[Q:] When Would You Prefer a SOSSAGE to a SAUSAGE? [A:] At about 100 msec. ERP Correlates of Orthographic Typicality and Lexicality in Written Word Recognition

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Abstract

■ Using a speeded lexical decision task, event-related potentials (ERPs), and minimum norm current source estimates, we investigated early spatiotemporal aspects of cortical activation elicited by words and pseudowords that varied in their orthographic typicality, that is, in the frequency of their component letter pairs (bigrams) and triplets (trigrams). At around 100 msec after stimulus onset, the ERP pattern revealed a significant typicality effect, where words and pseudowords with atypical orthography (e.g., *yacht*, *cacht*) elicited stronger brain activation than items characterized by typical spelling patterns (*cart*, *yart*). At ~200 msec, the ERP pattern revealed a significant lexicality effect, with pseudowords eliciting stronger brain activity than words. The two main factors interacted significantly at around 160 msec, where words showed a typicality effect but pseudowords did not. The principal cortical sources of the effects of both typicality and lexicality were localized in the inferior temporal cortex. Around 160 msec, atypical words elicited the stronger source currents in the left anterior inferior temporal cortex, whereas the left perisylvian cortex was the site of greater activation to typical words. Our data support distinct but interactive processing stages in word recognition, with surface features of the stimulus being processed before the word as a meaningful lexical entry. The interaction of typicality and lexicality can be explained by integration of information from the early form-based system and lexicosemantic processes. ■

INTRODUCTION

Reading—the practice of using visual symbols in myriad combinations to refer to meaningful entities—is a recently evolved ability unique to humans. The skills necessary to associate a letter string with a meaning are acquired over several years of intensive learning, usually in childhood. In normal readers, this learning results in a fast, accurate, and almost automatic process, allowing people to read and integrate into context several words per second without much attentional effort. The neural mechanisms underlying this process are naturally of outstanding interest to cognitive neuroscientists who study language.

One vital approach to unveiling the characteristics of the language system is to find the parameters that modulate its performance. In reading, many behavioral studies have been conducted to determine the critical parameters, often focusing on the measurement of reaction times (RTs) and accuracy in the orthographic lexical decision task, where subjects have to decide whether each of a series of letter strings represents an existing word. A frequent assumption is that successful discrimination of real words from pseudowords requires the reader to complete all stages of word recognition until a given stimulus has been found in memory. The speed of positive lexical decisions is thus often taken to reflect the time necessary to match a familiar letter string to an item in memory, and stimulus factors that influence speed and accuracy are typically interpreted as revealing important information about this matching process (e.g., Gernsbacher, 1984; Whaley, 1978).

Behavioral studies suggest that written word recognition relies on different sources of information, which can be roughly classified into two kinds: (i) surface properties, such as the length of a letter string or the frequency of its component letter combinations (bi-/trigram frequency) and (ii) lexicosemantic properties, such as a target word's frequency or imageability. Both kinds of information can influence speed and accuracy of lexical decision (e.g., Balota & Chumbley, 1984; Gernsbacher, 1984; Whaley, 1978), and this presents something of a challenge for interpreting behavioral data because the characteristics of the targets and distractors can dramatically shift the balance between reliance on the two

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general classes of information. For instance, effects of orthographic variables are most pronounced when the nonword distractors are easily discriminable from the words on the basis of their surface properties (Siakaluk, Sears, & Lupker, 2002). In contrast, if targets and distractors are closely matched for surface properties, participants must rely on the retrieval of lexicosemantic information about the real words to make accurate decisions (Binder et al., 2003). Understanding the mechanisms by which these factors contribute to word recognition seems critical; but it is difficult to disentangle them from behavioral data alone because accuracy and RT measures conflate these influences.

Recent evidence suggests that under the specialized conditions of focal brain lesions, surface and lexicosemantic properties can dissociate as sources of information in lexical decision. Semantic dementia (SD) is a neurodegenerative condition in which focal anterior temporal lobe atrophy produces a profound and relatively pure impairment to semantic memory. Patients with SD have major deficits in comprehending the meanings of spoken and written words (Hodges, Patterson, Oxbury, & Funnell, 1992; Snowden, Neary, Mann, Goulding, & Testa, 1992), but it is now well documented across a number of different languages that they can accurately read aloud words and pseudowords with regular spelling-to-sound correspondences (Fushimi et al., 2003; Rozzini, Bianchetti, Lussignoli, Cappa, & Trabucchi, 1997; Diesfeldt, 1992; Patterson & Hodges, 1992). Thus, patients with SD appear to have degraded knowledge of the lexicosemantic properties of words, but relatively preserved knowledge of typical surface properties of the written and spoken language and the mappings between them. One study tested 22 patients with SD in a two-alternative forced-choice lexical decision task in which each target word was either orthographically more typical than a paired pseudoword distractor (e.g., *rot* vs. *racht*) or orthographically less typical relative to the distractor (e.g., *yacht* vs. *yot*) (Rogers, Lambon Ralph, Hodges, & Patterson, 2004). Regardless of patient severity or target word frequency, patients with SD performed well when the real word was orthographically more typical than the distractor (*rot* vs. *racht*). When the reverse was true (*yacht* vs. *yot*), patients showed significant impairments that were modulated by both the frequency of the target word and the severity of the semantic impairment. Most strikingly, when the real word was orthographically atypical and of low frequency, the more severe patients reliably preferred the pseudoword to the real word, and thus had lexical decision scores significantly *below* chance. In other words, severely impaired patients reliably chose as ‘‘real’’ any typically structured letter string, and rejected as ‘‘not real’’ the less typical strings, regardless of which string was the real word. This finding suggests that when semantic knowledge degrades, orthographic properties form the basis of lexical decisions.

The two sources of information that influence lexical decision in healthy adults therefore appear to be at least singly dissociable by brain disease, suggesting that the processes that compute surface and semantic properties of words may be supported by different brain regions. These data also suggest that semantic knowledge plays a greater role in identifying words with atypical spelling patterns (see Patterson et al., 2006; Rogers, Lambon Ralph, Garrard et al., 2004, for a fuller account). Because the most prominent neuronal loss in SD is in anterior temporal cortex, we hypothesized that this brain region may contribute more strongly to the successful recognition of orthographically atypical words, whereas typical words may instead rely more on left perisylvian areas (for a review, see Pulvermüller, 1999). We consider these areas as part of a wider network responsible for the representation and processing of semantic information that includes, in addition, the middle/posterior temporal lobe and left inferior frontal cortex, as well as sensory association areas (Thompson-Schill, 2003; Bookheimer, 2002; Pulvermüller, 2001; Price, 2000).

Although these observations and considerations are suggestive, they tell us little about the time course and the stages of processing at which surface and lexicosemantic properties exert their effects in the healthy system. From a neuroanatomical perspective, it is clear that visually presented words will first activate cortical regions in occipital and posterior inferior temporal lobes where visual information is processed (McCandliss, Cohen, & Dehaene, 2003), and only later will engage areas involved in language comprehension, such as perisylvian regions and more anterior parts of the temporal lobe. Thus, on one hand, one might suppose that the surface properties of visually presented letter strings will exert their effects earliest in processing, in more posterior cortical regions, whereas lexicosemantic effects will only be observed in more anterior regions, somewhat later in processing. On the other hand, axonal conduction times allow for rapid and reciprocal activation along these pathways, raising the possibility that even early in processing, surface characteristics and lexicosemantic properties will interact (Pulvermüller, 1999).

These neuroanatomical considerations find their counterpart in cognitive theories of word recognition. So-called ‘‘form-first’’ theories (e.g., the open-entry model, see Forster, 1999) postulate that the surface form of a word must be computed before its lexicosemantic properties are accessed, whereas ‘‘cascaded’’ models (e.g., McClelland, 1979) suggest that the processes that compute surface and lexicosemantic properties interact early on. Both kinds of theories appear to account for much of the behavioral data (see Forster & Hector, 2002, for a useful discussion). It would therefore be of outstanding interest to reveal the time course of the earliest stages of word processing and, in particular, the stage at which orthographic information begins to interact with lexicosemantic representations. Methods from neuroscience may prove especially informative in elucidating both the cognitive and neural architectures that support visual word recognition.

Event-related brain potentials (ERPs) reveal coherent stimulus-related postsynaptic activity in the cortex with millisecond temporal resolution, hence are ideally suited for investigating the time course of cortical activation during language processing. Few ERP studies have systematically assessed the relative impact of the two different types of information that contribute to lexical decisions; but there is evidence for differences between words and pseudowords ~200 msec after onset (Hinojosa, Martin-Loeches, & Rubia, 2001; Martin-Loeches, Hinojosa, Gomez-Jarabo, & Rubia, 1999; Sereno, Rayner, & Posner, 1998). At ~160 msec after written word onset, researchers have reported neurophysiological differences between word types (Pulvermüller, Lutzenberger, & Birbaumer, 1995) and interactions between a surface feature (word length) and a lexicosemantic variable (word frequency) (Assadollahi & Pulvermüller, 2001, 2003).

