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The time course of visual word recognition as revealed by linear regression analysis of ERP data

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EEG correlates of a range of psycholinguistic word properties were used to investigate the time course of access to psycholinguistic information during visual word recognition. Neurophysiological responses recorded in a visual lexical decision task were submitted to linear regression analysis. First, 10 psycholinguistic features of each of 300 stimulus words were submitted to a principal component analysis, which yielded four orthogonal variables likely to reflect separable processes in visual word recognition: Word length, Letter n-gram frequency, Lexical frequency and Semantic coherence of a word's morphological family. Since the lexical decision task required subjects to distinguish between words and pseudowords, the binary variable Lexicality was also investigated using a factorial design. Word–pseudoword differences in the event-related potential first appeared at 160 ms after word onset. However, regression analysis of EEG data documented a much earlier effect of both Word length and Letter n-gram frequency around 90 ms. Lexical frequency showed its earliest effect slightly later, at 110 ms, and Semantic coherence significantly correlated with neurophysiological measures around 160 ms, simultaneously with the lexicality effect. Source estimates indicated parieto-temporo-occipital generators for the factors Length, Letter n-gram frequency and Word frequency, but widespread activation with foci in left anterior temporal lobe and inferior frontal cortex related to Semantic coherence. At later stages (>200 ms), all variables exhibited simultaneous EEG correlates. These results indicate that information about surface form and meaning of a lexical item is first accessed at different times in different brain systems and then processed simultaneously, thus supporting cascaded interactive processing models.

Keywords: Visual word recognition; Lexical decision; Word frequency; Lexicality; LSA; Source estimation

Introduction

Recognising one of the many thousands of written words known by a normal adult is a complex, multi-stage process involving an anatomically distributed neural system (Coltheart et al., 1977; Grainger and Jacobs, 1996; Fiez and Petersen, 1998; Pulvermüller, 2001; Turkeltaub et al., 2002; Jobard et al., 2003; Mechelli et al., 2003; Davis, 2004). This process must involve an analysis of the letters and letter combinations that make up the form of each word and the retrieval of lexico-semantic and morpho-syntactic information associated with the word form. Access to word-specific information is extremely rapid, starting within the first 200 ms after visual onset (Sereno and Rayner, 2003). However, the speed and efficiency of the recognition process are affected by a variety of different properties of written words and the contexts in which they occur.

Behavioural effects of psycholinguistic variables

A substantial body of empirical work has quantified the influence of various properties of written words on the speed of recognition, as revealed by responses in behavioural tasks such as naming, semantic categorisation and lexical decision. It has long been established, for example, that words with high frequency of occurrence (which individuals encounter and use frequently in their daily lives) are recognised and responded to more quickly than low frequency words (Rubinstein et al., 1970; Scarborough et al., 1977; Whaley, 1978; Gernsbacher, 1984). Naturally, given the multiple processing stages involved in word recognition, several other factors can also affect the speed of recognition. For instance, variables that quantify visual properties of written words (such as their length or orthographic typicality) significantly affect the speed of word recognition (Whaley, 1978; Andrews, 1997; Forster and Hector, 2002; Pecher et al., 2005), reflecting their influence on the processing of visual word forms. Similarly, semantic properties of written words (such as the presence of ambiguity or the concreteness of their meanings) also alter the speed of recognition due to their influence on meaning-based processes (Eviatar et al., 1990; Rodd et al., 2002). By evaluating different combinations of form, meaning and frequency variables on the speed of word recognition, behavioural investigations can reveal the properties of the multiple processing stages potentially involved in visual word recognition.

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ERPs/ERFs in the study of visual word recognition

An effective method for investigating the neural processes involved in word recognition is to combine these behavioural manipulations with on-line monitoring of brain activity using event-related potentials (ERPs) or fields (ERFs). These techniques measure changes in electric voltage or magnetic field on or above the scalp, evoked by electrical activity in the brain produced when participants read words (e.g., Rugg et al., 1986; Kutas and Federmeier, 2000; Pulvermüller, 2001; Halgren et al., 2002; Friederici, 2004). ERPs/ERFs possess an advantage over many behavioural measures since they reflect neural processing on a continuous millisecond by millisecond basis. In contrast, behavioural measures such as reaction times represent the combination of all processing stages (from early perceptual processing to decision making) up to the time at which the behavioural response (e.g., button press) is made. A number of studies have used ERP/ERF techniques to study the earliest influences on word processing in the brain occurring already at 100–200 ms after word onset (Pulvermüller, 1999; Sereno and Rayner, 2000).

Among those studies reporting early ERP effects of word recognition, Assadollahi and Pulvermüller (2003) and Hauk and Pulvermüller (2004) found main effects of Word length around 100 ms, with long words showing larger amplitude responses than short ones. From these studies, however, we cannot determine whether this effect is due to the greater luminance, number of letters, syllables or orthographic neighbourhood size since these variables were confounded with each other. An early effect (~100 ms) of "orthographic structure", or Letter n-gram frequency of a word form, quantified as bigram or trigram frequencies, has recently been found suggesting that this factor could also influence ERP responses to written words (Hauk et al., in press).

Effects of Word frequency on evoked responses have typically been reported as occurring after the first physiological signs related to features of the visual word form. For instance, an MEG study by Assadollahi and Pulvermüller (2003) found an interaction between Word length and Frequency, with short words exhibiting a frequency effect around 150 ms but long words at around 240 ms. Other studies have also shown early neurophysiological reflections of Word frequency around 150 ms (Sereno et al., 1998; Hauk and Pulvermüller, 2004). At this latency, high frequency words consistently produce lower amplitudes than low frequency words. An early difference (~110 ms) has sometimes been seen between words and pseudowords, in one case already at 110 ms (Sereno et al., 1998) and in most studies around 200 ms (Dehaene, 1995; Martin-Loeches et al., 1999; Hinojosa et al., 2001; Hauk et al., in press). Lexico-semantic variables have been found to influence brain responses at 160 ms after visual word onset (Pulvermüller et al., 1995), or even earlier (Pulvermüller et al., 2001).

Although a pattern is emerging from these studies that the earliest electrophysiological effects, around 100 ms, are related to surface features of written words, which are subsequently followed around 150–200 ms by lexicality and semantic word properties, the results are still partly inconsistent and electrophysiological data on early word recognition are still sparse. A possible reason for inconsistencies is that most studies only looked at one or two word parameters at a time, such that the whole picture has to be constructed out of several different studies. Furthermore, early electrophysiological effects might be smaller in amplitude than later ones (e.g., in the N400 time range), such that they were either overlooked or not detected due to a lack of sensitivity of the methods.

Factorial versus regression designs

Most electrophysiological and neuroimaging studies have used factorial designs, where stimuli are grouped into distinct categories (e.g., words vs. pseudowords, long words vs. short words, etc.), and ERP averages are computed across all items of each category. Corresponding values are computed for individual subjects. The category-specific average ERPs are then compared with each other using parametric statistical analyses, usually analyses of variance (Picton et al., 2000). Factorial designs are easy to apply, and the interpretation of their results is relatively straightforward. In cases where stimuli fall into discrete categories (such as words and pseudowords), these designs are the optimal approach. However, psycholinguistic variables are in many cases continuous, as with Word length or Lexical frequency. Although these continuous variables can be grouped into categories (for example, high vs. low frequency words), this procedure has been shown to reduce the amount of experimental variance that can be explained and results in a substantial loss of statistical power (Cohen, 1983; Harrell, 2001; Baayen, 2004).

A further problem with dichotomising continuous variables arises if items in factorial sets are also to be matched on other variables (e.g., matching on Word length while varying Word frequency). This category grouping can require the selection of unusual or atypical words. This is a particular problem if the confounding variables are highly correlated with the variable of interest, for example, a factorial comparison of whole-word and stem frequency counts may necessitate the inclusion of words that have particularly high-frequency plural forms which are by definition unusual (see Baayen et al., 1997; Ford et al., 2003).

One method that overcomes both of these problems is to use regression analyses in which the experimenter tests for a linear relationship between the predictor variable (e.g., Word frequency) and the data (e.g., reaction times). This method makes use of the full continuous distribution of stimulus parameters and avoids problems related to the dichotomisation and matching of stimulus sets. However, to date, the regression approach has not been applied to EEG/MEG data. In this paper, we demonstrate an application of regression analysis in a study of visual word recognition. In any case, as we argue below, the traditional factorial analysis approach for ERP data is actually a special case of this form of regression analysis.

In EEG analysis, regression coefficients that express the slope of the best-fitting linear relationship between evoked electrical activity and predictor variables (such as Word frequency) can be determined for individual time points in individual subjects on an electrode-by-electrode basis. From this stage onwards, these event-related regression coefficients (ERRCs) can be processed just like ERP signals, taking the place of "difference waves". Therefore, in order to test whether a variable predicts a significant amount of variation in the data, one only needs to test the regression coefficients of all subjects associated with this variable against zero. This regression approach has previously been suggested for behavioural data using a similar repeated measures designs (Lorch and Myers, 1990). Mapping ERRCs and their significance parameters for all variables individually over time can inform us about the time course of processes related to different kinds of information (form, frequency, meaning, etc.). A related regression method has been applied to ERP data by Dien et al. (2003), who instead of averaging trials across items for each subject averaged trials across subjects for each item and computed correlations on the resulting data. However, the approach we chose here, calculating ERRCs over all items for each subject individually and submitting regression coefficients to statistical analysis, is arguably more appropriate as it takes into account the most relevant sources of inter-subject variance (Lorch and Myers, 1990).

