

www.elsevier.com/locate/ynimg NeuroImage 42 (2008) 423-436

# The early context effect reflects activity in the temporo-prefrontal semantic system: Evidence from electrical neuroimaging of abstract and concrete word reading

Miranka Wirth,<sup>a</sup> Helge Horn,<sup>a,\*</sup> Thomas Koenig,<sup>a</sup> Annick Razafimandimby,<sup>c</sup> Maria Stein,<sup>a</sup> Thomas Mueller,<sup>a</sup> Andrea Federspiel,<sup>a</sup> Beat Meier,<sup>b</sup> Thomas Dierks,<sup>a</sup> and Werner Strik<sup>a</sup>

<sup>a</sup>University Hospital of Psychiatry, Bern, Switzerland

<sup>b</sup>University of Bern, Institute of Psychology, Bern, Switzerland

<sup>c</sup>Groupe d'Imagerie Neurofonctionnelle, UMR 6194, CNRS, CEA, Universities of Caen and Paris 5, Caen, France

Received 8 November 2007; revised 17 March 2008; accepted 19 March 2008 Available online 7 April 2008

Spatial and temporal characteristics of lexico-semantic retrieval are frequently examined with semantic context (i.e., priming) paradigms. These paradigms measure context (i.e., priming) effects in word processing evoked by semantically related context. Besides the well-known attentiondependent N400 context effect (>250 ms), recent studies demonstrate early automatic context effects in the P1-N1 time period (<200 ms). However, in visual word presentation the semantic origin of these early effects remains debated. This study examined spatio-temporal activation dynamics of the early context effect as well as the modulation of the effect by differences in structure and accessibility of verbal semantics existent in abstract and concrete words. The early context effect was measured in visually displayed words that followed semantically related single-word context. Spatial and temporal aspects of the effect were analyzed by applying topographic and source analyses on the word-triggered Event Related Potentials. The early context effect was enhanced in abstract compared to concrete words as indicated by a difference in the occurrence of P1-N1 transition map and a corresponding topographic dissimilarity (116-140 ms). This concretenessdependent modulation demonstrates the sensitivity of the early context effect to structural differences in verbal semantics. Furthermore, the topographic difference was explained by enhanced activation in the left inferior prefrontal cortex for related compared to unrelated words in addition to temporo-parietal generators recruited in both conditions. The result suggests automatic feedforward processing of context-related information in temporo-prefrontal brain regions critical to semantic analysis. Taken together our findings show that the early context effect reflects activation processes in verbal semantic memory. © 2008 Elsevier Inc. All rights reserved.

-

*Keywords:* Semantic memory; Language; Semantic priming; Inferior frontal gyrus; Temporal cortex; Concreteness; N400

\* Corresponding author. University Hospital of Psychiatry, Murtenstrasse

21, CH-3010 Bern, Switzerland. Fax: +41 31 930 9961.

*E-mail address:* horn@puk.unibe.ch (H. Horn). Available online on ScienceDirect (www.sciencedirect.com).

1053-8119/\$ - see front matter  ${\ensuremath{\mathbb C}}$  2008 Elsevier Inc. All rights reserved. doi:10.1016/j.neuroimage.2008.03.045

# Introduction

Research questions of when, where and how semantic information is retrieved during word recognition are frequently addressed by the neurophysiological examination of semantic context (i.e., priming, congruity) effects in healthy subjects (see Kutas and Federmeier, 2000 for review) and patient populations (e.g., Giffard et al., 2001; Kuperberg et al., 2007; Moss and Tyler, 1995). Such context effects refer to modulations in the processing of a word evoked by prior presentation of semantically related context and have been identified by behavioural (response time and accuracy, Meyer and Schvaneveldt, 1971), hemodynamic (Giesbrecht et al., 2004; Kotz et al., 2002; Matsumoto et al., 2005; Rossell et al., 2003), Event Related Potential (ERP) and magnetencephalographic (MEG) measurements (Kutas and Federmeier, 2000; Pylkkanen and Marantz, 2003, respectively).