The current ERP/lexical decision study orthogonally manipulated lexicality (words vs. well-matched pseudowords) and orthographic typicality (measured by bigram and trigram frequency); the latter is a variable interpretable in terms of surface form features that has not previously been investigated by means of ERPs. Both real word targets and pseudoword distractors could be either orthographically typical (e.g., *cart*, *yart*, *sossage*, *fossil*) or atypical (e.g., *yacht*, *cacht*, *sausage*, *fausil*), so that accurate lexical decisions could not be achieved solely from the structure of the surface form, but required retrieval of lexicosemantic properties. Equal and relatively high proportions (60%) of typical and atypical pseudowords were homophones of target words, which should also minimize reliance on phonological familiarity as a basis for lexical decision. The purpose of this study was not to single out ERP effects for these particular linguistic variables, but rather, by manipulating them, to tap into separable brain processes related to the analysis of surface form versus lexicosemantic information of letter strings.

To the extent that structural and lexicosemantic properties are computed by separate processes, these should be reflected by main effects of typicality and lexicality, respectively, in the ERP signal. To the extent that these processes interact with one another, they should produce reliable interactions in the ERP signal. If there are some stages at which these processes are independent and others at which they interact, the sequence of such stages should be revealed by the temporal ordering of these components. Furthermore, although ERP methodology is not ideally suited for neuroanatomical localization of cognitive functions, source estimation of these ERP effects can provide working hypotheses about the parts of the brain that contribute to the respective processes.

METHODS

Subjects

Fourteen monolingual, English-speaking, right-handed subjects (6 women, 8 men; mean age 23.3 years, SD = 5.3 years) entered the analysis, after data from 3 subjects were discarded due to high noise levels. None of them reported a history of neurological illness or drug abuse, and all had normal or corrected-to-normal vision. Handedness as determined by a standardized procedure revealed a mean laterality quotient of 78 (SD = 25) (Oldfield, 1971). Informed consent was obtained from all subjects and they were paid for their participation. This study was approved by the Cambridge Psychology Research Ethics Committee.

Stimuli

The word and pseudoword stimuli were based on those used in a previous study (Rogers, Lambon Ralph, Hodges, et al., 2004), which employed a two-alternative forced-choice lexical decision (LD) paradigm, in which subjects were confronted on each trial with a word and a pseudohomophonic pseudoword (e.g., *drew*/*driew* or *view*/*vew*) and asked to choose the real word. Furthermore, these pairs actually comprised quartets, in the sense that the surface–orthographic relationship between *drew* and *driew* is identical to the one between *view* and *vew*. The crucial manipulation in the Rogers, Lambon Ralph, Hodges, et al.(2004) study was that in one pair of each matched quartet, the word was less orthographically typical (as measured by positional bigram and trigram frequencies) than its pseudohomophone (as in the pairs *view* and *vew* or *yacht* and *yot*); in the corresponding pair, orthographic typicality favored the real word, as in *drew* and *driew* or *rot* and *racht*. It should be noted that Rogers et al. employed a somewhat special interpretation of the term pseudohomophone: that is, some of the pseudowords would almost certainly not, in isolation, be pronounced by most participants in an identical fashion to their word mates. *Racht* is a pseudohomophone of *rot* only in the sense of its orthographic and phonological matching to the pair *yacht* and *yot*.

In the present experiment, which employed yes/no rather than forced-choice LD so that we could measure RTs, the stimulus items from Rogers, Lambon Ralph, Hodges et al. (2004) were supplemented with an additional 24 items per condition for use in a preliminary rating study (with N = 12 participants) of multiple word parameters. On the basis of these ratings and the subsequent elimination of 10 items per condition, the real word stimuli (N = 50/cell) were matched across high/low typicality on CELEX written frequency per million, imageability, action relatedness, and object relatedness as rated on 7-point scales (see Table 1). We could not find homophonic pseudowords for all of the target words while still keeping the essential manipulation/matching

Table 1. Average Values for Letter Length, Neighborhood Size (*N*), Positional Bigram and Trigram Frequencies for Typical and Atypical Words and Nonwords, and Mean Values for CELEX Word Frequency and Rated Imageability, Action Association, and Object Association for Typical and Atypical Words

	Typical Words	*Atypical Words*	*Typical Pseudowords*	*Atypical Pseudowords*
Length	5.36	5.46	5.24	5.58
N	5.28	0.78	4.90	1.54
Positional bigram	3873	1758	3951	2270
Positional trigram	418	123	492	167
Frequencies per million	9.4	8.2	NA	
Imageability	5.6	5.8		
Action relatedness	3.5	3.4		
Object relatedness	4.7	4.3		

of stimulus quartets for orthographic typicality; but an equal number (30) of the 50 stimuli in each typicality pseudoword condition were homophones of their real-word partners. The remainder were orthographically similar pseudowords that maintained the quartet constraint but were not homophones (e.g., the pair *caribou/carabond* matched to the pair *vagabond/vagibou*). All of the stimuli are listed in Appendix A, with homophonic pairs indicated in the last column of that table. Mean values for letter length, orthographic neighborhood size, summed positional bigram frequency, and summed positional trigram frequency for each condition are provided in Table 1. Between-items analyses of variance (ANOVAs) revealed no significant differences between conditions in string length. As intended, high/low typicality conditions differed significantly in summed positional bigram frequency, $F_i(1,196) = 31.73$, $p < .0005$, summed positional trigram frequency, $F_i(1,196) = 22.55$, $p < .0005$, and as well in orthographic neighborhood size, $F_i(1,196) = 42.12$, $p < .0005$. Within each typicality condition, words and pseudowords were well matched on these factors, so that the participants' lexical decisions could not be based upon these surface features.

Procedure

Subjects performed a standard yes/no lexical decision task. They were instructed to respond to words and pseudowords by pressing a button with their left index finger or left middle finger, respectively. A short practice run preceded the experiment proper to ensure that subjects were comfortable with the task. White letter strings were presented on a dark gray background on a computer screen approximately 1.5 m in front of the subject, with the size of each stimulus not exceeding a visual angle of 4°. Each stimulus was presented for 100 msec to minimize the likelihood of eye movements. The stimulus onset asynchrony (SOA) varied between 2.5 and 3 sec. A fixation cross was shown in the center of the screen during the whole experiment. Each subject was presented with a different sequence of the same stimuli, which contained all quartets of stimuli as described above. Breaks of about 10 sec duration occurred after every 50 stimuli, with the whole session lasting about 15 min. Stimulus delivery and response collection was controlled by the Experimental Run Time System software (ERTS, BeriSoft Cooperation, Frankfurt, Germany).

Data Recording

The electroencephalogram (EEG) was measured in an electrically and acoustically shielded EEG booth at the MRC Cognition and Brain Sciences Unit in Cambridge, UK. Data were recorded from 64 Ag/AgCl electrodes mounted on an electrode cap (Easycap, Falk Minow Services, Herrsching-Breitbrunn, Germany) using SynAmps amplifiers (NeuroScan Labs, Sterling, VA), arranged according to the extended 10/20 system. Data were acquired with a sampling rate of 500 Hz. Recording reference for the EEG channels was Cz. The electrooculogram (EOG) was recorded bipolarly through electrodes placed above and below the left eye (vertical) and at the outer canthi (horizontal).

Preprocessing of ERP Data

The continuously recorded data were band-pass filtered at 1–20 Hz and transformed to average reference. Epochs of 900-msec duration, including a 100-msec baseline interval, were averaged for each stimulus category. Epochs with incorrect responses or with peak-to-peak potential differences larger than 100 μV in at least one EEG or EOG channel were rejected. For each channel the mean amplitude of a 100-msec prestimulus interval was subtracted at all time points.

Behavioral Analysis

RTs were recorded with respect to the onset of the stimuli. Responses occurring more than 2000 msec after stimulus onset were considered as incorrect. ANOVA analyses on RTs and error rates of correct responses were performed by item as well as by subject.

Statistical ERP Analysis

The classical approach to ERP analysis assumes that changes in brain states are primarily reflected in distinct

ERP components, such as P100 of the visual evoked potential, which labels a positive deflection at posterior electrode sites around 100 msec. These amplitude modulations should be best detectable at or around their peaks in time and space. However, the neural mechanisms determining the temporal and spatial structure of the ERP signal are not yet fully understood. It is possible that the effects of interest, in our case those of lexicality and typicality, are independent and might not be detected by such an analysis.

