Event-related potentials and the semantic matching of faces. *Neuropsychologia*, *27*, 913-922.
- Barrett, S. E., & Rugg, M. D. (1990). Event-related potentials and the phonological matching of pictures. *Brain and Cognition*, *14*, 201-212.
- Beauregard, M., Chertkow, H., Bub, D., Murtha, S., Dixon, R., & Evans, A. (1997). The neural substrate for concrete, abstract, and emotional word lexica: A positron emission tomography study. *Journal of Cognitive Neuroscience*, *9*, 441-461.
- Bentin, S. (1987). Event-related potentials, semantic processes, and expectancy factors in word recognition. *Brain and Language*, *31*, 308-327.
- Bentin, S. (1989). Electrophysiological studies of visual word perception, lexical organization, and semantic processing: A tutorial review. *Language and Speech*, *32*, 205-220.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551-565.
- Bentin, S., Kutas, M., & Hillyard, S. A. (1993). Electrophysiological evidence for task effects on semantic priming in auditory word processing. *Psychophysiology*, *30*, 161-169.
- Bentin, S., & McCarthy, G. (1994). The effect of immediate stimulus repetition on reaction time and event-related potentials in tasks of different complexity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 130-149.
- Bentin, S., McCarthy, G., & Wood, C. C. (1985). Event-related potentials, lexical decision and semantic priming. *Electroencephalography and Clinical Neurophysiology*, *60*, 343-355.
- Benton, A. L. (1975). Developmental dyslexia: Neurological aspects. *Advances in Neurology*, *7*, 2-41.
- Besson, M., Fischler, I., Boaz, T., & Raney, G. (1992). Effects of automatic associative activation on explicit and implicit memory tests. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*, 89-105.
- Bookheimer, S. Y., Zeffiro, T. A., Blaxton, T., Gaillard, W., & Theodore, W. (1995). Regional cerebral blood flow during object naming and word reading. *Human Brain Mapping*, *3*, 93-106.
- Campbell, R. T. L., & Regard, M. (1986). Face recognition and lipreading: A neurological dissociation. *Brain*, *109*, 509-521.
- Carr, T. H., & Pollatsek, A. (1985). Recognizing printed words: A look at current models. In D. Besner, T. G. Waller, & G. E. MacKinnon (Eds.), *Reading research: Advances in theory and practice 5* (pp. 1-82). New York: Academic Press.
- Chertkow, H., Bub, D., Beauregard, M., Hosen, C., & Evans, A. (in press). Visual and orthographic components of single word processing: A positron tomography study. *Brain*.

- Chwilla, D. J., Brown, C. M., & Hagoort, P. (1995). The N400 as a function of the level of processing. *Psychophysiology*, *32*, 274-285.
- Coltheart, M. (1985). Cognitive neuropsychology and the study of reading. In O. S. M. Marin & M. I. Posner (Eds.), *Attention and performance X*. Hillsdale, NJ: Erlbaum.
- Coltheart, M., Patterson, K. E., & Marshall, J. C. (1980). *Deep dyslexia*. London: Routledge and Kegan Paul.
- Damasio, A. R., & Damasio, H. (1983). The anatomic basis of pure alexia. *Neurology*, *33*, 1573-1583.
- Deacon, D., Breton, F., Ritter, W., & Vaughan, H. G., Jr. (1991). The relationship between the N2 and the N400: Scalp distribution, stimulus probability, and task relevance. *Psychophysiology*, *28*, 185-200.
- Demonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., Rascol, A., & Frackowiak, R. S. J. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, *115*, 1753-1768.
- Donchin, E. . Surprise! . . . Surprise? *Psychophysiology*, *18*, 493-513.
- Ducan-Johnson, C. C., & Donchin, E. (1982). The P300 component of the event-related brain potentials as an index of information processing. *Biological Psychology*, *14*, 1-52.
- Echallier, J. F., Perrin, F., & Pernier, J. (1992). Computer-assisted placement of electrodes on the human head. *Electroencephalography and Clinical Neurophysiology*, *82*, 160-163.