The present study

To establish the processing sequence associated with the extraction of word form, lexical and meaning-related information in the early stages of visual word recognition, we performed an exhaustive regression analysis on early latency ranges in the electrophysiological response, considering all relevant variables describing the form, frequency and meaning of a set of written words. To conduct these regression analyses, we needed to ensure not only that each predictor variable is related to a specific aspect of word recognition but also that the predictor variables are themselves mutually independent. Because of the degree of intercorrelation between many standardly used lexical variables – for example Word length and Word frequency – we used principal component analysis (PCA) to extract a set of four orthogonal variables from a larger representative set. From an original set of 10 psycholinguistic variables that had been previously reported to influence visual word recognition, we found that 4 orthogonal components explained approximately 80% of the variance and yet retained theoretically important distinctions between different properties of written words. We therefore selected these four PCA factors and applied a rotation procedure such that the individual factors were orthogonal and yet could still be categorised according to the domain of information they carry about the stimuli (as determined by the loadings of each PCA factor on the original 10 variables). The four components derived from this procedure can be described as encoding: (1) Frequency (correlating strongly with word form and morphemic frequency measures such as lemma and cumulative morpheme frequency and family size (Schreuder and Baayen, 1997)), (2) Length (correlating positively with number of letters and syllables, but negatively with orthographic neighbourhood size), (3) Orthographic Letter n-gram frequency (correlating positively with bigram and trigram frequency) and (4) Semantic coherence of the morphological family of a stimulus word (Ford et al., 2003), a relatively new variable quantifying the consistency of the meanings of morphologically related word forms. For example, the morphological family of *help* (e.g., *helper*, *helpful*, *helpmeet*) shows high Semantic coherence as all the words are clearly related to the meaning root form. Indeed, dictionary definitions for such words typically include the root word, e.g., *helper* "one who (or that which) helps" (Oxford English Dictionary). In contrast, the morphological family of *depart* shows low Semantic coherence. Although *departure* is clearly related to *depart*, other morphological relatives such as *department* are not related in meaning to *depart*. The Semantic coherence measure was derived from the analysis of a multidimensional semantic space extracted using Latent Semantic Analysis (Landauer and Dumais, 1997). In addition, the effect of the variable Lexicality (contrasting real words and pseudowords) was analysed using a factorial approach on event-related potentials. The difference between words and pseudowords has been widely investigated, thus the use of this variable in our study makes our data comparable to previous studies. We note that lexicality is a factorial variable that potentially impacts on many stages of the recognition process — since pseudowords have an unfamiliar appearance, lack any established meaning and have zero frequency for our participants. It is therefore of interest to consider which of the predictor variables has most in common with lexicality.

A critically important question in our study concerns the neural localisation of these various effects in the brain. Few of the previous studies on early ERP effects in visual word recognition used source estimation procedures. Although the neural generators of an ERP or ERF signal cannot be uniquely determined from electrophysiological data alone, meaningful inferences can still be made using distributed source analysis (see, e.g., Hämäläinen and Ilmoniemi, 1984; Dale and Sereno, 1993; Grave de Peralta Menendez et al., 1997; Fuchs et al., 1999; Hauk, 2004; Michel et al., 2004). These techniques can make use of a minimum of modelling assumptions and yield an estimate for the source activity underlying the measured signal that can be compared with neuroimaging (fMRI/PET) or neuropsychological (lesion studies) findings. We will apply to the data a standard distributed source solution, called minimum norm estimation (Hauk, 2004), in order to estimate the brain areas differentially affected by different word parameters.

In summary, this study for the first time uses a regression approach to scrutinise the neurophysiological correlates of important psycholinguistic variables in visual word recognition. Our goal in doing this was to answer the following questions:

- Which psycholinguistic variables are reflected in the human electrophysiological response to written words at early latencies?
- Do the onsets of the earliest neurophysiological correlates of the psycholinguistic variables reflect distinct stages of processing in visual word recognition? For example: Do form-related variables affect neural correlates of word recognition prior to effects of Word frequency and of semantic variables?
- Are there time points when the brain response simultaneously reflects a range of psycholinguistic variables, such as form, frequency and semantic information, thus indicating cascaded or parallel processing of information of different types in word recognition?

Results will be presented for four regression coefficients and one factorial variable that reflect the timing and operation of elementary processes during visual word recognition. Distributed source analysis yields estimates of the neuronal generators of the most relevant effects and provides us with an estimated localisation of the brain networks involved in the fast and efficient recognition of visually presented words.

Methods

Subjects

Twenty right-handed monolingual native speakers of British English were entered into the final analysis (11 female, 9 male). Their mean age was 22 years (SD 3). All had normal or corrected-to-normal vision, reported no history of neurological illness or drug abuse and had at least 14 years of education (school and higher education). Handedness was determined according to a simplified version of Oldfield's handedness inventory (Oldfield, 1971), revealing a mean laterality quotient of 85 (SD 25). Five subjects were initially removed from the data set due to extensive systematic eye blinking or other artefacts. 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

Three hundred monomorphemic English nouns were selected that were either lexically unambiguous nouns or, if lexically ambiguous, were used much more frequently as nouns than as members of other lexical categories (mean noun:verb frequency ratio, 22:1, CELEX database; Baayen et al., 1993). Homophonic words were excluded by checking all words in the Wordsmyth on-line dictionary (Parks et al., 1998). All words were between three and six characters in length, and most were monosyllabic.

Corpus-based lexical information previously shown to influence response times in lexical decision was obtained for all stimulus words. Four Lexical frequency measures were obtained from the CELEX database, word form frequency plus three morphemic frequency measures. These were lemma (or inflectional word stem) frequency, cumulative morpheme frequency and family size (e.g., Bradley, 1979; Clahsen et al., 1997; Schreuder and Baayen, 1997; Sereno and Jongman, 1997). At the surface form level, the average frequency of its letter bigrams and trigrams was calculated for each word along with Word length counted in number of letters. Furthermore, the number of lexical neighbours (words that can be derived from a given word by exchanging one letter) was used to estimate the orthographic neighbourhood density (Coltheart's N) (Coltheart et al., 1977).

We also obtained a corpus-based semantic measure that quantifies the degree to which words sharing a root morpheme (e.g., *gold*, *golden*, *goldsmith*) are related to each other in meaning, i.e., a measure of morpho-semantic coherence (Ford et al., 2003), which in the following will be referred to as "Semantic coherence". This measure was derived using Latent Semantic Analysis (LSA) (Landauer and Dumais, 1997), which measures the likelihood of words appearing in the same discourse context. For example, the words *baker* and *flour* are likely to appear in similar kinds of texts, whereas this is not the case for the words *baker* and *hypocrisy*. A matrix of words and the frequency with which they co-occur with specific other words in a particular text is created, and this matrix is converted to vectors in multidimensional space for each word. The cosine of the angle between the vectors of two words indicates the degree to which they have been found in similar contexts. Critically, this measure has been found to correlate well with subjective semantic relatedness ratings of word pairs (Rastle et al., 2000). For example, this measure accurately captures the difference between semantically transparent and semantically opaque morphologically related words, e.g., *government–govern* = 0.68, *department–depart* = 0.04. For the morphological family of each stimulus word used in the experiment, the mean semantic relatedness LSA score was calculated by averaging the LSA cosine measures over all pairs of stem and morphological variant in the family. This resulted in a corpus-based measure of the morpho-semantic coherence of the morphological family of each stimulus word (Semantic coherence).

Table 1
The time course of visual word recognition

	WF	FS	CMF	SC	BG	TG	N	Len	Syll
LF	0.953	0.681	0.523	0.323	0.191	0.216	0.118	−0.035	−0.057
WF		0.658	0.516	0.341	0.190	0.205	0.076	−0.001	−0.042
FS			0.655	−0.017	0.174	0.180	0.217	−0.148	−0.231
CMF				−0.141	0.169	0.158	0.051	−0.044	−0.107
SC					−0.004	0.047	0.035	−0.058	−0.009
BG						0.406	0.084	0.039	−0.069
TG							0.169	0.031	0.023
N								−0.691	−0.410
Len									0.487

Correlation matrix for psycholinguistic variables taken into the PCA analysis. Abbreviations as in Fig. 1.

As many of these variables are highly correlated (Table 1), which may lead to problems of collinearity in regression analyses, they were reduced to 4 variables by means of principal components analysis (PCA). The PCA, using varimax rotation, produced 4 orthogonal vectors, with their relationship with the original variables shown in Fig. 1. The first PCA component ("Frequency") showed a strong positive correlation with the four frequency variables. The second PCA component ("Word length") showed strong correlations with length, syllables (positive) and neighbourhood density (negative). The third PCA component ("Letter n-gram frequency") showed strong positive correlations with bigram and trigram frequency. The fourth PCA component ("Semantic coherence") showed the strongest positive correlation with the new semantic coherence measure based on LSA. It also showed moderate positive correlation with word form and lemma frequencies and negative correlation with cumulative morpheme frequency. However, we take the strong Semantic coherence correlation to be dominant here.

Three hundred pseudowords were created according to the orthographic and phonotactic rules of British English. Those were matched for length and bigram frequency to the real words. Pseudowords did not include letters or letter combinations that could be interpreted as prefixes or suffixes.

Procedure

Participants performed a lexical decision task. White letter strings were presented on a gray background on a computer screen. Each stimulus was presented for 100 ms. The stimulus onset asynchrony (SOA) varied between 2.5 and 3 s. A fixation cross was shown in the center of the screen when no letter strings were present. Subjects were instructed to press one button of a response box with the index finger of their left hand in response to a real word and another button with the middle finger of the same hand in response to a pseudoword. Each subject was presented with a different sequence of stimuli. Subjects were instructed to minimise eye and body movements throughout the experiment. The stimulus delivery and response collection was controlled by the Experimental Run Time System software (ERTS, BeriSoft, Germany).