We therefore applied a hierarchical analysis strategy and divided our analysis into two distinct steps:

1. ''Restrictive'' analysis: Only peaks in the time course and the topography of the ERP were analyzed. This enabled direct comparison of our results with previous results from similar studies and also avoids the serious problem of multiple comparisons by restricting the number of statistical tests to a minimum.
2. ''Exhaustive'' analysis: Parameter distributions summarizing results for several electrodes in relevant time ranges were computed. This allowed us to confirm that effects found by the classical approach are indeed specific to certain time ranges or electrodes. Where the exhaustive analysis reveals new effects, these have to be carefully interpreted in the light of previous findings and existing theories, taking into account the increased likelihood of false positives.

Following this strategy, we initially determined latencies of peaks in the root-mean-square (RMS:

$$\sqrt{(1/63)\sum_{i=1:63} p_i^2},$$

with p_i the voltage at the ith electrode) of the raw ERP curves averaged across all conditions. These occurred at 112, 158, 210, 326, and 552 msec (Figure 1). We identified further prominent peaks in the RMS curves of the differences between words and pseudowords as well as typical and atypical items at 240, 512 (both for lexicality), and 284 msec (typicality). For these latencies, we selected electrodes at local extrema of the potential distribution for analysis. Where two or more electrodes were selected, those entered the statistical analysis as a factor corresponding to laterality. These data were subjected to repeated measures ANOVAs with the factors lexicality, typicality, and—where applicable—laterality. Greenhouse–Geisser correction of the degrees of freedom was applied where appropriate. The same analysis was applied to average voltages from 20-msec time windows around the RMS peaks. However, because they did not reveal a qualitatively different pattern of results, those data will not be reported.

For the exhaustive analysis, paired two-tailed t tests were computed at each electrode for time ranges identified by the initial RMS analysis. These were interpolated and presented like usual ERP distributions. This procedure is common in metabolic imaging studies and has recently attracted interest in the field of EEG and magnetoencephalography (MEG) analysis (Michel et al., 2004). Because the results from this analysis are compared to those of the more restricted approach, we present these maps at a significance threshold of $p < .05$ uncorrected. We do not imply by this that every ''effect'' visible in these images can be interpreted as statistically reliable. Note that for those electrodes and latencies that were selected for the restricted analysis, the statistical parameter distributions show identical values; that is, the exhaustive analysis comprises the restricted analysis, but adds further information. That way, we did not merely test whether an effect was present at certain electrodes, but, in addition, whether an effect was specific to these electrodes. Where specific effects are scrutinized in further detail, the relevant analyses are described in the Results section.

Source Estimation

The potential distribution recorded at the scalp surface can in principle be explained by infinitely many generator configurations inside the brain. In particular, the depth of the sources cannot be determined by the data alone. In the absence of any reliable a priori assumptions about the number and location of generators, the minimum norm solution, for example, obtained using the Moore–Penrose pseudoinverse, has been suggested as a reasonable approach: Any generator distribution that explains the recorded data contains this solution, but possibly also sources that do not produce any measurable signal at the scalp surface signals (Hauk, 2004; Hämäläinen & Ilmoniemi, 1994). Solutions obtained by the minimum norm method are therefore predicted by the data, and are not just ''consistent'' with the data. This method does not rely on assumptions about the number or approximate location of the sources, but is biased toward solutions with minimal overall source strength.

Our implementation followed the procedure of Hauk (2004), which yields a blurred two-dimensional projection of the true source distribution within the brain. The purpose of this analysis was to estimate possible generators for the significant effects revealed by our ERP analysis. We therefore applied this method to our grand-mean data for different conditions and subsequently computed the subtractions corresponding to significant contrasts in our ANOVA analysis. To assess the reliability of the differences, we used a procedure similar to that of Dale and Sereno (1993); that is, the estimated source strengths were thresholded according to their signal-to-noise ratio (SNR). The SNR was computed at each dipole location by dividing the source strength of each dipole by its standard deviation of the source strengths within the baseline interval. Activation was

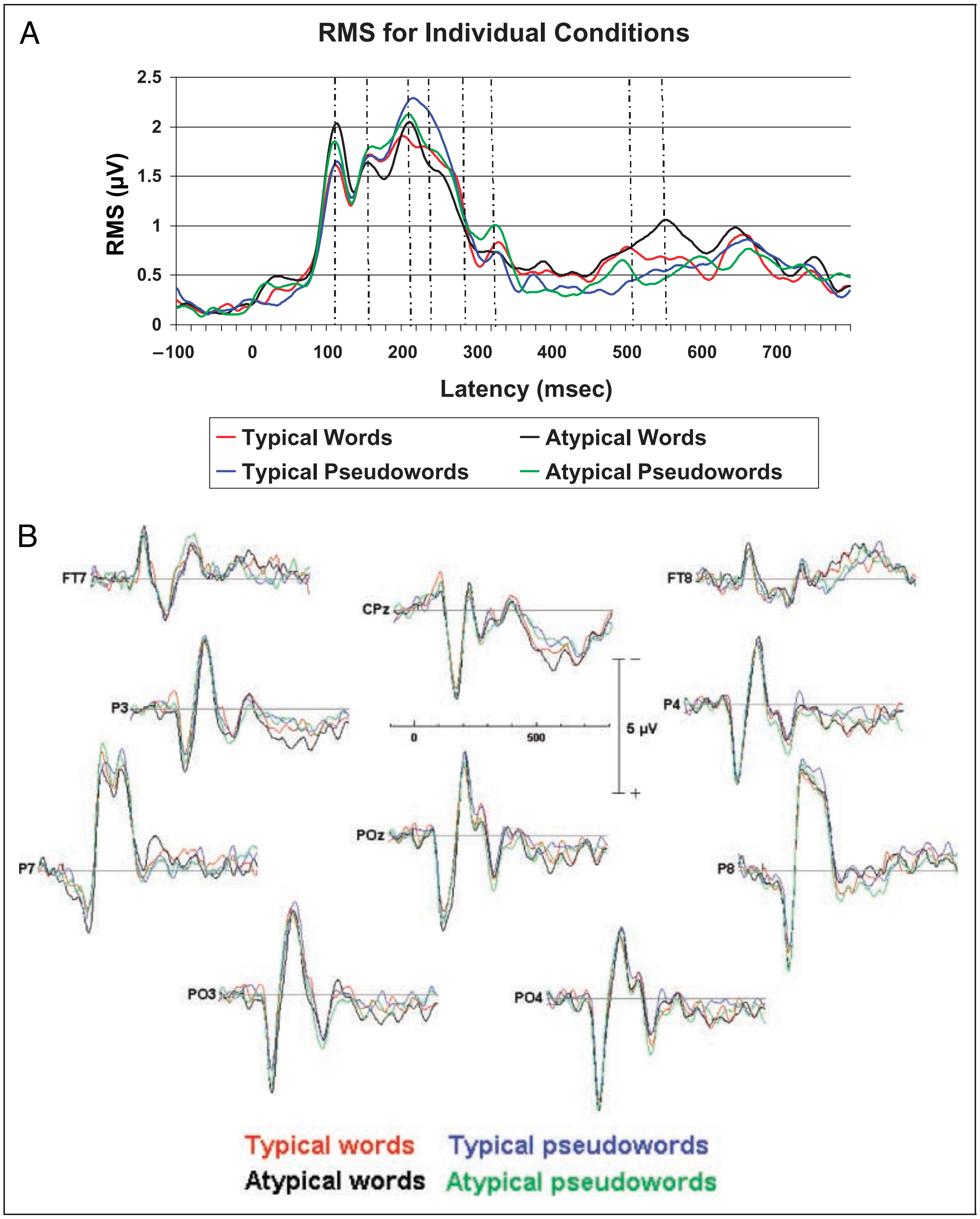


Figure 1. Time course of ERP data. (A) Root-mean-square (RMS) curves for individual conditions. Latencies selected for analysis are marked for the RMS curves. (B) Voltage curves for selected electrodes.

displayed as nonzero when the SNR exceeded a value of 2 (see Figure 5).