- Ellis A. W., Flude, B. M., & Young, A. W. (1987). "Neglect dyslexia" and the early visual processing of letters in words. *Cognitive Neuropsychology*, *4*, 439-464.
- Ellis, A. W., & Young, A. W. (1996). *Human cognitive neuropsychology: A textbook with readings*. Hove & London: Erlbaum Psychology Press.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in primate visual cortex. *Cerebral Cortex*, *1*, 1-47.
- Frith, C. D., Friston, K. J., Liddle, P. F., & Frackowiak, R. S. J. (1991). A PET study of word finding. *Neuropsychologia*, *29*, 1137-1148.
- Frith, C. D., Kapur, K. J., Friston, P. F., Liddle, P. F., & Frackowiak, R. S. J. (1995). Regional cerebral activity associated with the incidental processing of pseudo-words. *Human Brain Mapping*, *3*, 153-160.
- Frost, J. A., Springer, J. A., Binder, J. R., Hammeke, T. A., Bellgowan, P. S. F., Rao, S. M., & Cox, R. W. (1997). Sex does not determine functional lateralization of semantic processing: Evidence from fMRI. *Proceedings of the Third International Conference of the Society for Human Brain Mapping*. Copenhagen, April.
- George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, *4*, 65-76.
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, *24*, 95-112.
- Glushko, R. J. (1979). The organization and activation of orthographical knowledge in reading aloud. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 674-691.
- Henderson, V. W. (1986). Anatomy of posterior pathways in reading: A reassessment. *Brain and Language*, *29*, 199-233.
- Henik, A., Friedrich, F. J., & Kellogg, W. A. (1983). The dependence of semantic relatedness effects upon prime processing. *Memory and Cognition*, *11*, 366-373.
- Henik, A., Friedrich, F. J., Tzelgov, J., & Tramer, S. (1994). Capacity demands of automatic processes in semantic priming. *Memory and Cognition*, *22*, 157-168.
- Hillyard, S. A., & Kutas, M. (1983). Electrophysiology of cognitive processing. *Annual Review of Psychology*, *34*, 33-61.
- Hinton, G. E., & Shallice, T. (1991). Lesioning an attractor network: Investigations of acquired dyslexia. *Psychological Review*, *98*, 74-95.
- Holcomb, P. J. (1986). ERP correlates of semantic facilitation. In W. C. McCallum, R. Zappoli, & F. Denoth (Eds.), *Electroencephalography and clinical neurophysiology supplement 38. Cerebral psychophysiology: Studies in event-related potentials*. Amsterdam: Elsevier.
- Holcomb, P. J. (1993). Semantic priming and stimulus degradation: Implications for the role of the N400 in language processing. *Psychophysiology*, *30*, 47-61.
- Holcomb, P. J., & Neville, H. J. (1990). Auditory and visual semantic priming in lexical decision: A comparison using event-related brain potentials. *Language and Cognitive Processes*, *5*, 281-312.
- Howard, D., Patterson, K., Wise, R., Brown, W. D., Friston, K., Weiller, C., & Frackowiak, R. (1992). The cortical localization of the lexicons. Positron emission tomography evidence. *Brain*, *115*, 1769-1782.
- Imbs, P. (1971). *Dictionnaire des fréquences: Vocabulaire littéraire des XIX^e et XX^e siècles*. Nancy, France: CNRS.
- Jared, D., & Seidenberg, M. S. (1991). Does word identification proceed from spelling to sound to meaning? *Journal of Experimental Psychology: General*, *120*, 358-394.
- Kutas, M., & Hillyard, S. A. (1980). Event-brain potentials to semantically inappropriate and surprisingly large words. *Biological Psychology*, *11*, 99-116.
- Kutas, M., & Hillyard, S. A. (1982). The lateral distribution of event-related potentials during sentence processing. *Neuropsychologia*, *20*, 579-590.
- Kutas, M., & Hillyard, S. A. (1989). An electrophysiological probe of incidental semantic association. *Journal of Cognitive Neuroscience*, *1*, 38-49.