Data recording

The electroencephalogram (EEG) was measured in an electrically and acoustically shielded EEG chamber at the MRC Cognition and Brain Sciences Unit in Cambridge, UK. Data were

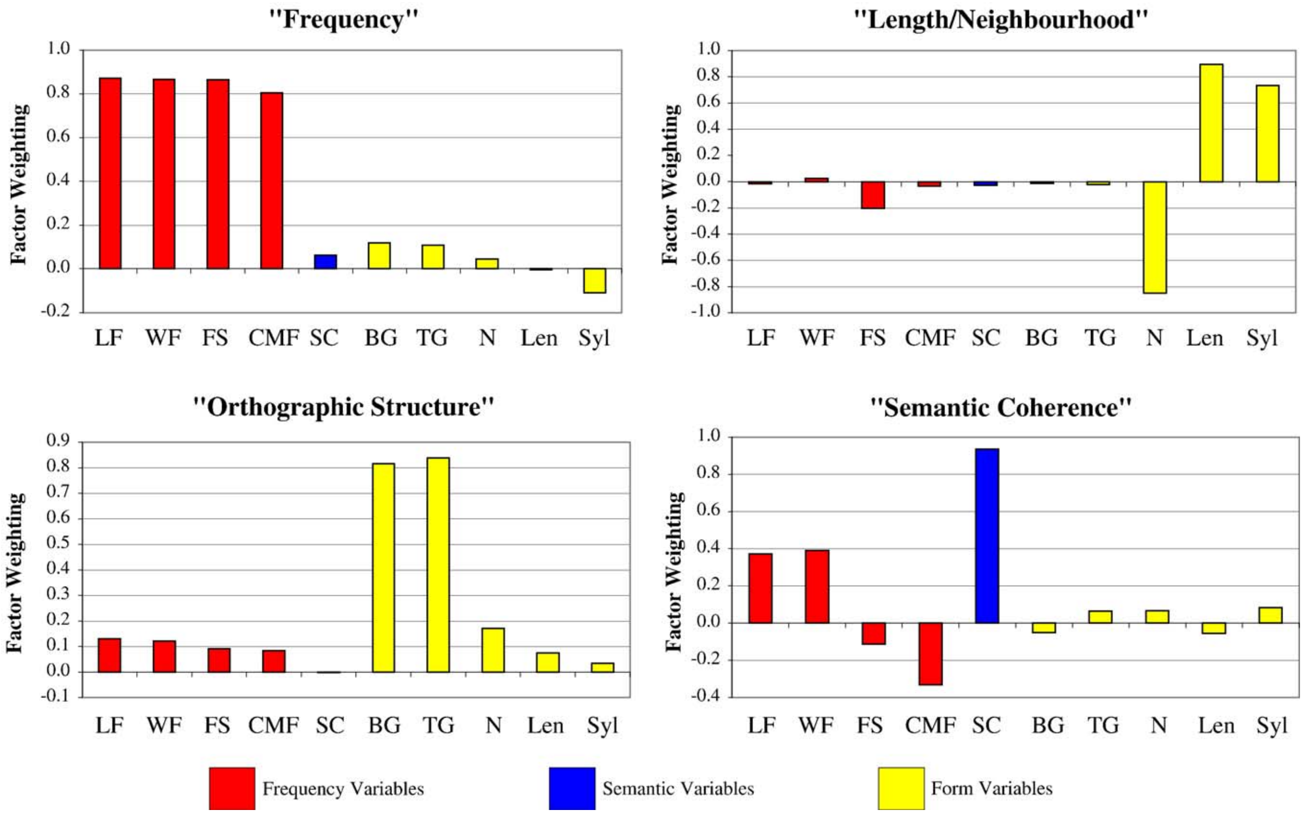

Fig. 1. Descriptive statistics for the stimuli employed in the regression analysis: correlations among the four eigenvectors extracted from the PCA with the individual variables (factor loadings). LF: lemma frequency; WF: word form frequency; FS: family size; CMF: cumulative morpheme frequency; SC: semantic coherence; BG: bigram frequency; TG: trigram frequency; N: orthographic neighbourhood size; Len: number of letters; Syl: number of syllables.

recorded from 65 Ag/AgCl electrodes, all of which were mounted on an electrode cap (EasyCap, Falk Minow Services, Herrsching-Breitbrunn, Germany) except the lower vertical EOG electrode which was placed below the right eye, using SynAmps amplifiers (NeuroScan Labs, Sterling, USA). Electrodes were arranged according to the extended 10/20 system. Data were sampled at 500 Hz with a band-pass filter 0.1–100 Hz. Cz was used as recording reference for the EEG channels. The EOG was recorded bipolarly through electrodes placed above and below the left eye (vertical) and at the outer canthi (horizontal).

Pre-processing of ERP data

The continuously recorded data were divided into epochs of 800 ms length, starting 100 ms before stimulus onset. Trials with peak-to-peak potential differences larger than 100 μV in at least one EEG or EOG channel were rejected as were trials in which incorrect responses were given. For each channel, the mean amplitude of a 100 ms baseline interval was subtracted at all time points, and data were converted to average reference.

Regression analysis

Most previous ERP studies employed factorial designs, that is, stimuli were grouped into two or more categories and the corresponding ERP responses were then averaged. Differences among the mean of these categories were usually assessed using ANOVAs, and the "difference waves" were displayed to show the magnitude of the effects. In our study, we computed event-related regression coefficients (ERRCs) for each of the four orthogonal variables for each subject. This was done at each electrode and for each time sample (i.e., every 2 ms). The resulting data set therefore strongly resembled "normal" ERP data, that is, we obtained spatio-temporal information for each variable. Because each variable was normalised to zero mean and unit standard deviation, the regression coefficients can be interpreted as "microvolts per standard deviation" of the corresponding variable. We describe below the details of this regression procedure and how it relates to classical factorial designs.

In both factorial designs and linear regression designs, a weighted sum $\sum_{i=1}^{N} w_i d_i$ of all valid EEG epochs is computed, where the d_i are the data values (e.g., voltages for one channel and one time point) for individual trials i $(1\ldots N)$, N is the number of trials, and w_i the weighting coefficients. The w_i values would be chosen as a step function in a factorial design (i.e., 1 for one category of stimuli (e.g., frequent words), -1 for another (e.g., infrequent words)) or would correspond to the continuous variable of interest in a linear regression analysis (e.g., frequency values for individual words). Linear regression analysis can therefore be considered as a generalisation of the factorial design, which better exploits the full range of stimulus parameters. An estimate for the slope of the regression line can be calculated for each individual subject and subjected to group statistical analysis (Lorch and Myers, 1990). If z-transformed predictor variables are applied to

ERP data, the resulting beta-values represent "signal change in microvolts per standard deviation of the predictor variable".

Since the operation applied to the data is linear, any further linear operation R_M we want to perform on all trials can be performed on the weighted average to get the same result, i.e., $R_M = \sum_{i=1}^{N} w_i M D_i = M\sum_{i=1}^{N} w_i D_i$. This would be the case, for example, for linear estimation techniques often employed in distributed source analyses of EEG and MEG data (Hämäläinen and Ilmoniemi, 1994; Grave de Peralta Menendez et al., 1997; Hauk, 2004).

Statistical analysis

The main purpose of this analysis was to identify which of the four predictor variables generated reliable differences in the ERRC responses and to determine the latency ranges in which they exhibit significant effects. Because the predictor variables that were entered into the regression analysis were mutually orthogonal, this can be achieved by comparing the result for each variable separately against the zero distribution. This was done using paired two-tailed t tests.

Previous reports on early modulation of the word-evoked response described in the literature are quite sparse, as outlined in Introduction. Furthermore, we investigated the effects of one variable, Semantic coherence (based on the LSA measure), that to the best of our knowledge has not previously been described in the ERP literature. For these reasons, we will present an exhaustive analysis of the whole early time range from 70 to 240 ms (Fig. 4), as well as time window analyses focussing on prominent peaks of the RMS curves in Fig. 2 (Figs. 5 and 6). Significance maps are presented at a lenient threshold (0.05 uncorrected). As will be discussed later, this makes our results comparable to previous studies that either did not address the problem of multiple comparisons at all or reported results for individual electrodes at uncorrected thresholds. More importantly, results from previous studies allow us to perform hypothesis-driven tests at specific electrodes and time points (e.g., for Word length effects around 100 ms at occipital electrodes), which are now included as part of the significance maps.

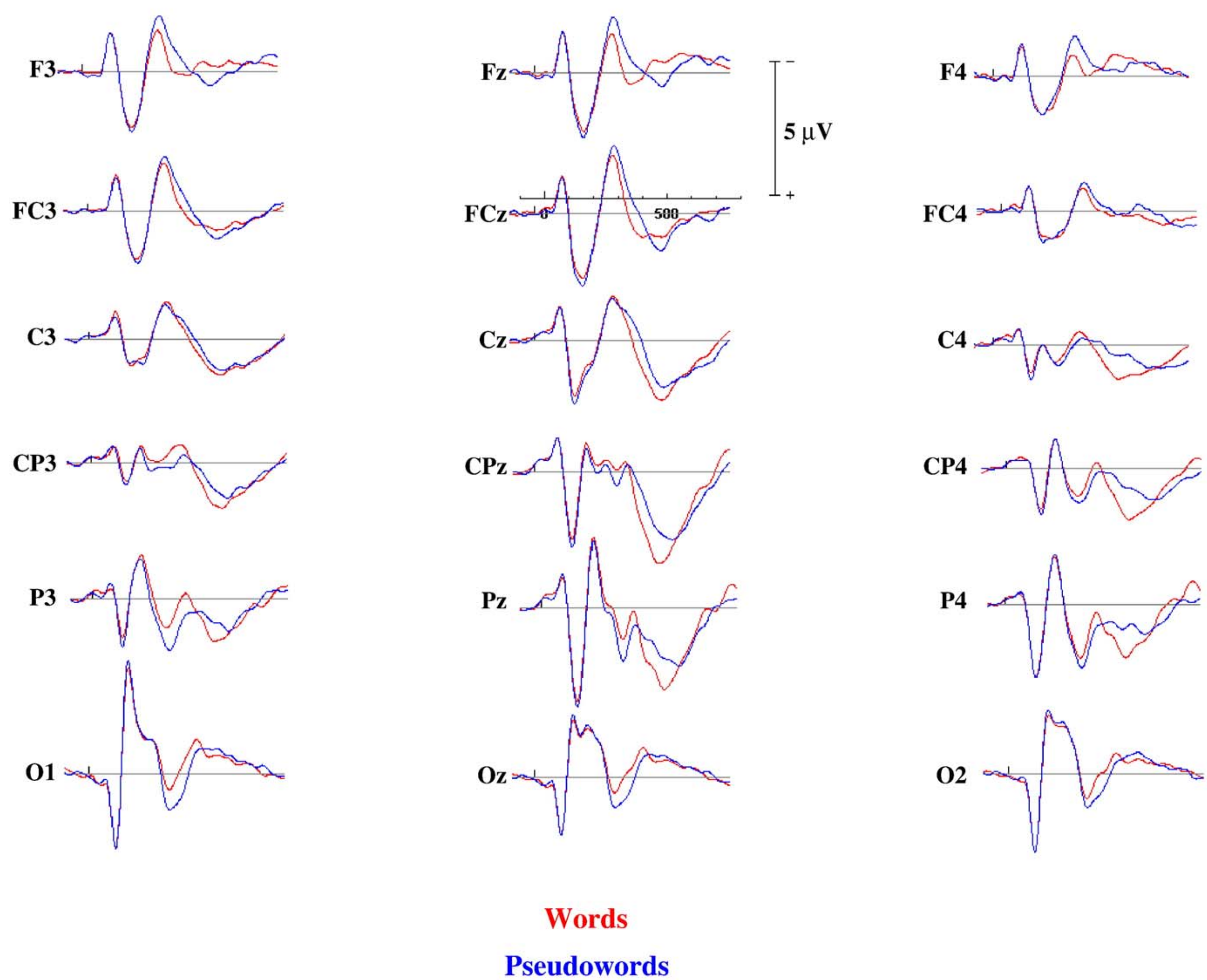

Fig. 2. Grand-average ERP wave forms for words (red) and pseudowords (blue) separately for a sub-set of electrodes. Data were average-referenced with respect to all 63 electrodes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Topographical ANOVA analysis