RESULTS

Behavioral Data

Mean correct RTs and overall error rates are displayed in Table 2. These data were analyzed by ANOVAs including the within-subjects and between-items factors of lexicality (two levels) and typicality (two levels). The results revealed a reliable main effect of lexicality in RT, $F_S(1,13) = 11.52$, $p = .005$; $F_i(1,196) = 14.95$, $p < .0005$, and a marginally reliable effect on accuracy, $F_s\,(1,13) = 4.73$, $p = .049$; $F_i\,(1,196) = 3.63$, $p = .058$. These data, however, reflect something of a speed/error trade-off, as RTs were significantly faster to words than pseudowords, but error rates were lower to pseudowords than words. The main effect of typicality was reliable by subjects but not items in both RT and accuracy, $F_s(1,13) = 7.88$, $p = .015$; $F_i(1,196) = 2.08$, $p = .151$;

Table 2. Summary of Behavioral Results of the Lexical Decision Task (Average RTs and Error Rates) as a Function of Lexicality and Typicality

	Reaction Time (msec)	*Error Rate (%)*
Typical words	730	15.57
Atypical words	721	15.57
Typical pseudowords	806	12.29
Atypical pseudowords	779	10.00

and $F_s(1,13) = 8.58, p = .012$; $F_i(1,196) = 0.24, p = .623$. The interaction between lexicality and typicality was not significant for either latency or accuracy, $F_s(1,13) < 1$; $F_i(1,196) < 1$; and $F_s(1,13) = 2.05, p = .175$; $F_i(1,196) < 1$. Planned comparisons revealed that the negative impact of orthographic typicality for pseudowords was significant by subjects but not items for both latency and error rate, $F_s(1,13) = 15.39, p = .002$; $F_i(1,196) < 1$ and $F_s(1,13) = 10.95, p = .006$; $F_i(1,196) < 1$. No reliable effects of typicality were observed for words in either RT or error rate, $F_s(1,13) < 1$; $F_i(1,196) = 2.29$, $p = .132$ and $F_s(1,13) < 1$; $F_i(1,196) < 1$).

Event-related Potentials

Figure 1 shows the RMS of the raw ERP curves, with peaks revealed at 112, 158, 210, 326, and 552 msec. As indicated in the Introduction, our investigation focuses on the earliest stages of word recognition, prior to the likely onset of decision processes. We therefore examined effects of typicality and lexicality at the RMS peaks prior to 250 msec. The significant effects are summarized in Table 3. Figures 2–5 only show amplitudes or topographies that relate to main effects or interactions in the ERP that reached significance in the ANOVA analyses.

Main Effects of Typicality

There was a marginally significant effect of typicality at 112 msec, with atypical items producing larger positivities than typical ones at posterior electrodes, $F(1,13) = 3.47, p = .085$. Because such an early effect of typicality is of particular interest and because the effect was in the expected direction (i.e., larger amplitudes for the more difficult to process atypical items), we chose to investigate this effect in more detail. Visual inspection of the time range between 84 and 112 msec revealed a stable topography for the difference between atypical and typical items. An ANOVA analogous to the previous one performed at 100 msec revealed a main effect of typicality, $F(1,13) = 8.21$, $p < .02$ (Figure 2A). The topographies of the ERP and the p values for this effect

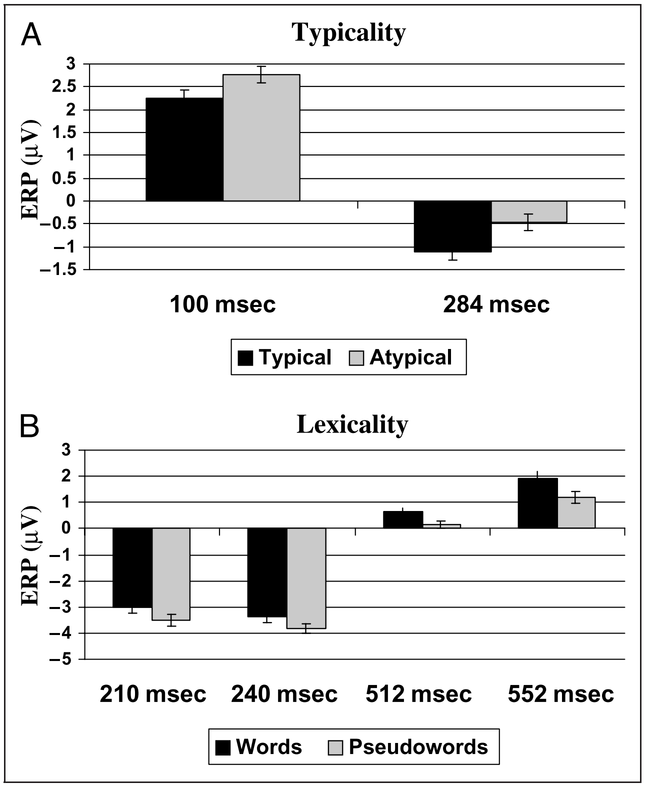


Figure 2. Bar graphs for significant main effects of the restrictive ERP analysis. Grand-mean voltages are plotted for electrodes at peaks in the ERP distribution at the corresponding latencies (see Table 3). Error bars show the standard error of the mean after between-subject variability has been removed, appropriate for repeated measures comparisons (Loftus & Masson, 1994). (A) Main effects of typicality. (B) Main effects of lexicality.

Table 3. All Significant p Values of the Initial ANOVA Analysis at Several Latencies

	100 msec, PO3/4	*158 msec, P7/8*	*210 msec, P7/8*	*240 msec, P7/8*	*284 msec, POz*	*512 msec, CP3/4*	*552 msec, CPz*
Lex	–	–	0.051	0.041	–	0.005	0.009
Typ	0.01	–	–	–	0.004	–	–
Lat	–	–	–	–	n.a.	–	n.a.
Lex × Typ	–	0.01	–	–	–	–	–
Lex × Lat	–	–	–	–	n.a.	–	n.a.
Typ × Lat	–	–	–	–	n.a.	–	n.a.
Lex × Typ × Lat	–	0.001	–	–	n.a.	–	n.a.

Electrode labels refer to electrodes at peaks in the ERP distribution at the corresponding latencies that were chosen for statistical analysis. Empty cells refer to nonsignificant ($p > .1$) effects. Lex = lexicality; Typ = typicality; Lat = laterality; n.a. = not applicable, i.e., the factor or interaction was not included in the analysis.

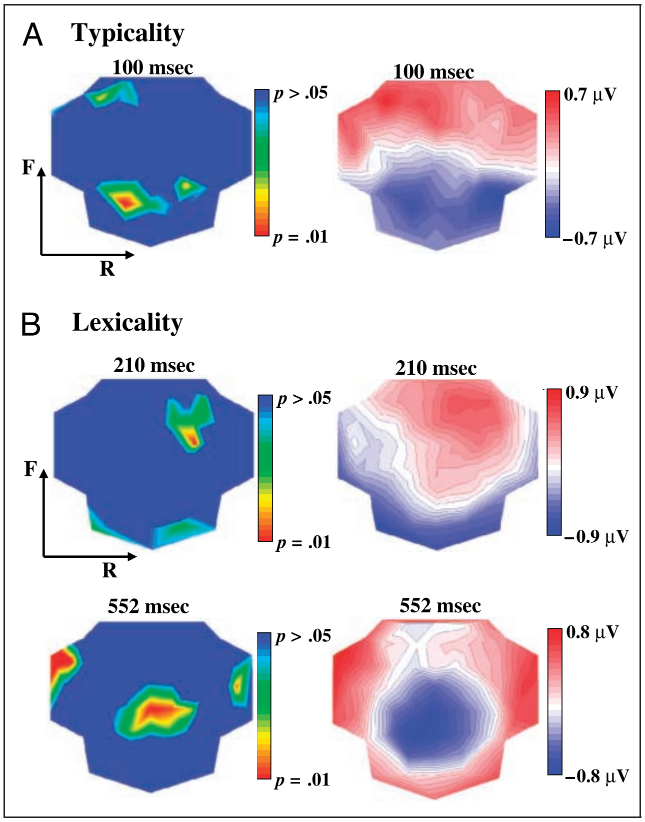


Figure 3. ERP topographies of early main effects. Maps were interpolated and projected on a two-dimensional plane. The p values based on paired two-tailed t tests are shown on the left, whereas the corresponding ERP amplitudes are presented on the right. F = front; R = right. (A) Main effect of typicality (typical minus atypical) at 100 msec. (B) Main effects of lexicality (pseudowords minus words) at 210 and 552 msec, respectively.

are presented in Figure 3A, which demonstrate that this effect has a standard distribution of a word evoked potential. Significant p values occur only around peaks in the ERP distribution, supporting their interpretation as genuine ERP effects. The main effect of typicality was also significant at 284 msec, $F(1,13) = 12.26$, $p < .005$, where typical items elicited larger negative ERP amplitudes than atypical ones (Figure 2A).

Main Effects of Lexicality

The effect of lexicality was significant at 240 msec, $F(1,13) = 5.15$, $p < .05$); 512 msec, $F(1,13) = 11.69$, $p < .005$; and 552 msec, $F(1,13) = 9.26$, $p < .01$; and approached significance at 210 msec, $F(1,13) = 4.60$, $p = .051$. Figure 2B reveals that pseudowords produced consistently more negative potentials than words at the selected electrodes at all these latencies. Previous studies have reported similar more negative-going potentials for pseudowords compared to words around 200 msec at posterior electrode sites (Hinojosa et al., 2001; Martin-Loeches et al., 1999). Figure 3B confirms that the main effect of lexicality (pseudowords minus words) at 210 msec also follows this pattern, and that ERP differences are significant near to the peak electrodes. Considering that Table 3 reports results from F tests, although less stringent one-tailed t tests would have been justified, the main effect of lexicality at 210 msec can be viewed as a replication of previous findings. Figure 3B also shows the topography of the lexicality effect at 552 msec (pseudowords minus words), which is characterized by a centroparietal negativity peaking around electrodes Pz, CPz, and P1. Such a pattern has consistently been reported for pseudowords or words that occur in a specific context with low probability (e.g., Friederici, 2004; Kutas & Federmeier, 2000).