- Kutas, M., Hillyard, S. A., & Gazzaniga, M. S. (1988). Processing of semantic anomaly by right and left hemispheres of commissurotomy patients. *Brain*, *111*, 553-576.
- Kutas, M., Lindamood, T. E., & Hillyard, S. A. (1984). Word expectancy and event-related potentials during sentence processing. In S. Kornblum & J. Requin (Eds.), *Preparatory states and processes* (pp. 217-234). Hillsdale, NJ: Erlbaum.
- Kutas, M., McCarthy, G., & Donchin, E. (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, *197*, 792-795.
- Kutas, M., & Van Petten, C. (1988). Event-related brain potential studies of language. *Advances in Psychophysiology*, *3*, 139-187.
- Lauter, J., Herscovitch, P., Formby, C., & Raichle, M. E. (1985). Tonotopic organization in human auditory cortex revealed by positron emission tomography. *Hearing Research*, *20*, 199-205.
- Marshall, J. C. (1986). The description and interpretation of aphasic language disorder. *Neuropsychologia*, *24*, 5-24.
- Maunsell, J. H. R., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience*, *10*, 395-367.
- Mazziotta, J. C., Phelps, M. E., Carson, R. E., & Kuhl, D. E. (1982). Tomographic mapping of human cerebral metabolism: Auditory stimulation. *Neurology*, *32*, 921-937.
- McCallum, W. C., Farmer, S. F., & Pocock, P. V. (1984). The effects of physical and semantic incongruities on auditory event-related potentials. *Electroencephalography and Clinical Neurophysiology*, *59*, 477-488.
- McCarthy, G., Blamire, A. M., Puce, A., Nobre, A. C., Bloch, G., Hyder, F., Goldman-Rakic, P., & Shulman, R. G. (1994). Functional magnetic resonance imaging of human prefrontal

- cortex activation during a spatial working memory task. *Proceedings of the National Academy of Science U. S. A.*, *91*, 8690-8694.
- McCarthy, G., Blamire, A. M., Rothman, D. L., Gruetter, R., & Shulman, R. G. (1993). Echo-planar magnetic resonance imaging studies of frontal cortex activation during word generation in humans. *Proceedings of the National Academy of Science U. S. A.*, *90*, 4952-4956.
- McCarthy, G., & Donchin, E. (1981). A metric of thought: A comparison of P300 latency and reaction time. *Science*, *211*, 77-80.
- McCarthy, G., & Nobre, A. C. (1993). Modulation of semantic processing by spatial selective attention. *Electroencephalography and Clinical Neurophysiology*, *88*, 210-219.
- McCarthy, G., Nobre, A. C., Bentin, S., & Spencer, D. D. (1995). Language-related field potentials in the anterior-medial temporal lobe: 1. Intracranial distribution and neural generators. *Journal of Neuroscience*, *15*, 1080-1089.
- McClelland, J. L. (1979). On the time-relations of mental processes: An examination of systems of processes in cascade. *Psychological Review*, *86*, 287-330.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: 1 An account of basic findings. *Psychological Review*, *88*, 375-407.
- Morton, J. (1969). Interaction of information in word recognition. *Psychological Review*, *88*, 375-407.
- Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, *372*, 260-263.
- Nobre, A. C., & McCarthy, G. (1994). Language-related ERPs: Modulation by word type and semantic priming. *Journal of Cognitive Neuroscience*, *6*, 233-255.
- Nobre, A. C., & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: 2. Effects of word type and semantic priming. *Journal of Neuroscience*, *15*, 1090-1098.
- Patterson, K. E., & Kay, J. (1982). Letter-by-letter reading: Psychological descriptions of a neurological syndrome. *Quarterly Journal of Experimental Psychology*, *34A*, 411-441.
- Patterson, K. E., Marshall, J. C., & Coltheart, M. (1985). *Surface dyslexia*. London: Erlbaum.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*, 184-187.
- Perrin, F., Pernier, J., Bertrand, O., & Giard, M. H. (1987). Mapping of scalp potentials by surface plane interpolation. *Electroencephalography and Clinical Neurophysiology*, *66*, 75-81.