Lexico-semantic context effects arise in the verbal–linguistic semantic system. This network mainly consists of left-lateralized temporal, parietal and inferior–prefrontal brain regions (Jobard et al., 2003; Price, 2000; Vigneau et al., 2006). Within this cortical network neural activity is modulated in response to context exposure as previously shown by neuroimaging (Copland et al., 2007; Giesbrecht et al., 2004; Kotz et al., 2002; Matsumoto et al., 2005; Mummery et al., 1999; Rissman et al., 2003; Rossell et al., 2003) and ERP/MEG localization studies (Frishkoff et al., 2004; Halgren et al., 1994; Helenius et al., 1998; Marinkovic et al., 2003).

High-temporal resolution ERP/MEG methods further indicate that semantic representations can be accessed during early (<200 ms, e.g. Hauk et al., 2006; Ortigue et al., 2004; Pulvermuller et al., 2001; Skrandies, 1998; Sysoeva et al., 2007) and late (~250–600 ms, Kutas and Federmeier, 2000; Salmelin and Kujala, 2006) time intervals following word presentation. In the same time ranges, studies report electro-/magneto-physiological context

effects which are presumably linked to functionally-distinct retrieval processes inherent to long-term memory, that is, controlled and automatic retrieval functions (Miyashita, 2004). The well-studied electrophysiological probe of late semantic processing is the N400 context effect. This ERP modulation describes the characteristic N400 amplitude increase starting at around 250 ms in words that pursue unrelated compared to related context (Kutas and Federmeier, 2000; Kutas and Hillyard, 1980). Because the N400 context effect is altered by the amount of attention directed to semantics (Bentin et al., 1993; Chwilla et al., 1995; McCarthy and Nobre, 1993), it is mainly thought to index controlled (i.e., attention-dependent, explicit) semantic processes (see Kutas and Federmeier, 2000, for review). In addition, recent studies demonstrate early (~ 120-190 ms) electro-/ magneto-physiological context effects in seen (Michel et al., 2004b; Rossell et al., 2003; Sereno et al., 2003; Wirth et al., 2007) and spoken (Shtyrov and Pulvermuller, 2007) words applying active and passive (i.e., no response) paradigms. The early context effects are not attributable to a premature onset of the N400 effect (Michel et al., 2004b; Sereno et al., 2003). Moreover, these early ERP modulations are unaffected by group differences in controlled semantic processes (Wirth et al., 2007) and arise independent of focussed attention (Shtyrov and Pulvermuller, 2007). Thus, conclusions can be drawn that early context effects emerge from automatic (i.e., attention-independent, implicit) processes that apparently underlie the initial semantic access.

However, in reading words, doubt is cast on the semantic origin of early context effects for two reasons: First, prior ERP studies (Michel et al., 2004b; Wirth et al., 2007) did not address the influence of top– down (expectancy generation, Neely, 1977, 1991) and bottom–up intralexical processing that might contribute to the generation of context effects (Fodor, 1983). Further, in acoustic word presentation, early context integration was shown to engage the temporo-prefrontal semantic retrieval system starting at around 115ms post word onset (Shtyrov and Pulvermuller, 2007). For visually displayed words, however, the neurophysiologic mechanisms underlying the early effect lack detailed examination.

The present ERP study therefore aims to examine the semantic origin of early context effects in visually presented words using two approaches: We trace spatial and temporal activation dynamics of the effects by the application of electrical neuroimaging, i.e., a stepwise procedure of topographic and source analysis techniques (Murray et al., 2004 for similar approach). At the same time, we assess the sensitivity of the early context effect to differences in structure and accessibility of verbal semantics. Thus, electrical neuroimaging is conducted in abstract (e.g., "motive") and concrete (e.g., "frog") words. As previously shown, these word categories exhibit dissimilar context effects in the N400 (Holcomb et al., 1999; West and Holcomb, 2000) and response measurements. This has been demonstrated in a series of behavioural studies where abstract words yielded stronger effects of related vs. unrelated context exposure compared to concrete words (Schwanenflugel et al., 1988; Schwanenflugel and Shoben, 1983; Schwanenflugel and Stowe, 1989). Notably, these concreteness effects are attributed to variations in the structure and hence accessibility of contextual representations stored in the common verbal semantic system (Brandsford and McCarrell, 1974; Kieras, 1978) existing beyond dissimilarities in non-verbal semantics (Paivio, 1971, 1986, 1991; see Kounios and Holcomb, 1994; Swaab et al., 2002 for empirical support).