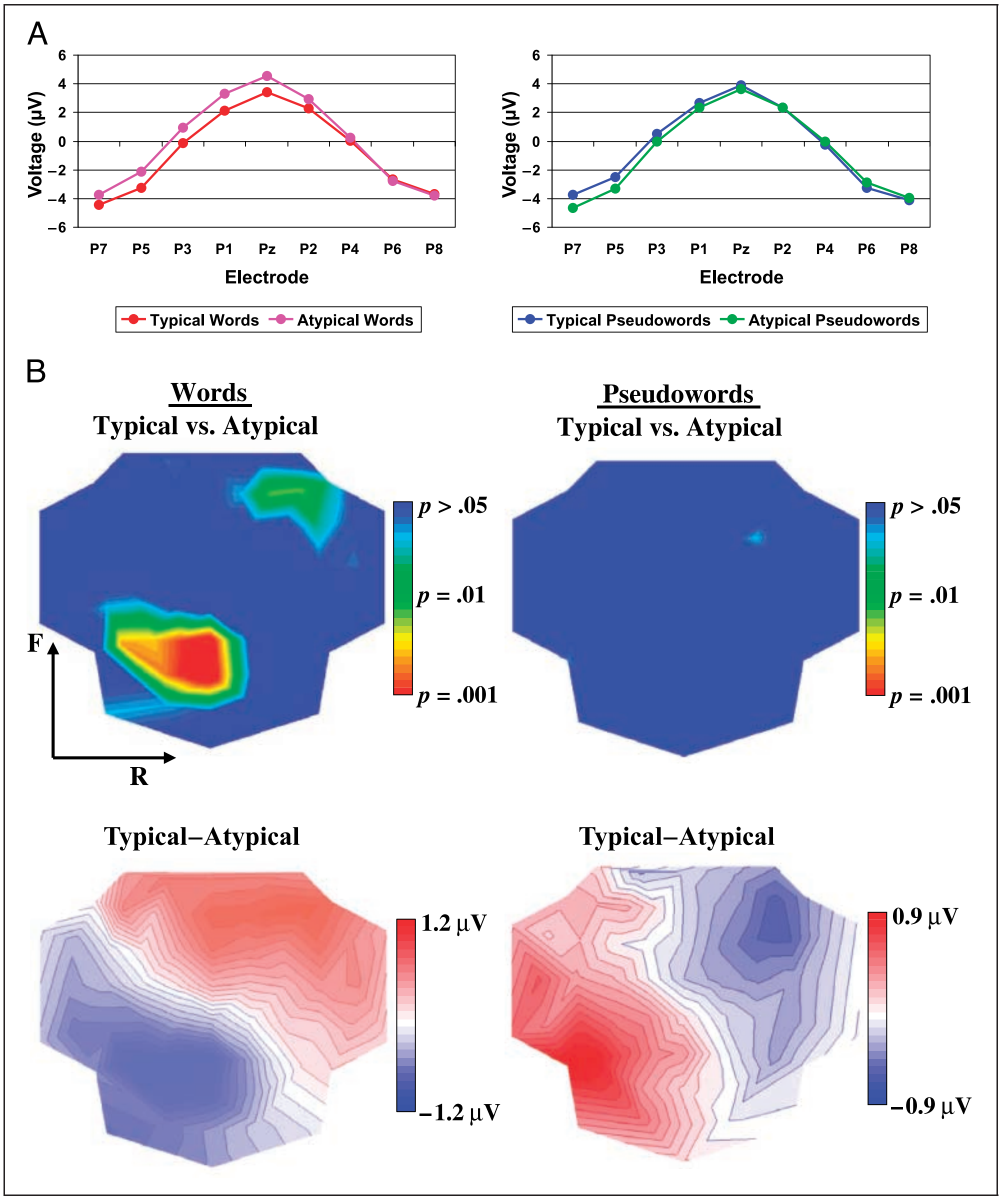
ERP: Interaction of Lexicality and Typicality

Located temporally between the main effects of these two variables, a significant interaction of lexicality and typicality occurred at 158 msec in the analysis for peak electrodes P7/Pz/P8, $F(2,26) = 11.96$, $p < .001$, Greenhouse–Geisser $\varepsilon = 0.98$. To study the distribution of this effect in more detail, we first performed an ANOVA on a line of nine electrodes connecting the peak electrodes, that is, P7, P5, P3, P1, Pz, P2, P4, P6, and P8. This confirmed a highly significant interaction of lexicality by typicality by laterality, $F(8,104) = 13.42$, $p < .001$, Greenhouse–Geisser $\varepsilon = 0.39$ (Figure 4A). The effect remained significant after vector normalization (McCarthy & Wood, 1985), $F(8,104) = 9.92$, $p < .001$, Greenhouse–Geisser $\varepsilon = 0.33$. The post hoc tests, together with statistical tests at all other electrodes, are shown in Figure 4B. The comparison of typical words with atypical words was significant over the left hemisphere at parietal electrodes P5, P3, P1, and Pz of the electrode line previously analyzed. Typical words produced larger negativities than atypical ones over the left hemisphere. For pseudowords, only electrode P7 reached significance. The effect is lower in amplitude and in the reverse direction of the word effect, with atypical pseudowords eliciting more negative potentials at centroparietal recording sites.

Source Localization

Most previous ERP studies investigating visual word recognition have based their conclusions solely on the ERP signals (Hauk & Pulvermüller, 2004; Sereno & Rayner, 2000; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Osterhout, Bersick, & McKinnon, 1997). Information about possible brain generators of the neurophysiological effects is, however, of substantial interest, and this requires estimation of the sources of the effects measured at the surface. The questions in this study were (a) whether it would be possible to assign the typicality and lexicality effects to clear cortical sources

Figure 4. Statistical results on the interaction Lexicality × Typicality × Laterality at 158 msec. (A) Grand-mean voltages are plotted for selected posterior electrodes as a function of electrode, lexicality, and typicality. (B) Statistical parametric maps (top) and ERP topographies (bottom) for the typicality contrast, separately for words (left) and pseudowords (right). Maps are displayed as in Figure 3.



and (b) whether these sources could be related to areas known to be involved in word processing from functional imaging and other ERP and/or lesion studies. For example, the posterior inferior left temporal lobe is reliably activated in fMRI studies of orthographic processing (Mechelli et al., 2005; McCandliss et al., 2003); superior temporal and other perisylvian sources of ERP signals appear to distinguish early between words and pseudowords (Pulvermüller, 2001); and, as part of a widespread cortical network involved in semantic processing (see, e.g., Thompson-Schill, 2003; Martin & Chao, 2001), the anterior temporal cortex may play a special role that is highlighted by both structural and functional imaging in patients with semantic dementia (Mummery, Patterson, Price, et al., 2000; Mummery, Patterson, Wise, et al., 1999) and also by some functional imaging studies of normal participants (Kellenbach, Hovius, & Patterson, 2005; Rogers, et al., in press; Tyler et al., 2004; Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Devlin et al., 2000; Scott, Blank, Rosen, & Wise, 2000; Mummery, Patterson, Hodges, & Wise, 1996). Source estimates were therefore obtained for the earliest and clearest ERP effects, that is, the main effect of typicality at 100 msec, the main effect of lexicality at 210 msec, and the typicality effect for words at 158 msec. We used a minimally constrained procedure to estimate the sources of our signals (Hauk, 2004; Hämäläinen & Ilmoniemi, 1994), and our conclusions will take into account the general resolution limits of the procedure.