The goal of this study was to identify the time course of the electrophysiological brain response for several distinct psycholinguistic variables. This can be achieved by testing the regression coefficients for the group of subjects against the zero distribution for each variable separately since the variables were constructed to be mutually orthogonal. Nevertheless, an interesting question is whether the topographies of these regression coefficients differ between variables. Together with our source estimation results, this would provide additional evidence that there are different neural generators responsible for the effect of different variables.

This can be answered by an interaction analysis including a factor describing the topography of the ERP or ERRCs. We therefore selected 9 electrodes (F7, Fz, F8; T7, Cz, T8; P7, Pz, P8) that captured the most prominent peaks in the topographies presented in Figs. 5 and 6, which were grouped into the factors Gradient (anterior–posterior, 3 levels) and Laterality (left–right, 3 levels). Interactions of these factors with two or more variables were computed for time ranges where more than one variable showed significant effects simultaneously. Because in this analysis we are interested in topographical effects rather than mere amplitude differences, vector normalisation according to McCarthy and Wood (1985) was performed on a single-subject level. Topographies can be considered as vectors with their elements corresponding to different electrodes. The question of whether two topographies differ with respect to a common scaling factor, or with respect to shape, is equivalent to asking whether the vectors are only different in length or also differ in direction. Normalising the lengths of these vectors, and subsequently testing for differences, can therefore provide further information on the nature of the observed effects (Dien and Santuzzi, 2004). This makes the pattern of results more comparable to previous studies and serves as an intermediate step between ERP and source analysis since different patterns of source distributions should be reflected in topographical differences of the surface signal. Greenhouse–Geisser correction of degrees of freedom was applied where appropriate.

Source analysis

Minimum norm source estimates were obtained for regression coefficients and difference ERPs, respectively, that showed significant effects in the statistical analysis. In the case of noiseless data, this method produces the unique solution among the infinitely many possible ones that explains the data completely but has minimal overall source strength in the least squares sense (Hämäläinen and Ilmoniemi, 1984; Bertero et al., 1985). This property also asserts that the solution does not contain any "silent sources", i.e., sources that do not produce any measurable signal at the recording electrodes (Hämäläinen and Ilmoniemi, 1984; Hauk, 2004). When noise has to be taken into account, the "smoothness" of the solution can be controlled by a "regularisation parameter" (often referred to as "λ") (Bertero et al., 1988)—the higher this parameter is set, the less variance the solution explains in the data, but the smoother the source distribution.

The implementation used for our analysis followed the suggestion of Hauk (2004). The method 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 and regression analysis. We therefore applied this method to our grand mean data for different variables. 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 ratios (SNR). The SNR was computed at each source location by dividing each source strength by its standard deviation within the baseline interval. Activation was displayed as non-zero when the SNR exceeded a value of 2 (see Fig. 7).

Results

Behavioural analysis

Mean reaction times (RTs) and error rates are presented in Table 2. Paired two-tailed t tests revealed that RTs were significantly faster for words compared to pseudowords (571 ms vs. 648 ms), both by items ($t(598) = -21.3$, $P < 0.001$) and by subjects ($t(19) = -8.3$, $P < 0.001$). The effect for error rates (ERs) was significant by items ($t(598) = -2.1$, $P < 0.05$) but only approached significance by subjects ($t(19) = -1.1$, $P = 0.07$), pseudowords being slightly more error-prone than words (5.3% vs. 4.2%).

ERP analysis

The grand-average ERP curves for words and pseudowords separately are shown for selected electrodes in Fig. 2. The first prominent peaks occur around 100 ms, with virtually identical positive amplitudes for both words and pseudowords at occipital electrodes (O1, Oz, O2). This is followed by a negative deflection around 160 ms, lasting until after 200 ms, with responses to pseudowords being more negative than those to words at occipital sites. The posterior negativity was strongly left lateralised (see for example ERPs at O-electrodes, Fig. 2), as reported earlier (Dehaene, 1995; Pulvermüller et al., 1995). For both early peaks, polarity was reversed at frontal electrodes. They were followed by a negative deflection most prominent at frontal electrodes around 300 ms, and a large positive peak maximal at centro-parietal electrodes peaking around 500 ms, where pseudowords again exhibited more negative-going (thus less positive) potentials than words.

To summarise the time course of the word-evoked ERP and ERRCs, signal-to-noise ratios (SNRs) derived from root-mean-square values (RMS) are presented in Fig. 3. The transformation into SNRs permits better comparison between ERPs – such as those for the word–pseudoword difference – and ERRCs which would otherwise appear in different physical units. In Fig. 3A, the RMS was computed for the word-evoked potential as displayed in Fig. 2, and the SNR was obtained by dividing the RMS values at each time point by the mean RMS of the baseline interval. In Fig. 3B, the same procedure was applied to the regression coefficients for each word parameter separately. In parts of the following

Table 2
The time course of visual word recognition

	Reaction time		Error rate	
Words	570.9	SD 46.1	4.2	SD 5.7
Pseudowords	647.5	SD 42.0	5.3	SD 6.0

Summary of behavioural data.

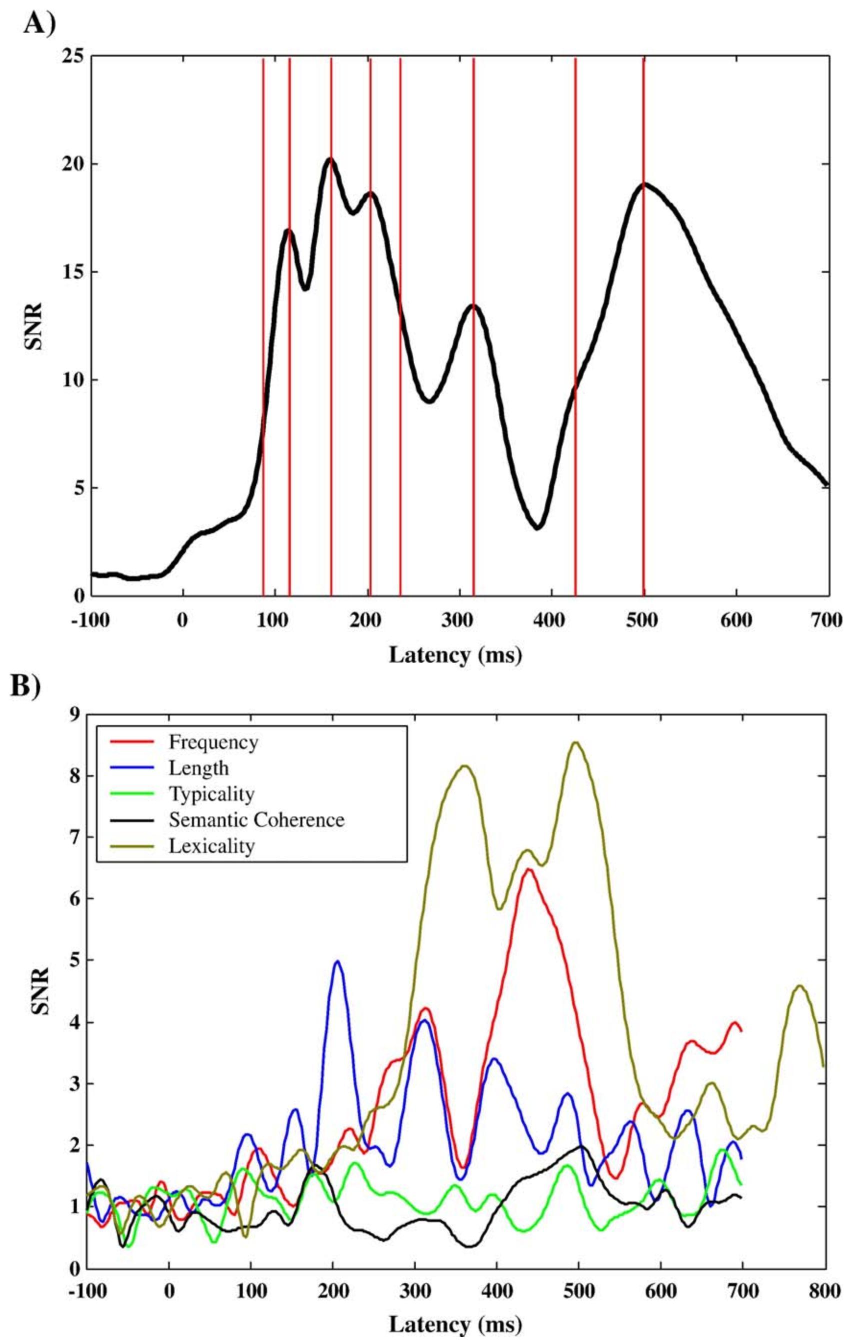

Fig. 3. (A) Time course of SNRs of the RMS values computed on the grand mean across all words and subjects. Latencies used for more detailed analysis are marked by vertical red lines. (B) SNRs of the RMS values for event-related potentials (ERPs) and event-related regression coefficients (ERRCs) of individual variables, respectively.