We hence reason that if the early context effect reflects bottomup retrieval of verbal semantics, neural responses in the leftlateralized temporo-parietal and possibly inferior prefrontal brain regions should be altered in related compared to unrelated words. Secondly, we anticipate that word-concreteness will modulate the early context effect due to existing differences in verbal semantic representations between abstract and concrete words. The expected localization and concreteness-dependent modulation will provide evidence for the semantic foundation of the early context effect.

The current study employs a single-word context paradigm consisting of abstract and concrete words. According to the aims of the study, we restrict the ERP analysis to the comparison of context effects in abstract and concrete words. Topographic and source analysis methods serve to elucidate the neurophysiologic mechanisms underlying obtained waveform changes. In contrast to the traditional waveform analysis, topographic methods are free of reference choice and simultaneously include the information measured at all electrodes. Moreover, strength-independent topographic testing detects changes in the spatial distribution of the electric field potential and hence the neural generator configuration, irrespective of the electric field strength. Thus, context effects are measured in the temporal occurrence of topographically-defined ERP components of interest (Michel et al., 2004b; Wirth et al., 2007) identified on the basis of scalp-wide transient topographic patterns. These formerly termed microstates (Lehmann et al., 1987; see Michel et al., 2001 for review) are proposed to represent the electrophysiological correlate of cortical metatability (Friston, 1997), a term that describes the functional synchronization of distributed local networks into distinct transient large-scale networks (e.g., Bressler and Kelso, 2001; Fingelkurts and Fingelkurts, 2004; Varela et al., 2001). The microstate-based ERP analysis thus supplements neuroimaging studies by providing a window into spatio-temporal dynamics of language-evoked large-scale network activity (e.g., Brandeis et al., 1994; Khateb et al., 2003; Stein et al., 2006).

#### Materials and methods

# Subjects

Twenty-two paid subjects participated in the study. They gave their written informed consent to the procedure, which was approved by the Ethics committee of the Canton of Bern. All participants were right handed (Oldfield, 1971), had normal or corrected to normal vision and reported they were free of medication or drugs. Two data sets were rejected because of defective electroencephalogram (EEG) recordings. In the final set, the data of 20 (10 women) participants (mean<sub>age</sub>=24.6, SD<sub>age</sub>=2.6) were included. The same subject group was presented in an earlier study (Wirth et al., 2007).

# Stimuli

The stimulus list consisted of 180 German noun-noun combinations. (It should be noted that each word only appeared once throughout the experiment.) The first word will be referred to as the 'index word'; the second word as the 'final word'. The combinations included 90 abstract and 90 concrete word pairs, which varied in the strength of relatedness, i.e., semantically related, indirectly related and unrelated. For indirectly related words, the noun-noun sequence was semantically related via an intermediate node (e.g., Tiger-Lion, Stripe=intermediate node). Each of the two sets of 90 abstract and 90 concrete words contained 30 related, 30 indirectly related and 30 unrelated word pairs. The indirectly related word pairs, however, served only as filler words, the reason for which is given below.

Special care was taken in the development of the stimulus material: Abstract and concrete nouns were selected from the word lists published in Hager and Hasselhorn (1994), Weisbrod et al. (1999) and Baschek et al. (1977) or were translated from the MRC Psycholinguistic database (Coltheart, 1981). Words were combined with the aim of maximizing differences in semantic association strength between related and unrelated conditions within each word category (see Weisbrod et al., 1999, for a similar procedure). The word pairs were rated by 60 psychology students of the University of Bern on a scale from 1 to 5 (1=not semantically assciated; 5=very strongly semantically associated). This procedure has been described in a previous study (Wirth et al., 2007). The following rating values were computed for the concrete conditions: unrelated word pairs were classified as semantically low associated (Co/UR: Mean [M]=1.1, SD=0.1), related word pairs as highly associated (Co/R: M=4.5, SD=0.2) and indirectly related word pairs as at an intermediate level of association (M=2.9, SD=0.8). Comparable rating values were obtained for the abstract word conditions: unrelated (Ab/UR: mean=1.6, SD=0.2), related (Ab/R: M=4.4, SD=0.2) and indirectly related (M=2.9, SD=0.4) word pairs.