The source estimation results are displayed in Figure 5. At 100 msec, atypical items (words and pseudowords) produced stronger activation than typical ones in several areas bilaterally. The two most prominent effects are a broad activation in a right inferior pos-

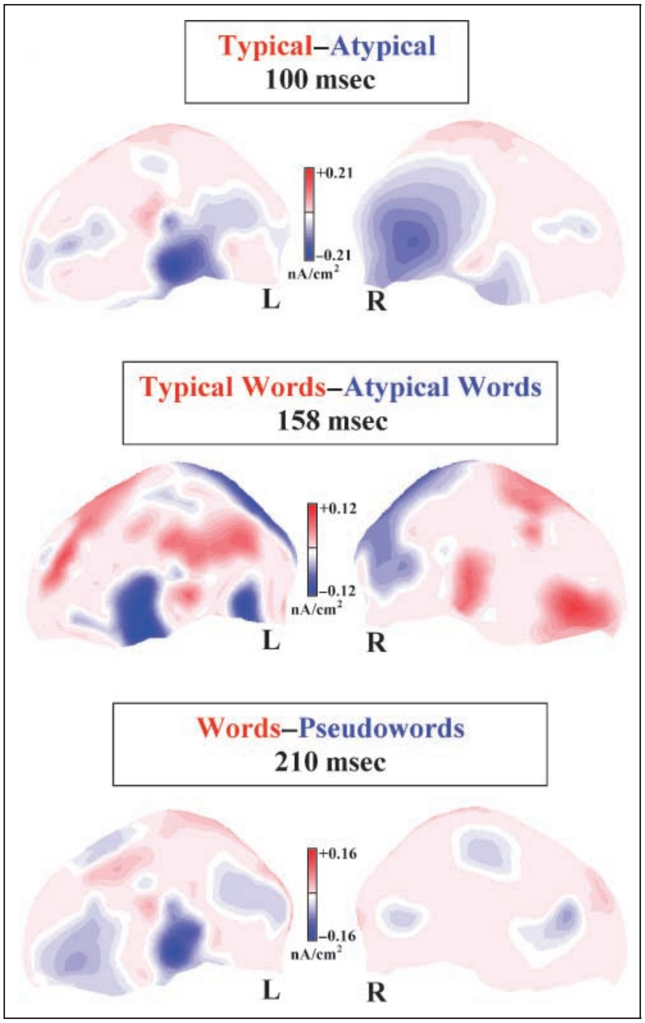


Figure 5. Source estimates computed on the grand-mean ERP displayed for the left (L) and the right (R) hemisphere, respectively. Source strengths are only displayed as nonzero at locations where their SNRs (actual source strengths divided by their standard deviations of the baseline interval) were higher than 2. Red and blue colors distinguish the direction of effects according to labels within each figure.

terior region and a more focal activation in the left midposterior inferior temporal lobe. At 158 msec, atypical words produced larger activation than typical words at two inferior locations in the left hemisphere, anterior and posterior to the region sensitive to typicality at 100 msec, and, additionally, in a more dorsal centroparietal area. The anterior focus associated with atypical words is in/near the left temporal pole. Typical words elicited stronger activation than atypical ones in prefrontal and superior central areas in both hemispheres, in the left temporoparietal areas, and in the right temporal lobe. The dominant activation for the lexicality effect at 210 msec, where pseudowords yielded more activation than words, was located in the middle/posterior extent of the inferior temporal lobe, close to the largest left hemisphere peak at 100 msec.

DISCUSSION

Behavioral Effects

Past research has generally shown slower/less accurate responses to orthographically typical pseudowords and faster/more accurate responses to orthographically typical words (Holcomb, Grainger, & O'Rourke, 2002; Forster & Shen, 1996; Sears, Hino, & Lupker, 1995). In light of these findings, the current behavioral results may seem surprising: We found an effect of typicality on decisions to pseudowords that was reliable by subjects but not by items, and no hint of a typicality effect for decisions to words. Recall, however, that to ensure that decisions were based on lexicosemantic rather than surface information, we (a) matched the pseudowords closely to the words on bigram/trigram frequency, thus removing general orthographic familiarity as a decision basis and (b) arranged that more than half of the pseudowords would be clear pseudohomophones of target words (e.g., *abyss* and *abiss*, *cymbal* and *simble*), thus reducing the value of phonological familiarity as a decision basis. Furthermore, previous research has demonstrated that the influence of orthographic typicality on decision times to real words is attenuated as the words and pseudowords become more similar in terms of their surface properties (Siakaluk et al., 2002; Forster & Shen, 1996; Sears et al., 1995; Andrews, 1989). We therefore conclude that high orthographic typicality did not facilitate word decisions in the present study because participants relied largely upon lexicosemantic rather than surface information as a basis for lexical decision (Binder et al., 2003). In support of this claim, rated imageability proved a significant predictor of both RTs and error rates to words, $B = -61.30$, $t(1,92) = -6.07$, $p < .0005$ and $B = -10.61$, $t(1,92) = -6.03$, $p < .0005$. Such an interpretation fits well within a distributed model of lexical processing in which semantic information forms an important component of the basis for lexical decision (Plaut, 1997).

Spatiotemporal Pattern of the ERP

The ERP results suggest that between 80 and 250 msec after stimulus onset, surface form and lexicosemantic properties of words are computed by processes that operate independently in early and later phases of word recognition, but interact in an intermediate phase. The earliest effect of typicality in our data occurred around 100 msec, and no hint of a lexicality effect was observed in this range, consistent with a conclusion that orthographic structure rather than lexicosemantic information is being processed at this time. Previous studies have already suggested neurophysiological correlates of surface form features such as word length in this latency range (Hauk & Pulvermüller, 2004; Assadollahi & Pulvermüller, 2003; Sereno et al., 1998). In our study, atypical items produced stronger current sources than typical ones bilaterally. In principle, amplitude differences between conditions can be caused by several factors, such as the number of active synapses constituting the sources, the depth and orientation of sources, or synchrony of neurons. In our case, we can reasonably assume that similar types of stimuli (typical and atypical letter strings) in the same task and at an early stage of processing modulate similar neuronal systems, but to different degrees. With regard to the early typicality effect, this is reflected in larger amplitudes for atypical items compared to typical ones. We therefore argue that although YACHT is a familiar word and YART is not, in some sense the word-recognition system ''prefers'' YART, or at least processes it more efficiently, at this point in its computations.

The cortical source estimates for this early activation are consistent with a generator in the left midposterior fusiform gyrus, which has been reported to respond strongly to the visual forms of words and pseudowords relative to strings of consonants that could not be words (McCandliss et al., 2003; Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002; Cohen et al., 2000). Consonant strings are not orthographically atypical, but instead are impossible (illegal), which means that they can easily be dismissed as nonwords, resulting in low levels of activation in this area (Cohen et al., 2002). Our results therefore suggest that this area that contributes generally to form-based visual processing is an important site in distinguishing typical from possible but atypical letter strings (although see Price & Devlin, 2003, for evidence that this region is also involved in other language processes).

The very early typicality effect was followed by a significant interaction of lexicality, typicality, and laterality at 158 msec in the ERP, driven by a robust typicality effect in the left hemisphere for words but not pseudowords. The source estimation for this effect indicated a left-lateralized region of the anterior temporal cortex that was activated more strongly for atypical than typical-words. This source corresponds to the region of cortex most affected both structurally and metabolically in SD (e.g., Mummery, Patterson, Price, et al., 2000; Mummery, Patterson, Wise, et al., 1999), and the correspondence is of particular note because patients with SD become increasingly insensitive to lexicality as their comprehension diminishes, ultimately basing their lexical decisions predominantly on orthographic typicality (Rogers, Lambon Ralph, Hodges, et al., 2004). Thus, the ERP and source localization data from the current work, together with behavioral data from SD, are consistent with two hypotheses: (a) that lexicosemantic knowledge—knowledge particular to letter strings that constitute meaningful words in the language—is supported at least in part by representations in the left anterior temporal lobe; (b) that interaction between more posteriorly based orthographic processing and more anteriorly based semantic processing is more critical for recognition of orthographically atypical than typical words.

The source estimates for the typicality effect at 158 msec also revealed greater activation for typical relative to atypical words in left perisylvian areas, especially in regions extending from Wernicke's area around the angular gyrus to the posterior/inferior region of the parietal cortex and in the prefrontal cortex. Evidence from neuropsychology and functional imaging certainly implicates these regions in language processing, and it has been argued that perisylvian circuits become more tightly linked internally the more frequently a word and its constituent parts are processed together (Pulvermüller, 1999, 2001); this notion would predict a stronger engagement of these areas during reading of orthographically typical words (Pulvermüller, 1999, 2001). The indication from our current results that a left temporoparietal region responds more strongly to words with typical spellings at an early (~160 msec) stage may also fit with the suggestion of some researchers that this region is important in learning to integrate orthographic with phonological information (McCrory, Mechelli, Frith, & Price, 2005; Pugh et al., 2001).

Lexicality effects were observed at 210 and 240 msec, with no hint of modulation by orthographic typicality. Somewhat surprisingly, source estimates suggested more activity for pseudowords compared to words in a midposterior region of the left inferior temporal lobe, almost identical to the main source peak for the typicality effect ~100 msec earlier. As this activation followed the Typicality × Lexicality interaction, which was explained by differential activation in anterior temporal and perisylvian areas, one may suggest that the more anterior and superior lexicosemantic processes feed back to the areas in the inferior temporal lobe that process the orthographic structure of words. For instance, feedback activation from lexicosemantic representations may help to ''clean up'' or stabilize letter-string representations in the posterior cortex, consistent with the well-known interactive activation and competition model of word recognition (McClelland, 1979); alternatively, the letter string might be reprocessed in order to search for alternative interpretations of the input or possible errors.