analyses, we focussed on RMS peaks for the word-evoked potential in Fig. 3A. The choice of time ranges based on these RMS peaks was motivated by previous studies that reported electrophysiological effects of several variables for peaks around 100 ms ("P1") (Sereno et al., 1998; Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004; Hauk et al., in press), 160 ms ("N1") (Pulvermüller et al., 1995; Sereno et al., 1998; Assadollahi and Pulvermüller, 2003; Sereno et al., 2003; Hauk and Pulvermüller, 2004; Hauk et al., in press), 200 ms (Dehaene, 1995; Martin-Loeches et al., 1999; Pulvermüller et al., 1999; Rudell et al., 2000; Hinojosa et al., 2001; Hauk and Pulvermuller, 2004), between 300 and 400 ms (Osterhout et al., 1997; King and Kutas, 1998; Embick et al., 2001; Pylkkanen and Marantz, 2003) and at later latencies (Polich and Donchin, 1988; Rugg, 1990; Kutas and Federmeier, 2000; Friederici, 2004). RMS peaks in our data occurred at 114 ms, 160 ms, 202 ms, 314 ms and 500 ms. Because there were gaps between some of the peaks where the RMS was still clearly different from zero, we also selected the latencies 90 ms, 244 ms and 425 ms. All these latencies are marked by vertical lines in Fig. 3A. For display and statistical analysis, average topographies were computed for latency ranges of 20 ms around these peaks that showed a stable topography. These time windows were 80–100 ms, 100–120 ms, 140–180 ms, 202–222 ms, 234–254 ms and 304–324 ms. For later time ranges in which topographies remained stable over longer time intervals, broader time ranges were chosen, namely, 400–450 ms and 450–550 ms.

Fig. 3B indicates that the regression coefficients of the variables included in the study produce activity with differential time courses. The "classical" factor Lexicality (words minus pseudowords) produces SNRs around 2 from about 150 ms onwards, with largest peaks occurring later around 350 ms and 500 ms. Length and Frequency reach SNRs of approximately 2 already around 100 ms. While Length then produces its largest amplitudes around 200 ms and 300 ms, Frequency does so around 300 ms and 450 ms. Letter n-gram frequency and Semantic coherence variables generally have the lowest SNRs, the former showing its first noticeable deflection from baseline around 100 ms, the latter shortly after 150 ms and then again later around 500 ms. Although a more detailed analysis of these effects will be postponed to later sections of this paper, note that the earliest peak associated with Letter n-gram frequency occurs together with the other surface form variable, Length, earlier than any other peaks. Furthermore, the comparatively small peaks of Semantic coherence coincide with those of Lexicality, which is the other factor thought to reflect lexico-semantic processing.

Fig. 4 shows grand-average topographies and significance maps for time windows around latencies selected from the RMS analysis (Fig. 3A) that exhibited significant effects. The first effects are produced around 100 ms by the surface variables Length and Letter n-gram frequency followed at a short delay by Frequency. Both Semantic coherence and Lexicality follow around 160 ms, but only Lexicality maintains significant effects at 202 ms and 244 ms. At 202 ms, Length, Frequency and Lexicality exhibit significant effects simultaneously. We now turn to a more detailed discussion of this pattern of effects.

The earliest significant responses for Length were seen at 90–100 ms. Length is associated with positive regression coefficients at electrodes that show a positive potential on average (maximum at electrode P8). Thus, the longer the words, the larger the positivity at this latency. A further positive correlation was seen around 200 ms. This is in accordance with previous studies reporting Word length effects in this latency range (Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004). Consistent with the Assadollahi and Pulvermüller (2003) study, the sources of the length effect were primarily present in bilateral temporo-occipital areas (Fig. 7).

The negative regression coefficients at posterior electrodes for Letter n-gram frequency mean that word stimuli with high bi- or trigram frequencies produced less positive amplitudes than items with low frequency of their letter pairs or triplets. The most negative amplitudes were found at electrode P7. The corresponding electrode above the right hemisphere (P8) showed negative regression coefficients as well but failed to reach significance. Hauk et al. (in press) found similar effects of bigram and trigram frequency at bilateral parieto-occipital electrodes. Source estimates produced activation associated with Word length in a left inferior temporal area, matching the most prominent peak of activation found in the present study (see Fig. 7).

These effects of Length and Letter n-gram frequency were closely followed by a left-lateralised effect of Frequency around 110 ms. As with Letter n-gram frequency, the negative regression coefficients at left posterior electrodes around P7 show that increasing word frequencies correlate with decreasing positive amplitudes of ERP signals. As with Word length, this effect is consistent with the results of Hauk and Pulvermüller (2004), who also provide a review of previous frequency effects in the neurophysiological literature. A further frequency effect was found at 202 ms, where again higher frequency predicts lower amplitudes. Frequency produces largest source activation at 110 ms in a left posterior area, which shifts to more anterior regions in the left inferior temporal cortex at 202 ms, where it is accompanied by activity in an almost symmetrical location in the right hemisphere, and a further central occipital activation spot.

Effects of the lexico-semantic parameters Lexicality and Semantic coherence first occurred at about 160 ms for both Semantic coherence and Lexicality. This is the same point in time where Pulvermüller et al. (1995) found differential activation to matched words from different lexical categories with distinct meanings (grammatical function words and highly imageable content words). The general pattern found for the Lexicality contrast, with more positive-going (less negative) potentials for words than pseudowords at occipital electrode sites, has been reported in several previous studies and is sometimes referred to as the "recognition potential" (Rudell, 1991; Martin-Loeches et al., 1999; Rudell et al., 2000; Hinojosa et al., 2001; Hauk et al., in press). These studies found lexicality effects shortly after 200 ms, consistent with our effects at 202 ms and 244 ms. Other early neurophysiological differences between lexical and semantic word categories, which also suggest differential activation as a function of lexical and semantic information carried by the stimulus words, were reported by several studies (for example, Preissl et al., 1995; Hinojosa et al., 2001; Martin-Loeches et al., 2001; Pulvermüller et al., 2001). Consistent with this, the new variable Semantic coherence produced significant effects at 160 ms, simultaneously with the lexicality effect, around left-frontal electrode FT7 and parietal electrode P2. The general pattern of the ERRCs indicates that larger values of Semantic coherence predict larger ERP amplitudes. This pattern occurred in parallel to a lexicality effect at 160 ms but is not present at 202 ms and 244 ms.

Fig. 5 shows the topographies of all variables for the early time range 70–240 ms in steps of 10 ms, accompanied by the corresponding significance maps based on paired two-tailed *t* tests. This illustrates the time course of the effects summarised in Fig. 4 and demonstrates that they are indeed specific for the latency ranges chosen from the RMS curves of Fig. 3A.

Although our interest lies mainly in the early processes of visual word recognition, and thus the early time ranges of the ERP, we note that previous studies focussed primarily on effects occurring at later latencies. In Fig. 6, we therefore present topographies and significance maps for effects at latencies after 250 ms obtained from the RMS analysis based in Fig. 3, i.e., for time windows 304–324 ms, 400–450 ms and 450–550 ms. At around 314 ms, Length, Frequency and Lexicality show effects with similar topographical distributions, i.e., frontal positivity and left posterior negativity. Lexicality, Semantic coherence and Frequency produce similar patterns around 425 ms and 500 ms, with positive potentials at central or centro-parietal electrode sites. The Lexicality effect consists of responses to pseudowords being more negative than those to words, a pattern consistent with previously reported N400 effects for pseudowords (Holcomb and Neville, 1990; Kutas and Federmeier, 2000).

Topographical ERP analysis

To probe for the specific brain systems processing the information captured by the stimulus features Length, Letter n-