The abstract-concrete word categorization was further validated by rating all words for concreteness (1), imageability (2) and semantic association strength (3). Definition and rating procedures were taken from the publication of Baschek and colleagues (Baschek et al., 1977). Each of the dimensions was assessed in an independent group of healthy subjects (each with 16 subjects) all of whom did not participate in the EEG experiment. The following results were obtained: (1) Concreteness ratings were conducted on a 7-point scale (1: very abstract; 7: very concrete). Concrete words were defined as words that characterize something material and represent an actual substance or thing; words referring to something considered other than material objects were classified as abstract. As expected, concrete words obtained significantly higher ratings than abstract words (concrete: mean=6.5, SD=0.6, abstract: mean=2.6, SD= 1.0, P < 0.0001, unpaired *t*-test). (2) Imageability of the words was established from ratings on a 7-point scale ranging from 1 to 7 using standardized instructions. Imageability was defined on how difficult or easy it was to form perceptual images of the words (1: very difficult to form images; 7: very easy to form images). The mean imageability rating was 6.7 (SD=0.5) for concrete and 3.1 (SD=1.2) for abstract words (P < 0.0001, unpaired *t*-test). (3) The strength of semantic association was defined whether or not a given word evokes few or many associations (1: low semantic association strength; 7: high semantic association strength). The semantic association strength was 4.6 (SD=0.7) for concrete words and 3.6 (SD=1.0) for abstract words (P < 0.0001, unpaired *t*-test). These rating procedures validated the word categorization (abstract/ concrete). Furthermore concrete words were confirmed to be highly imageable and associated with more semantic context.

The index and final words critical to data analysis were further matched for word brightness, word frequency and word length (selected values are reported below with mean/standard deviation) across the 4 experimental conditions, concrete/related (Co/R), concrete/unrelated (Co/UR), abstract/related (Ab/R), abstract/unrelated (Ab/UR). Word brightness values were obtained as following: First, the brightness-weighted sum of (white and grey) pixels defining each letter of the Courier New Font was extracted. Next, the letter-specific count was summarized for each word. Written words frequencies were extracted from the Leipzig Wortschatz Datenbank (http://www.wortschatz.uni-leipzig.de) where logarithmic word frequency classes range from 0 (= high frequency) to 25 (= low

frequency). The following mean word frequencies values were measured: index word (Co/R: 11.7/2.4, Co/UR: 12.7/ 2.7, Ab/R: 10.5/2.1, Ab/UR: 11.4/2.3) and final word (Co/R: 12.0/2.5, Co/UR: 13.3/1.5, Ab/R: 10.7/1.4, Ab/UR: 11.2/2.0). Mean word lengths are given below: index word (Co/R: 5.3/1.0, Co/UR: 5.7/1.2, Ab/R: 5.8/ 1.5, Ab/UR: 6.1/1.7), final word (Co/R: 5.8/1.3, Co/UR: 6.0/1.5, Ab/R: 6.3/1.4, Ab/UR: 6.0/1.4). Importantly, ANOVAs on the word measurements rendered the critical interactions of the factors word position (index/final), concreteness (abstract/concrete) and context (related/unrelated) insignificant (all P's  $\geq 0.4$ ). Further, we tested potential effects in the difference data for each noun-noun combination: Notably, there were no significant interactions (all P's  $\geq$ 0.1) between the factors concreteness and context in the ANOVAs in these differences for word frequency, length and brightness values. In addition, the difference in brightness values was calculated for each letter position within each word pair and subjected to multivariate ANOVAs; the interactions between the factors concreteness and context were insignificant (all P's  $\geq 0.1$ ) at all letter positions (1-9).