Although it might have been desirable in principle to control for neighborhood size while manipulating bi-/trigram frequency to quantify typicality, the strong correlation between these two measures (Westbury & Buchanan, 2002) in fact makes this separation difficult, especially in electrophysiological experiments, which require a large stimulus set. One may therefore ask whether our effects can be explained by the variation in the number of lexical neighbors, a variable known as Coltheart's *N* (Coltheart, Davelaar, Jonasson, & Besner, 1977). However, in our view this would not be plausible on the background of previous research. Holcomb et al. (2002) found a larger N400 generated by words with large neighborhoods as compared with small-neighborhood items, and this suggests that the neurophysiological correlates of Coltheart's *N* are to be expected at around 200 msec and later, not at 100 msec where we found the earliest effect of typicality. Interestingly, this study found larger amplitudes for items with larger neighborhoods. This would predict larger responses for typical items in our study, which is the opposite of what we found. In addition, it seems difficult to explain why an effect of *N* should become neurophysiologically manifest substantially earlier than that of lexicality. We therefore argue that the early main effect of typicality at ~100 msec is best interpreted in terms of surface features of word forms.

A later main effect of typicality was found at 284 msec, and effects of lexicality shortly after 500 msec. On the basis of the combination of facts (a) that these later effects occurred after words and pseudowords had already produced distinguishable brain responses shortly after 200 msec and (b) that this earlier lexicality effect was in turn preceded by a processing sequence involving early orthographic analysis and an interaction of orthographic and lexicosemantic processing, we argue that these later effects should be interpreted as postlexical. They might be related to the reevaluation and verification of information before the subjects commit themselves to a definite response.

In general, the data are consistent with the notion that word recognition results from two distinct but interacting processes: a structural component that computes the orthographic surface form of an observed letter string, which is sensitive to the distributional properties of combinations of letters in the language and is located more posteriorly in the brain; and a lexicosemantic component that encodes knowledge about meanings and other lexical properties of real words, situated in more anterior temporal lobe regions and in perisylvian language-related areas. Early in recognition, structural processes begin to construct an orthographic representation of the observed string, based partially on knowledge about which letters are likely to co-occur in the language. As a result, infrequent combinations of letters constitute more of a challenge for this process; and because it knows nothing of ''words'' per se, typicality but not lexicality effects are observed at this stage. The structural process feeds information forward to more anterior regions of the temporal lobe and perisylvian cortex that begin to activate candidate word/meaning representations. By this, we do not imply that anterior temporal lobe and perisylvian cortex are the only cortical areas that contribute to lexicosemantic processes. We rather suggest that these sites are the ones most consistently activated by the words and task employed in this study. The visual form of typical words can mostly be satisfactorily resolved by the posterior structural system; words with unusual spellings, however, do not benefit so much from structural processes, and must rely more heavily on interaction with the lexicosemantic system to settle to the correct representation. Hence, at ~160 msec, atypical words provoke more activation than do typical words. Feedback for real words from lexicosemantic representations—possibly reflecting top-down influences on the letter-string computation, or reanalysis of the word form in the case of nonmatches—produces the later-observed posterior lexicality effect at ~200 msec.

With regard to cognitive theories of word recognition, two results from the current study are of note. First, the effects we describe all occur within the first 250 msec after stimulus onset, before decision processes are likely to have begun. Advocates of form-first theories suggest that most of the behavioral evidence offered in support of cascaded theories can be explained in a strictly feed-forward paradigm by supposing that such effects occur in decision processes that operate after candidate word representations have been activated (Forster & Hector, 2002). Our ERP results indicate, however, that structural and lexicosemantic processes interact as early as 160 msec—likely too early to reflect decision processes. In this sense, the data are compatible with cascaded or interactive theories of word recognition.

Second, it is notable that the source for the early-occurring typicality effect and the later-occurring lexicality effect appears to be nearly identical, suggesting that lexical processes are exerting an influence in the very same region of cortex that is initially sensitive only to structural properties of letter strings. As indicated above, we construe this finding as revealing a top-down influence from lexicosemantic representations on surface-orthographic processes, so that, in this sense as well, our data support cascaded or interactive theories of word recognition.

In summary, the results suggest that word recognition is implemented in the human brain by a sequence of anatomically segregated but functionally linked and interactive neuronal systems responsible for the computation of structural and lexicosemantic properties of words.

APPENDIX: STIMULUS ITEMS

Atypical Word	*Typical Pseudoword*	*Typical Word*	*Atypical Pseudoword*	*Homophones*
abyss	abiss	amiss	amyss	X
acrylic	acrile	sterile	sterylic	
aisle	astle	castle	caisle	
cymbal	simble	thimble	thymbal	X
cyst	cest	vest	vyst	
debt	det	pet	pebt	X
drawl	drall	pall	pawl	X

APPENDIX. *(continued)*

Atypical Word	*Typical Pseudoword*	*Typical Word*	*Atypical Pseudoword*	*Homophones*
feud	fewd	shrewd	shreud	X
ghost	grost	grove	ghove	
giraffe	geraffe	germane	girmane	X
gnome	nome	node	gnode	X
guile	gire	mire	muire	
guru	gart	wart	wuru	
hyena	hainty	dainty	dyena	
idyll	idder	udder	udyll	
kangaroo	cangarew	cashew	kashoo	X
kayak	kaiack	hijack	hyjak	X
khaki	kackey	lackey	lhaki	X
kiwi	kint	lint	tiwi	
knife	nife	nine	knine	X
koala	coala	cobra	kobra	X
lamb	lam	dam	damb	X
limb	lim	rim	rimb	X
lynx	linx	minx	mynx	X
martyr	marter	garter	gartyr	X
niece	nease	grease	griece	X
numb	num	hum	humb	X
opaque	opake	partake	partaque	X
piano	peano	peanut	pianut	
pigeon	pigion	legion	legeon	X
platypus	platapes	parapets	paryputs	
polyp	pollop	dollop	dolyp	X
psalm	salm	salve	psalve	X
rhinoceros	reinoceros	reindeer	rhindeer	
ritzy	rissy	sissy	sitzy	
sausage	sossage	fossil	fausil	X
scissors	sissers	sinners	scinners	X
seize	seese	cheese	cheize	X
sleuth	slooth	booth	beuth	X
squirrel	shirrel	shin	squin	
tryst	trint	tint	tyst	
umbrella	ambrella	ambulance	umbulance	
vacuum	vacume	costume	costuum	X
view	vew	drew	driew	X
waltz	walp	scalp	scaltz	
weir	weer	sneer	sneir	X
yacht	yart	cart	cacht	
zebra	sebra	serpent	zerpent	
zephyr	zepple	topple	tophyr	
zodiac	zodash	awash	awiac	

Stimuli judged to be pseudohomophones are marked with an X in the column labeled ''Homophones.''

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REFERENCES

Andrews, S. (1989). Frequency and neighborhood effects on lexical access: Activation or search? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15,* 802–814.

Assadollahi, R., & Pulvermüller, F. (2001). Neuromagnetic evidence for early access to cognitive representations. *NeuroReport, 12,* 207–213.

Assadollahi, R., & Pulvermüller, F. (2003). Early influences of word length and frequency: A group study using MEG. *NeuroReport, 14,* 1183–1187.

Balota, D. A., & 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.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11,* 235–260.

Binder, J. R., McKiernan, K. A., Parsons, M. E., Westbury, C. F., Possing, E. T., Kaufman, J. N., & Buchanan, L. (2003). Neural correlates of lexical access during visual word recognition. *Journal of Cognitive Neuroscience, 15,* 372–393.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25,* 151–188.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M. A., & Michel, F. (2000).

The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123,* 291–307.

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain, 125,* 1054–1069.

Coltheart, M., Davelaar, E., Jonasson, J. T., & Besner, D. (1977). Access to the internal lexicon. In S. Dornic (Ed.), *Attention and performance* (Vol. 6, pp. 535–555). New York: Academic Press.

Crinion, J. T., Lambon-Ralph, M. A., Warburton, E. A., Howard, D., & Wise, R. J. (2003). Temporal lobe regions engaged during normal speech comprehension. *Brain, 126,* 1193–1201.

Dale, A. M., & Sereno, M. I. (1993). Improved localization of cortical activity by combining EEG and MEG with MRI cortical surface reconstruction: A linear approach. *Journal of Cognitive Neuroscience, 5,* 162–176.

Dehaene, S., Le Clec, H. G., Poline, J. B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport, 13,* 321–325.