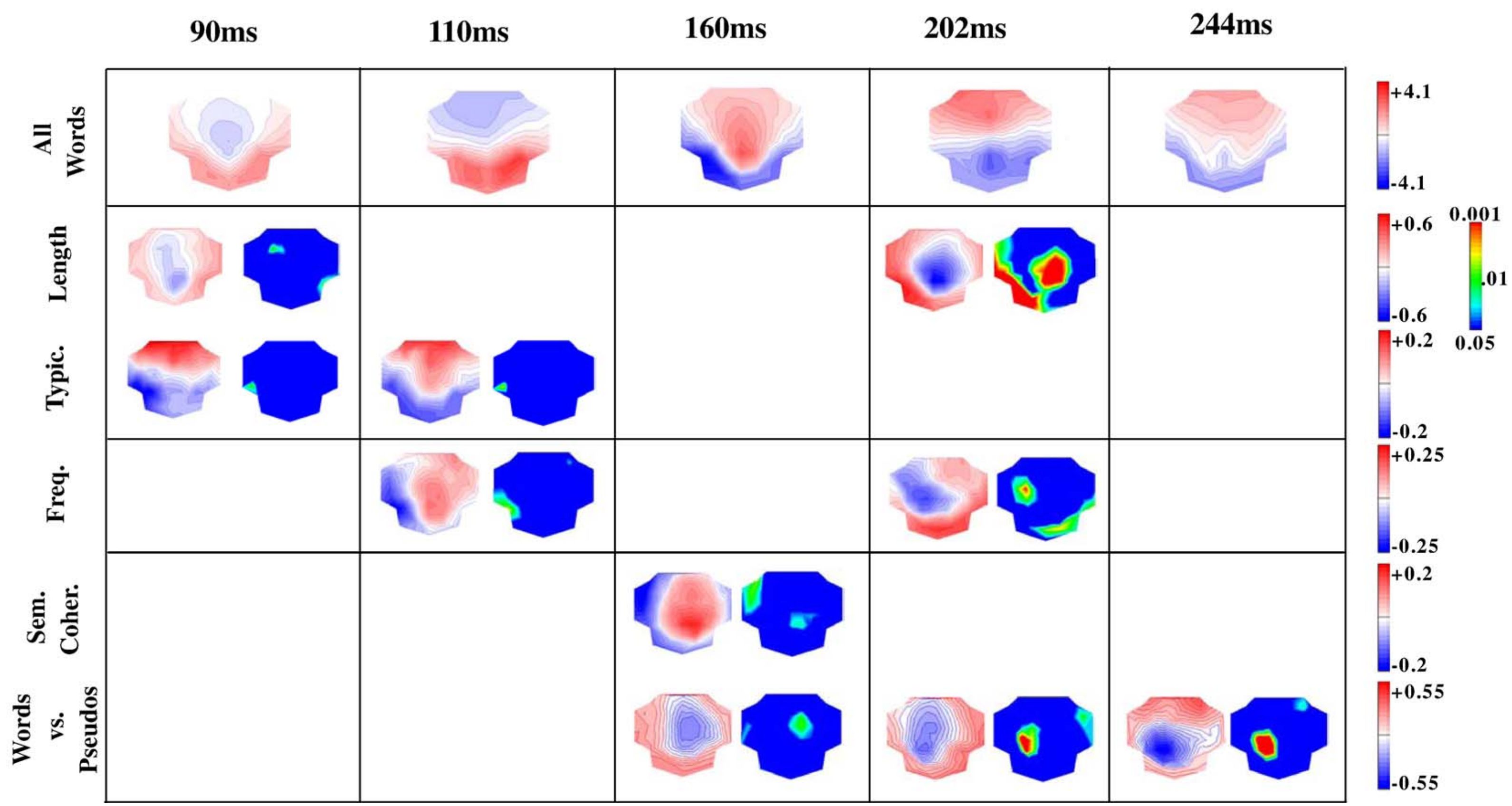

Fig. 4. Spatial distribution of ERPs and ERRCs, respectively, and their corresponding significance maps in the early time range 70–240 ms. Only maps of significant effects that occurred at latencies marked in the RMS curves of Fig. 3A are shown. The electrode array was unfolded into one plane in order to visualise the whole distribution as one map. The rainbow-coloured scale bars refer to the *p*-values, while the red–blue scale bars refer either to ERRCs (for the four PCA variables) or ERPs (Words vs. Pseudos, All Words). Typic.: Typicality; Freq.: Frequency; Sem. Coher.: Semantic coherence; Pseudos: Pseudowords.

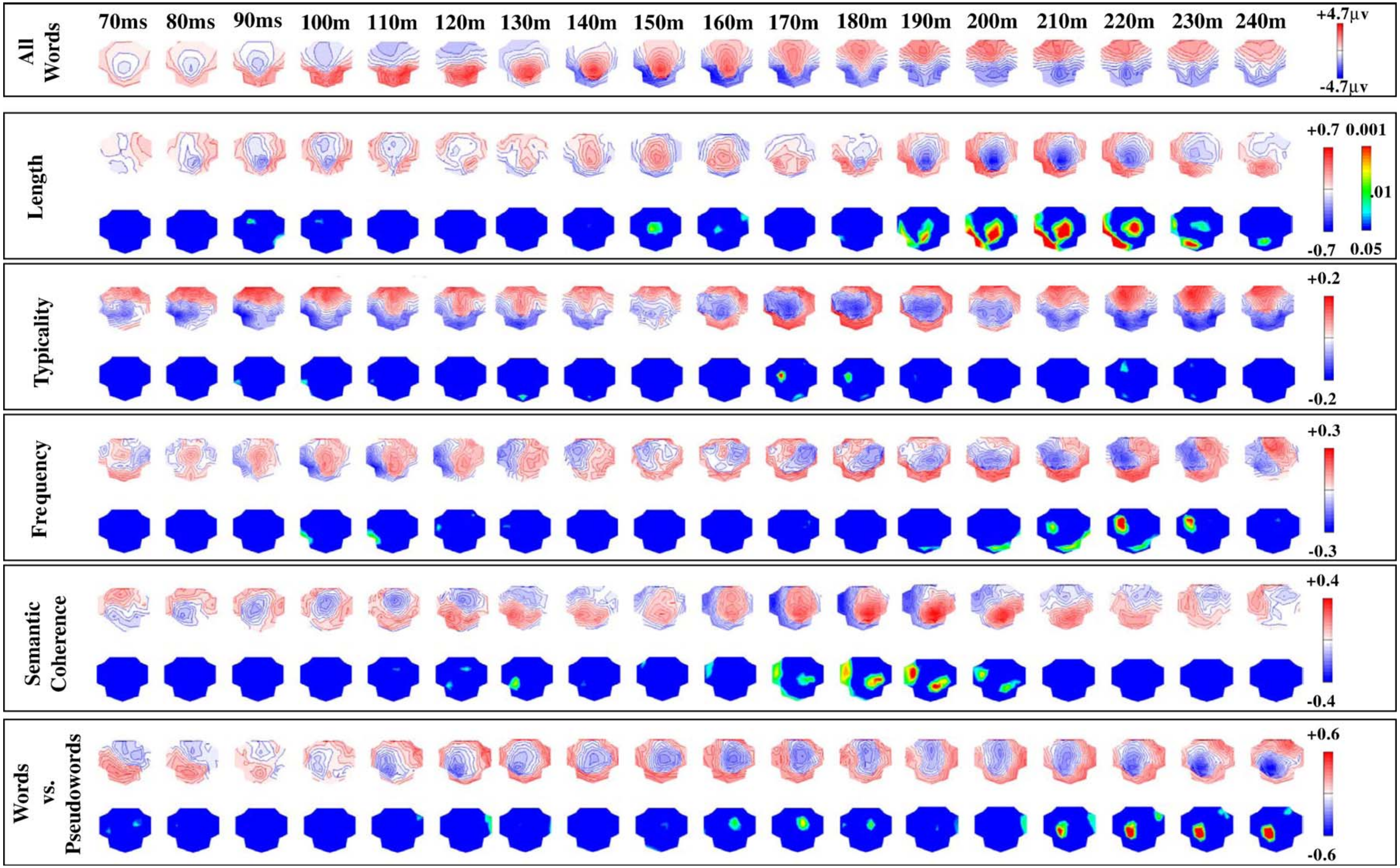

Fig. 5. Spatial distribution of ERPs or ERRCs (upper rows within frames), respectively, and their corresponding significance maps (lower rows within frames) between 70 and 240 ms in steps of 10 ms. The electrode array was unfolded into one plane in order to visualise the whole distribution as one map.

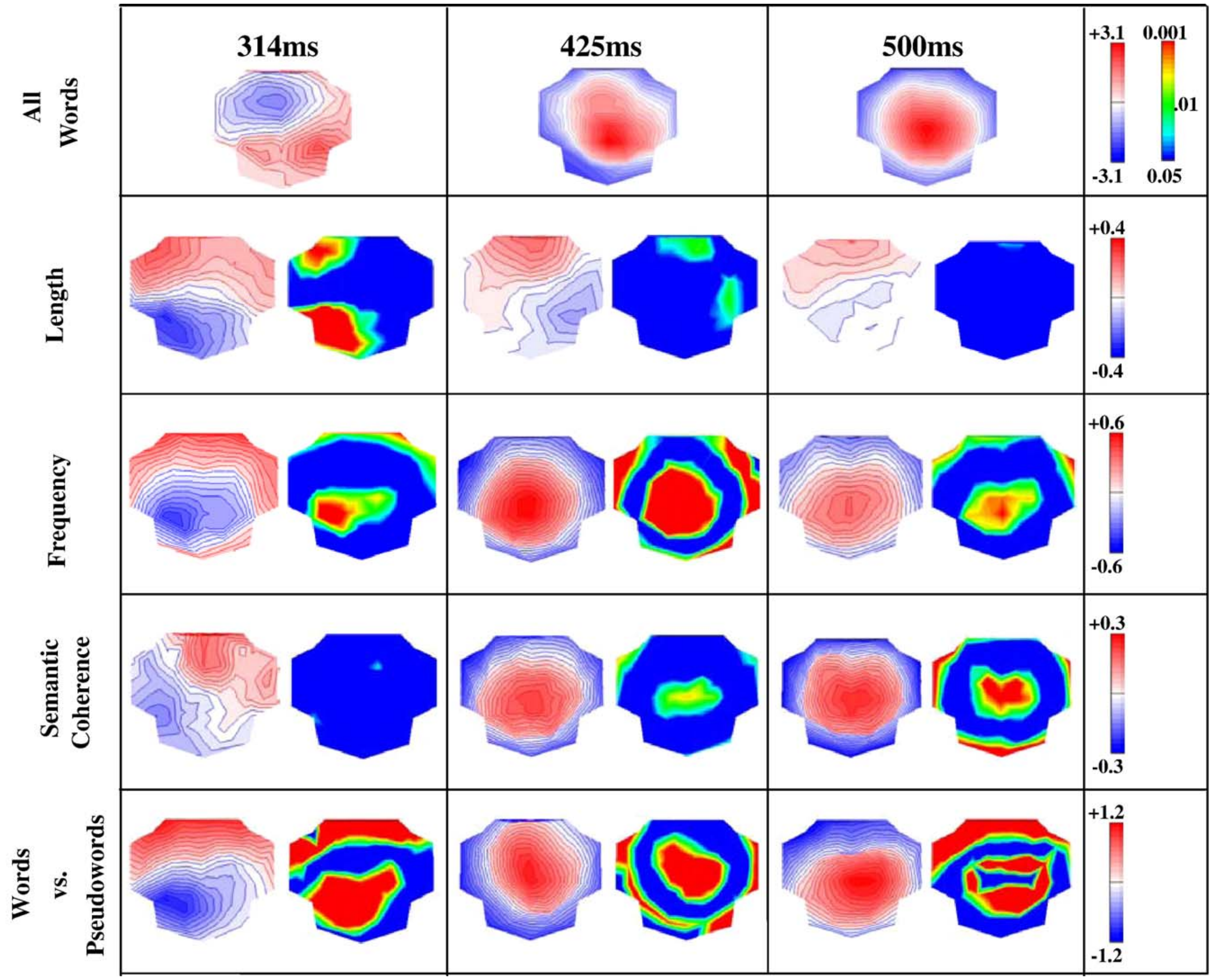

Fig. 6. As in Fig. 4, but for selected time ranges after 250 ms.

gram frequency, Lexical frequency and Semantic coherence, we used analyses of variance (ANOVAs) to look for interactions among these variables and the topography of the ERP or ERRCs, respectively. To do this, we selected 9 electrodes (F7, Fz, F8; T7, Cz, T8; P7, Pz, P8) that captured the most prominent peaks in the topographies presented in Figs. 4 and 6 and grouped these into the factors Gradient (anterior–posterior, 3 levels) and Laterality (left–right, 3 levels). The question addressed by these analyses was whether there are reliably different topographical activation patterns for the psycholinguistic variables, indicating different sets of neural generators for the processes related to the investigated variables.