# Procedure

A passive (i.e., no response) reading task was applied. Each trial consisted of the sequential presentation of index and final word (white on black in the centre of the computer screen); see Fig. 1A. The index word was presented for 935ms, immediately followed by the final word that was also shown for 935ms. The word pairs were presented in randomized order that was held contestant across subjects, each trial was separated by a fixation cross which remained for 1870 ms on the screen. Subjects were instructed to uphold fixation during the inter-stimulus interval and read the presented words silent and attentively. To maintain

# A: Experimental task



Fig. 1. Experimental task. (A) Schematic illustration of the word pair reading task in which final words were preceded by related or unrelated index words. (B) Displays of the  $2 \times 2$  factorial design. Word examples for the factorial combination of context (related/unrelated) and concreteness (concrete/ abstract) are provided.

attention, 30 blue squares were randomly mixed between the word pairs and subjects were asked to press a button when the square appeared. Top-down intralexical processing (e.g., expectancy generation, Neely et al., 1989; Neely, 1991) was minimized by the following prerequisites: Subjects were kept uninformed regarding the experimental conditions. Previous findings further indicate that expectancy is not active in the absence of external task demands (Brown et al., 2000). Moreover, the relatedness proportion, which may encourage expectancy generation (e.g., DeGroot, 1984; Neely et al., 1989), was reduced by adding the abovementioned indirectly related filler word pairs. (Indirectly related noun-noun combinations do not allow the strategic prediction of the final word.) Together with the squares, the indirectly related word pairs were discarded from the analysis procedure because they did not constitute a homogenous stimulus category. The present study thus employed a two-by-two factorial design with the factors context (related/unrelated) and concreteness (abstract/concrete); see Fig. 1B.

# EEG recording

The EEG measurement was conducted at the EEG lab of the Department of Psychiatric Neurophysiology, University Hospital of Psychiatry in Bern. The scalp EEG was recorded from 74 silver chloride electrodes mounted in an electrode cap in the extended 10-20 system. Cz served as recording reference; a ground electrode was placed at the lateral neck. Two additional electrodes recorded vertical eye movements. All impedances were kept below 25kOhms. and digitized at 250 Hz sampling rate. Offline, the EEG was corrected for eve-movement artefacts by removing those components identified by Independent Component Analysis (ICA, Tran et al., 2004) which clearly accounted for vertical and horizontal eye movements. The EEG data was then recalculated to common average reference. Epochs containing further artefacts (i.e., epochs with voltage exceeding  $+/-100\mu V$  or below  $0.50\mu V$ for 100 ms at any electrode site) were discarded in a semiautomatic artefact inspection. Artefact electrodes were replaced by linear interpolation between their neighbouring electrodes. This was measured as a total of 11 electrodes of the 74 times 20 traces. The EEG data was then band-pass filtered at 1.0Hz (12db/oct)-12.0Hz (24db/oct); surface EMG activity may go down to 12-15Hz (Gotman et al., 1981; O'Donnell et al., 1974). Finally the data was segmented into epochs starting from the onset of the final word to 600 ms post word onset. This specific point in time was set according to the temporal presence of the topographically-defined ERP components of interest. Individual ERPs were computed for the 4 experimental conditions (CoR, CoUR, AbR, AbUR, see above) with an average number of 28 trials per conditions over all subjetcs, a maximum of 30 and a minimum of 22 trials. Finally, the grand-mean ERPs to final words were calculated for each condition.