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Wilson, J., Moss, H. E., Matthews, P. M., & Tyler, L. K. (2000). Susceptibility-induced loss of signal: Comparing PET and fMRI on a semantic task. *Neuroimage, 11,* 589–600.

Diesfeldt, H. F. A. (1992). Impaired and preserved semantic memory functions in dementia. In L. Backman (Ed.), *Memory functioning in dementia* (pp. 227–263). Amsterdam: Elsevier.

Forster, K. I. (1999). The microgenesis of priming effects in lexical access. *Brain and Language, 68,* 5–15.

Forster, K. I., & Hector, J. (2002). Cascaded versus noncascaded models of lexical and semantic processing: The turple effect. *Memory and Cognition, 30,* 1106–1117.

Forster, K. I., & Shen, D. (1996). No enemies in the neighborhood: Absence of inhibitory neighborhood effects in lexical decision and semantic categorization. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 22,* 696–713.

Friederici, A. D. (2004). Event-related brain potential studies in language. *Current Neurology and Neuroscience Reports, 4,* 466–470.

Fushimi, T., Komori, K., Ikeda, M., Patterson, K., Ijuin, M., & Tanabe, H. (2003). Surface dyslexia in a Japanese patient with semantic dementia: Evidence for similarity-based orthography-to-phonology translation. *Neuropsychologia, 41,* 1644–1658.

Gernsbacher, M. A. (1984). Resolving 20 years of inconsistent interactions between lexical familiarity and orthography, concreteness, and polysemy. *Journal of Experimental Psychology: General, 113,* 256–281.

Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: Minimum norm estimates. *Medical and Biological Engineering and Computing, 32,* 35–42.

Hauk, O. (2004). Keep it simple: A case for using classical minimum norm estimation in the analysis of EEG and MEG data. *Neuroimage, 21,* 1612–1621.

Hauk, O., & Pulvermüller, F. (2004). Effects of word length and frequency on the human event-related potential. *Clinical Neurophysiology, 115,* 1090–1103.

Hinojosa, J. A., Martin-Loeches, M., & Rubia, F. J. (2001). Event-related potentials and semantics: An overview and an integrative proposal. *Brain and Language, 78,* 128–139.

Hodges, J. R., Patterson, K., Oxbury, S., & Funnell, E. (1992). Semantic dementia. Progressive fluent aphasia with temporal lobe atrophy. *Brain, 115,* 1783–1806.

Holcomb, P. J., Grainger, J., & O'Rourke, T. (2002). An electrophysiological study of the effects of orthographic neighborhood size on printed word perception. *Journal of Cognitive Neuroscience, 14,* 938–950.

Kellenbach, M. L., Hovius, M., & Patterson, K. (2005). A PET study of visual and semantic knowledge about objects. *Cortex, 41,* 121–132.

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences, 4,* 463–470.

Loftus, G., & Masson, M. (1994). Using confidence-intervals in within-subject designs. *Psychonomic Bulletin and Review, 1,* 476–490.

Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology, 11,* 194–201.

Martin-Loeches, M., Hinojosa, J. A., Gomez-Jarabo, G., & Rubia, F. J. (1999). The recognition potential: An ERP index of lexical access. *Brain and Language, 70,* 364–384.

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences, 7,* 293–299.

McCarthy, G., & Wood, C. C. (1985). Scalp distribution of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology, 62,* 203–208.

McClelland, J. L. (1979). On the time relations of mental processes: An examination of systems of processes in cascade. *Psychological Review, 86,* 287–330.

McCrory, E. J., Mechelli, A., Frith, U., & Price, C. J. (2005). More than words: A common neural basis for reading and naming deficits in developmental dyslexia? *Brain, 128,* 261–267.

Mechelli, A., Crinion, J., Long, S., Friston, K., Lambon Ralph, M., Patterson, K., McClelland, J. L., & Price C. J. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of Cognitive Neuroscience, 17,* 1753–1765.

Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & Grave De Peralta, R. (2004). EEG source imaging. *Clinical Neurophysiology, 115,* 2195–2222.

Mummery, C. J., Patterson, K., Hodges, J. R., & Wise, R. J. (1996). Generating 'tiger' as an animal name or a word beginning with T: Differences in brain activation. *Proceedings of the Royal Society of London, Series B, Biological Sciences, 263,* 989–995.

Mummery, C. J., Patterson, K., Price, C. J., Ashburner, J., Frackowiak, R. S., & Hodges, J. R. (2000). A voxel-based morphometry study of semantic dementia: Relationship between temporal lobe atrophy and semantic memory. *Annals of Neurology, 47,* 36–45.

Mummery, C. J., Patterson, K., Wise, R. J. S., Vandenbergh, R., Price, C. J., & Hodges, J. R. (1999). Disrupted temporal lobe connections in semantic dementia. *Brain, 122,* 61–73.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9,* 97–113.

Osterhout, L., Bersick, M., & McKinnon, R. (1997). Brain potentials elicited by words: Word length and frequency predict the latency of an early negativity. *Biological Psychology, 46,* 143–168.

Patterson, K., & Hodges, J. R. (1992). Deterioration of word meaning: Implications for reading. *Neuropsychologia, 30,* 1025–1040.

Patterson, K., Lambon Ralph, M. A., Jefferies, E., Woollams, A., Jones, R., Hodges, J. R., & Rogers, T. T. (2006).

"Pre-semantic" cognition in semantic dementia: Six deficits in search of an explanation. *Journal of Cognitive Neuroscience, 18,* 169–183.

Plaut, D. C. (1997). Structure and function in the lexical system: Insights from distributed models of word reading and lexical decision. *Language and Cognitive Processes, 12,* 767–808.

Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy, 197,* 335–359.

Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *Neuroimage, 19,* 473–481.

Pugh, K. R., Mencl, W. E., Jenner, A. R., Lee, J. R., Katz, L., Frost, S. J., Shaywitz, S. E., & Shaywitz, B. A. (2001). Neuroimaging studies of reading development and reading disability. *Learning Disabilities Research and Practice, 16,* 240–249.

Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences, 22,* 253–279; discussion 280–336.

Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences, 5,* 517–524.

Pulvermüller, F., Lutzenberger, W., & Birbaumer, N. (1995). Electrocortical distinction of vocabulary types. *Electroencephalography and Clinical Neurophysiology, 94,* 357–370.

Rogers, T. T., Hocking, J., Noppeney, U., Mechelli, A., Gorno-Tempini, M., Patterson, K., & Price, C. J. (in press). The anterior temporal cortex and semantic memory: Reconciling findings from neuropsychology and functional imaging. *Cognitive, Affective, and Behavioral Neuroscience.*

Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., & Patterson, K. (2004). Structure and deterioration of semantic memory: A neuropsychological and computational investigation. *Psychological Review, 111,* 205–235.

Rogers, T. T., Lambon Ralph, M. A., Hodges, J. R., & Patterson, K. (2004). Natural selection: The impact of semantic impairment on lexical and object decision. *Cognitive Neuropsychology, 21,* 331–352.

Rozzini, L., Bianchetti, A., Lussignoli, G., Cappa, S., & Trabucchi, M. (1997). Surface dyslexia in an Italian patient with semantic dementia. *Neurocase, 3,* 307–312.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123,* 2400–2406.

Sears, C. R., Hino, Y., & Lupker, S. J. (1995). Neighborhood size and neighborhood frequency effects in visual word recognition. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 876–900.

Sereno, S. C., & Rayner, K. (2000). The when and where of reading in the brain. *Brain and Cognition, 42,* 78–81.

Sereno, S. C., Rayner, K., & Posner, M. I. (1998). Establishing a time-line of word recognition: Evidence from eye movements and event-related potentials. *NeuroReport, 9,* 2195–2200.

Siakaluk, P. D., Sears, C. R., & Lupker, S. J. (2002). Orthographic neighborhood effects in lexical decision: The effects of nonword orthographic neighborhood size. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 661–681.

Snowden, J. S., Neary, D., Mann, D. M., Goulding, P. J., & Testa, H. J. (1992). Progressive language disorder due to lobar atrophy. *Annals of Neurology, 31,* 174–183.

Thompson-Schill, S. L. (2003). Neuroimaging studies of semantic memory: Inferring "how" from "where." *Neuropsychologia, 41,* 280–292.

Tyler, L. K., Stamatakis, E. A., Bright, P., Acres, K., Abdallah, S., Rodd, J. M., & Moss, H. E. (2004). Processing objects at different levels of specificity. *Journal of Cognitive Neuroscience, 16,* 351–362.

Westbury, C., & Buchanan, L. (2002). The probability of the least likely non-length-controlled bigram affects lexical decision reaction times. *Brain and Language, 81,* 66–78.

Whaley, C. (1978). Word–nonword classification time. *Journal of Verbal Learning and Verbal Behavior, 17,* 143–154.