For the variables Length and Letter n-gram frequency around 90 ms, this analysis revealed a significant interaction Condition-by-Laterality ($F(2,38) = 3.76$, $P < 0.05$, $\varepsilon = 1$) and a marginally significant effect for Condition-by-Gradient ($F(2,38) = 3.27$, $P < 0.06$, $\varepsilon = 0.84$). This indicates that these two variables produce brain responses with different topographies at this latency, possibly suggesting different neuronal generators. No significant interaction including the factor Condition was found for Frequency and Letter n-gram frequency around 110 ms (all $F < 1$). Lexicality and Semantic coherence produced a significant interaction Condition-by-Laterality around 160 ms ($F(2,38) = 11.5$, $P < 0.001$, $\varepsilon = 0.86$). However, the patterns of these variables in Fig. 5 indicate that one topography might be the inverse of the other. We therefore ran the same ANOVA on the same data again, but this time with the topographies for Semantic coherence multiplied by the value −1. There was no significant interaction including the factor Condition in this analysis (all $F < 1.6$, $P > 0.2$). For the time range around 212 ms, we included three variables Length, Frequency and Lexicality in the analysis. This produced interactions Condition-by-Laterality ($F(4,76) = 4.57$, $P < 0.01$, $\varepsilon = 0.81$) and Condition-by-Gradient ($F(4,76) = 11.5$, $P < 0.001$, $\varepsilon = 0.86$) and Condition-by-Gradient-by-Laterality ($F(4,76) = 2.47$, $P < 0.05$, $\varepsilon = 0.56$). Around 314 ms, the factor Condition with three levels Length, Frequency and Lexicality produced an only marginally significant interaction Condition-by-Laterality-by-Gradient ($F(8,152) = 1.93$, $P < 0.1$, $\varepsilon = 0.65$). In the late latency range 400–450 ms, the factor Condition with four levels Length, Frequency, Semantic coherence and Lexicality interacted with both Laterality ($F(6,114) = 3.48$, $P < 0.01$, $\varepsilon = 0.91$) and Gradient ($F(6,114) = 4.81$, $P < 0.001$, $\varepsilon = 0.54$), but only the interaction with Gradient remained after the level Length was removed ($F(4,76) = 3.89$, $P < 0.05$, $\varepsilon = 0.51$). Around 500 ms, Lexicality, Frequency and Semantic coherence were entered as a factor Condition, which resulted in interaction Condition-by-Laterality ($F(4,76) = 3.50$, $P < 0.05$, $\varepsilon = 0.75$), Condition-by-

Gradient ($F(4,76) = 17.74$, $P < 0.001$, $\varepsilon = 0.65$) and Condition-by-Gradient-by-Laterality ($F(8,152) = 2.42$, $P < 0.05$, $\varepsilon = 0.55$).

Source estimation

Using minimum norm techniques, source estimates were obtained for the effects summarised in Fig. 4 and are displayed in Fig. 7. Length effects are confined to posterior brain areas. Lateralisation changes from the right hemisphere at 90 ms to the left at 202 ms, confirming the pattern observed for the ERRCs in Fig. 4. The source estimate for Letter n-gram frequency at 90 ms shows the most prominent peak in a left-temporal area, corresponding to the pattern of the regression coefficients, but also a weaker activation spot at an approximately symmetrical location in the right hemisphere, and a further left-frontal focus with intermediate amplitude. Frequency produces largest activation at 110 ms in a left posterior area, which shifts to more anterior regions in the left inferior temporal cortex at 202 ms, where it is accompanied by activity in an almost symmetrical location in the right hemisphere, and a further central occipital activation spot.

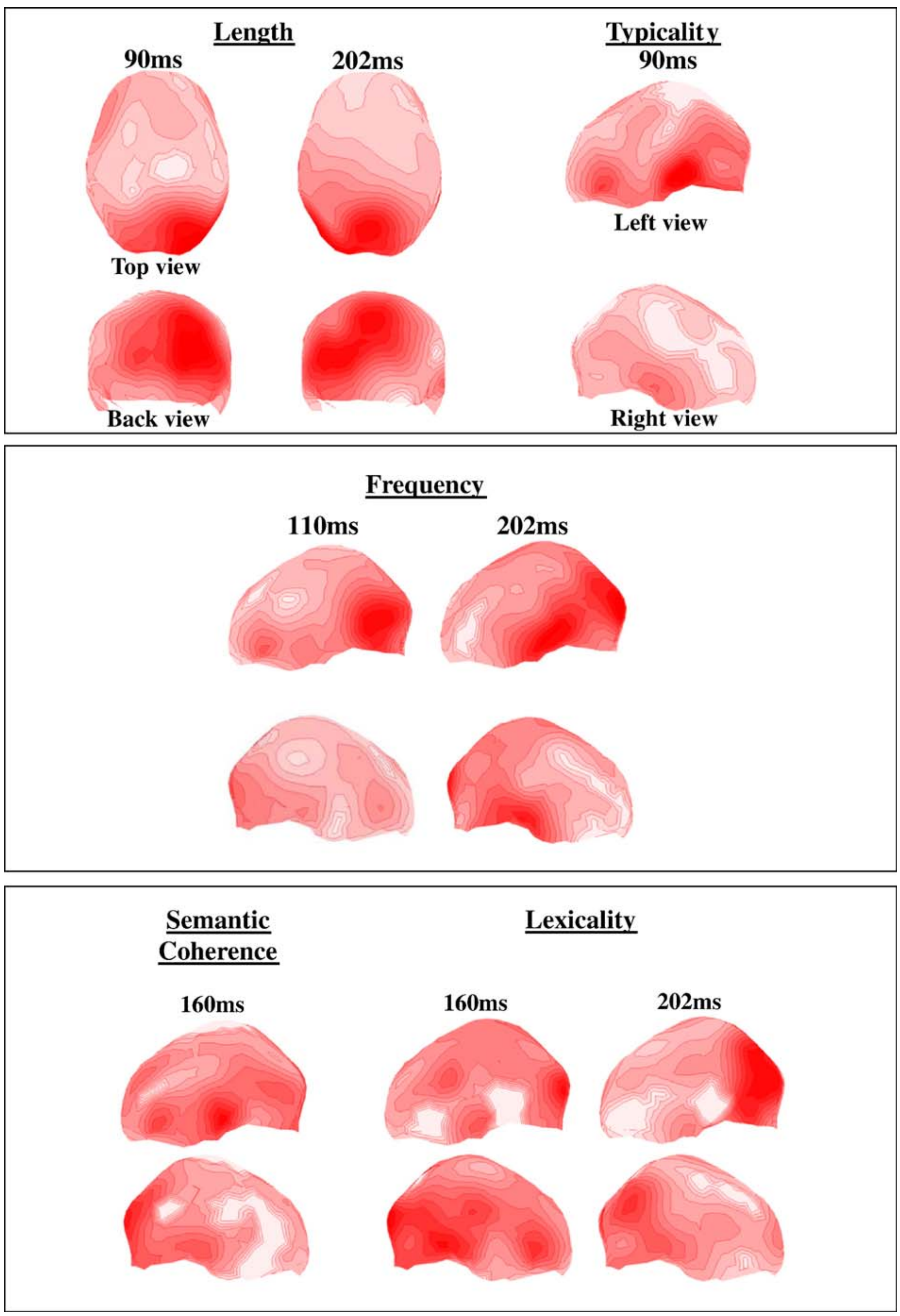

Fig. 7. Minimum norm source estimates for ERPs and ERRCs that showed significant effects in the analysis. Images are grouped into surface variables (Length and N-gram, top frame), Frequency (middle frame), and lexico-semantic variables (LSA and Lexicality, bottom frame). The original source strengths are displayed but thresholded at an SNR of 2. For Length, the brain surface is displayed in top view (top) and back view (bottom), while all others are shown in left and right view (top and bottom, respectively).

The source distribution associated with the Semantic coherence variable at 160 ms is not dominated by any single focus, with peaks occurring in left perisylvian cortex, in a left anterior temporal and a left inferior frontal area and also in a right inferior temporal and a centro-occipital area. This pattern is comparable to that of Lexicality produced at the same latency. At 202 ms, however, the source distribution for Lexicality is characterised by a left parietal activation focus and a weaker one at an almost symmetrical location in the right hemisphere.

Discussion

This study investigated the spatio-temporal effects of several psycholinguistic variables on the human ERP in a lexical decision task in order to monitor the basic processes involved in on-line visual word recognition. Multiple regression was used to gain sensitivity and avoid problems associated with stimulus matching related to classical factorial designs. Our main conclusions are based on statistical analyses performed on ERP amplitudes around peak latencies, but an exhaustive picture of the data is presented for the early latency range up to 250 ms. Distributed source estimates were obtained for significant effects.

Summary of effects in early latency ranges

Word length and Letter n-gram frequency were reflected in the electrophysiological response shortly before 100 ms. The ERP in this latency range has previously been shown to distinguish between written words and objects (Schendan et al., 1998). In our study, longer words and items with lower n-gram frequencies produced larger amplitudes than short words or words with high n-gram frequency, respectively, in accordance with previous results (Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004; Hauk et al., in press). The earliest lexical frequency effect in our study (110 ms) occurred earlier than the Word frequency effects reported by Sereno et al. (1998) (144 ms), Hauk and Pulvermüller (2004) (~160 ms) and Assadollahi and Pulvermüller (2003) (~150 ms), but went in the same direction (high frequency words showing lower amplitudes than low frequency ones) and was lateralised to the language-dominant left hemisphere. Effects of both Lexicality and Semantic coherence, two variables proposed to reflect lexico-semantic properties of words, started around 160 ms. The variables Length, Frequency and Lexicality exhibited effects in parallel around 200 ms. At later time points, between 300 and 500 ms, simultaneous and topographically similar effects were seen for Word length, Lexical frequency, Lexicality and Semantic coherence.