- Petersen, S. E., & Fiez, J. A. (1993). The processing of single words studied with positron emission tomography. *Annual Review of Neuroscience*, *16*, 509-530.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1989). Positron emission tomographic studies of the processing of single words. *Journal of Cognitive Neuroscience*, *1*, 153-170.
- Petersen, S. E., Fox, P. T., Snyder, A. Z., & Raichle, M. E. (1990). Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science*, *249*, 1041-1044.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25-42.
- Posner, M. I., Petersen, S. E., Fox, P. T., & Raichle, M. E. (1988). Localization of cognitive operations in the human brain. *Science*, *240*, 1627-1631.
- Posner, M. I., & Raichle, M. E. (1994). *Images of mind*. New York: Freeman.
- Praamstra, P., Meyer, A. S., & Levelt, W. J. M. (1994). Neurophysiological manifestations of phonological processing: Latency variations of a negative ERP component time-locked to phonological mismatch. *Journal of Cognitive Neuroscience*, *6*, 204-219.
- Price, C. J., Wise, R. J. S., Watson, J. D. G., Patterson, K., Howard, D., & Frackowiak, R. S. J. (1994). Brain activity during reading: The effects of exposure duration and task. *Brain*, *117*, 1255-1269.
- Pugh, K. R., Shaywitz, B. A., Constable, R. T., Shaywitz, S. E., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Shankweiler, D. P., Katz, L., Fletcher, J. M., & Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain*, *119*, 1221-1238.
- Rugg, M. D. (1984). Event-related potentials and the phonological processing of words and nonwords. *Neuropsychologia*, *22*, 435-443.
- Rugg, M. D. (1985). The effects of handedness on event-related potentials in a rhyme-matching task. *Neuropsychologia*, *23*, 765-775.
- Rugg, M. D. (1990). Event-related potentials dissociate repetition effects of high- and low-frequency words. *Memory and Cognition*, *18*, 367-379.
- Rugg, M. D., & Barrett, S. E. (1987). Event-related potentials and the interaction between orthographic and phonological information in a rhyme-judgment task. *Brain and Language*, *32*, 336-361.
- Schwartz, M. F., Saffran, E. M., & Marin, O. S. M. (1980). Fractionating the reading process in dementia: Evidence for word-specific point-to-sound associations. In M. Coltheart, K. E. Patterson, & J. C. Marshall (Eds.), *Deep dyslexia* (pp. 259-269). London: Routledge and Kegan Paul.
- Shallice, T., & Warrington, E. K. (1977). The possible role of selective attention in acquired dyslexia. *Neuropsychologia*, *15*, 31-41.
- Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word and naming. *Psychological Review*, *96*, 528-568.
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Constable, R. T., Shaywitz, S. E., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Fletcher, J. M., Shankweiler, D. P., Katz, L., & Gore, J. C. (1995). Sex differences in the functional organization of the brain for language. *Nature*, *373*, 607-609.
- Smith, M. C., Bentin, S., & Spalek, T. (submitted). *On the automaticity of semantic priming at short SOAs*.
- Smith, M. C., Theodor, L., & Franklin, P. E. (1983). The relationship between contextual facilitation and depth of processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*, 697-712.
- Van Essen, D. C., & DeYoe, E. A. (1995). Concurrent processing in the primate visual cortex. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 383-400). Cambridge, MA & London: MIT Press.
- Verleger, R., Jaskowski, P., & Wauschkuhn, B. (1994). Suspense and surprise: On the relationship between expectancies and P3. *Psychophysiology*, *31*, 359-369.
- Wise, R. J., Chollet, F., Hadar, U., Friston, K., Hoffner, E., & Frackowiak, R. (1991). Distribution of cortical neural networks involved in word comprehension and word retrieval. *Brain*, *114*, 1803-1817.
- Zatorre, R. J., Meyer, E., Gjedde, A., & Evans, A. C. (1996). PET studies of phonetic processing of speech: Review, replication, and reanalysis. *Cerebral Cortex*, *6*, 21-30.