Cascaded processing sequence

The finding that word-form-related variables show the earliest effects might not seem surprising. Logically, some analysis of the visual input must take place before any other information can be retrieved or computed. However, earlier studies on Word length were not able to decide whether the corresponding early effects were due to physical or linguistic stimulus properties (e.g., luminance versus number of letters or syllables) (Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004). The current study, together with that of Hauk et al. (in press), using bigram and trigram frequencies as variables, shows for the first time that processing complex features of the visual word form is reflected in the electrophysiological response around 100 ms after stimulus presentation.

These word-form-related processes can still overlap in time with lexico-semantic processes, that is, the analysis of the orthographic structure of a word does not necessarily have to be completed before semantic information can be activated (Pecher et al., 2005). Cascaded models of word recognition suggest, for example, that at any processing stage part of the available information is fed forward to following processing stages, which in turn can send feed back if the input resembles a familiar pattern, in our case a known word (e.g., McClelland, 1979; Rogers et al., 2004). Evidence for such a model from our data is provided by the early frequency effect around 110 ms that closely follows and partly overlaps with the earlier Length and Letter n-gram frequency effects. Note that, while Letter n-gram frequency describes the familiarity just of letter combinations, the variable Lexical frequency reflects the familiarity of an individual word and its morphologically related forms. The data therefore suggest that features of the visual word form and the word's lexical representations are accessed consecutively, but there is only a minimal delay between the timing of form-based and higher-order effects of Word frequency. Shortly after these early influences, at around 160 ms, ERPs distinguished between whether the input was a familiar word or an unfamiliar pseudoword. This effect of Lexicality coincided with an effect observed in the event-related regression coefficients (ERRCs) of a predictor variable encoding whether words had a consistent meaning across their morphological families (an effect of Semantic coherence). At later stages, around 200 ms and between 300 and 500 ms, the psycholinguistic variables investigated here were reflected simultaneously in the EEG, sometimes even by the same topographies. This pattern of initial serial activation and later parallel processing is consistent with the cascaded processing metaphor.

Semantic coherence

We used our ERRC analysis to investigate effects of Semantic coherence on electrophysiological responses. This analysis showed an early neurophysiological correlate at a point in time where earlier studies had suggested that lexico-semantic information is accessed. Our Semantic coherence variable was still slightly positively correlated with word form and lemma frequency and negatively correlated with cumulative morpheme frequency. However, the fact that the earliest effect of Semantic coherence coincided with that of lexicality and not of frequency indicates that this new variable produced an independent effect. This confirms that semantic information linked to a written word is processed by the brain within the first 200 ms after word onset, a position held by psycholinguistic models for some time but only recently substantiated by neurophysiological research (for a review, see Pulvermüller, 2001). Furthermore, the result suggests that not only the semantic properties of the stimulus word per se come into play at the neurophysiological level at early stages, but also the morphological family of this word, together with the semantic properties of this family. Since the neurophysiological effect relates to Semantic coherence computed at the level of the family, this suggests that members of the family of a stimulus are at least partially activated at the semantic level. We also note again that the effects of the variable Semantic coherence were present together with Lexicality effects at 160 ms, 314 ms and 500 ms but were absent at other time points when Lexicality was reflected (200–250 ms).

Late ERP effects

The largest effects of the variables Lexicality, Semantic coherence and Frequency occurred around 425 ms and 500 ms, i.e., clearly after the brain has already distinguished words from pseudowords. Furthermore, they are close to the time range in which subjects make their responses (average RT for words: 571 ms). This demonstrates the strength of ERP methodology to reveal effects of psycholinguistic variables in different latency ranges and therefore at different processing stages. We would like to argue that the early effects reported in this study reflect the initial phase of visual word recognition, including access and selection of lexical and semantic information, while the later effects are related to post-lexical processing.

In our study, pseudowords produced more negative potentials at central or centro-parietal electrode sites around 400–500 ms, similar to previous studies (Rugg, 1990; Kutas and Federmeier, 2000; Friederici, 2004). The topographies of effects in this time range for the different variables appear very similar, in particular, similar to the average topography of all words. This might reflect activity in a large-scale network that is not specific to any of the variables. We therefore suggest that the corresponding processes are not the primitive operations of visual word recognition but rather reflect the forming of associations, decision making or response planning, preparation and execution. Several quite different lexical properties are reflected by similar topographical patterns of the EEG between 300 and 500 ms, which indicates that these late components are not very specific to the type of linguistic information being processed.

Alternative views: Pylkkanen and Sereno

Much of recent literature based on MEG data has focussed on brain responses occurring later than 250 ms (Embick et al., 2001; Pylkkanen and Marantz, 2003; Pylkkanen et al., 2002; Stockall et al., 2004). These authors claim that MEG is able to resolve the processes underlying the established N400 component in ERP research in more detail and argue that processing of lexical information is reflected for the first time around 350 ms (Pylkkanen and Marantz, 2003). Other authors, however, have pointed out that both behavioural and ERP evidence suggest that single word recognition is accomplished within 250 ms after stimulus onset (Pulvermüller, 1999; Sereno and Rayner, 2000). A number of EEG and MEG studies provide evidence for this view (Pulvermüller et al., 1995; Sereno et al., 1998, 2003; Martin-Loeches et al., 1999; Hinojosa et al., 2001; Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004). The early effects are usually topographically specific, short-lived and therefore much more vulnerable than the widely distributed long-lasting late ones. Therefore, the reason for the absence of early effects in some MEG and EEG studies may be related to methodological features of the studies (for discussion, see Pulvermüller, 1999).

Based on eye-tracking and ERP results, Sereno and Rayner (2003) and Sereno et al. (1998) suggested a "time-line" of word recognition. Their time-line started with a difference between words and pseudowords reflected in the ERP at 112 ms followed by a Word frequency effect. This finding is in contrast with ours, where the earliest lexicality effect occurs around 160 ms, and is preceded by effects of surface form variables Length and n-gram frequency, as well as Lexical frequency. The exact timing of the relevant processes might depend on the stimulus material and tasks employed and certainly warrants further research. In general, however, our results and those of Sereno et al. (2003) and Sereno and Rayner (2003) support the view that lexico-semantic information is already retrieved within the first 150 ms after word onset.

Source estimation results

Source estimation suggested early modulation of occipital brain areas by Word length around 100 ms. This supports the view of Assadollahi and Pulvermüller (2003) and Hauk and Pulvermüller (2004) that this early effect mainly reflects "physical" properties of the stimuli. The source distribution at this latency was right-lateralised, which is consistent with the finding that Word length effects on behaviour are largest for words presented to the left visual hemifield (Ellis, 2004). A left infero-temporal brain focus was activated for Letter n-gram frequency around the same latency. An area in left fusiform gyrus (LFG) has consistently been described in fMRI studies on visual word recognition and has been labelled the "Visual Word Form Area" (McCandliss et al., 2003; Cohen et al., 2004; but see Price and Devlin, 2004). Activity in the LFG has been associated with the computation of an abstract visual word form from the visual input, performed by a neural system that was "tuned" for this purpose by learning and exposure to written language (McCandliss et al., 2003; Cohen et al., 2004). However, both an ERP study (Cohen et al., 2000) and a recent MEG study (Pammer et al., 2004) found activity associated with LFG only around 200 ms after word onset, which we suggest is too late to be likely to reflect involvement in early word form processing. Our study found an effect for Letter n-gram frequency that is consistent with a source in the LFG already around 100 ms, which is more realistic with respect to the timing of the corresponding process. This result is further confirmed by a recent ERP study on a related topic (Hauk et al., in press).

We also observed that Word frequency significantly modulated activity in left-lateralised regions of posterior temporal cortex. The source responsible for this effect appears to be posterior and superior to the source just described for Letter n-gram frequency, although post-hoc ANOVA on ERP topography did not reveal a significant interaction between these variables at that latency. One possible explanation for this pattern is that there is a single brain region that is modulated by both Word frequency and bi/trigram frequencies. Alternatively, two distinct sources might have been obscured in the ERRC analysis due to the lower spatial resolution of the ERRC surface signal compared to derived source estimates or due to large variation in the orientation of the sources across subjects. A similar argument was brought forward in a comparable situation by Hauk and Pulvermüller (2004). For example, this activation for Frequency might correspond to an area around the angular gyrus that has been found to be involved in both word form and semantic processing (Price, 2000). In either case, this activation could reflect early processing in perisylvian areas that mediates or interacts between the form analysis and the lexico-semantic system. A smaller peak of activation was also present in a left inferior frontal area, where a previous fMRI study found an effect of Word frequency (Fiebach et al., 2002).

In response to lexico-semantic variables (Lexicality in ERPs, Semantic coherence in ERRCs), we observed a widely distributed network to be modulated by these variables at around 160 ms. This network includes left perisylvian sources in inferior frontal and temporal cortices. This is consistent with the activation of anatomically distributed cell assemblies in left perisylvian cortex, which have been proposed to provide the neurobiological basis of the semantic processing of words (Pulvermüller, 1999). Around 200 ms, several variables produce clearly left-lateralised source constellations, sometimes in additional areas to those in which earlier activations were observed. These additional areas differed between the various predictor variables. This may suggest an interactive processing of different information types in different areas in visual word recognition. Occipital cortex (modulated by Length, possibly related to processing of visual information), left inferior temporal cortex (modulated by Frequency, possibly reflecting the mediation between the word form and lexico-semantic information) and parietal cortex (modulated by semantic word properties) may thus interact with perisylvian language areas in processing information about visually presented words.

Summary and conclusion

In conclusion, we have derived event-related regression coefficients from linear regression analysis of EEG data in order to reveal the time course of visual word recognition. We carefully chose several psycholinguistic variables modulating processes of word recognition. Each of these variables correlated with specific effects in the EEG signal and showed a distinct time course. We were able to separate EEG signatures of early visual analysis of the word form from those of the retrieval of lexico-semantic information. Source estimation results suggest that an area in left inferior temporal cortex processes information about the surface structure of a word within the first 100 ms after stimulus onset. Semantic variables instead modulate a widely distributed cortical network shortly after 150 ms. The parallel activation of several distinct brain regions, modulated by different variables, suggests an integration of different kinds of information at later stages (>200 ms). The proposed linear regression approach may be useful to study any of these processes separately in more detail, and the results of our exhaustive analysis can serve as a basis for further electrophysiological research into word recognition.

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