# Data analysis

The present study aimed to elucidate and compare spatiotemporal activation dynamics of the early context effect (i.e., the difference between related and unrelated conditions) in the ERP responses to abstract and concrete words. However, for completion we also analyzed the N400 context effect. The stepwise analysis procedure was conducted in particular time intervals centred around the temporal presence of topographically-defined ERP components of interest, namely the P1, N1 and N400, determined from prior ERP studies (Michel et al., 2004b; Sereno et al., 2003; Wirth et al., 2007). First, the data were analyzed with global ERP waveforms in order to outline concreteness-evoked modulations of context effects during the time intervals of interest. To elucidate the neurophysiologic mechanisms underlying waveform changes, a topographic microstate analysis was conducted which was further analyzed by means of the topographic fitting procedure and comparisons of map topography. Finally early topographic effects were estimated with the local autoregressive average inverse solution (LAURA, Grave de Peralta et al., 2001). Electrical neuroimaging has proved a valuable tool in recent ERP studies (e.g., De Santis et al., 2007; Murray et al., 2006; Ortigue et al., 2004) and will be described in the order of application.

# Global waveform analysis

Significant changes in the measured ERP responses were identified by computing data-point wise *t*-tests between conditions of interest. The method detects a significant ERP modulation between two experimental conditions at any given moment and each measured electrode site (in our case 74 electrodes). Thus the method specifies the temporal and spatial location of ERP modulations on the scalp surface. In practice we compared the context effects in abstract and concrete words as measured by the difference data sets between related and unrelated condition. Note, only changes at those electrodes were considered significant that exceeded the alpha criterion (p<0.05) for more than 5 consecutive data points (see Murray et al., 2004 for similar approach).

#### Descriptive microstate analysis of the grand-mean ERPs

The grand-mean ERPs of each experimental condition were clustered into periods of similar topography (Pascual-Marqui et al., 1995). These periods have been referred to as microstates (Lehmann et al., 1987). This method is based on the observation that scalp topographies do not change continuously but remain temporarily stable forming transient topographic states. As such the method constitutes a data-driven and objective manner of defining the ERP components according to their topographic pattern, thus including all measured electrodes. In detail, a spatial k-mean cluster analysis was performed on all the ERP topographies observed in any of the 4 normalized grand-mean ERPs. The procedure extracted the most dominant scalp topographies over time, here referred to as microstate maps. The optimal number of microstate maps was determined as the second minimum according to the modified cross-validation criterion (Pascual-Marqui et al., 1995). Then, the moment-bymoment topographies of the 4 grand-mean ERPs were assigned to the best-fitting microstate map based on spatial correlation. This assignment was smoothed over time (Pascual-Marqui et al., 1995) and a temporal criterion was introduced such that a microstate map had to be observed for at least 3 consecutive data points. The microstate assignment of the 4 experimental conditions was plotted and compared.

### Statistical validation of the microstate assignment

Changes in the assignment of microstate maps across experimental conditions were tested with the topographic fitting procedure in the individual ERPs (Brandeis et al., 1992; Michel et al., 1999; Michel et al., 2001). This topographic fitting procedure determines, within a pre-defined time-window (i.e., the time interval of fit), for how many time frames a given grand-mean microstate map fits the individual ERP data better than a set of other microstate maps. We selected all microstate maps occurring in any of the 4 grand-mean



Fig. 2. Average-referenced ERP waveforms for abstract (upper panel) and concrete (lower panel) final words. (A) ERP signals at 74 scalp electrodes for related (bold line) and unrelated (thin line) conditions. (B) Selected ERP curves at left frontal (F7) and parietal (Pz) electrode sites for related (black line) and unrelated (grey line) words. Noticeable, amplitude differences in the P1–N1 time period (around 100–200 ms) and around 400–600 ms in the N400 time interval are stronger pronounced in abstract compared to concrete words.

ERPs during the time intervals of context effects approximately outlined in the global waveform analysis. During these time periods, all individual ERP topographies were assigned moment by moment to the selected grand-mean microstate maps based on a best-fit criterion. For each subject, experimental condition and microstate map of interest, the total count of time points assigned to the microstate map was extracted from the ERPs. This count will be referred to as map occurrence and was measured in timeframes. Note, in the respective figures the count was transferred to ms (i.e., one timeframe corresponds to 4 ms at 250 Hz sampling rate). The values were subjected to repeated-measurement ANOVAs with concreteness (abstract/concrete) and context (related/unrelated) as within-subject factors. The factor sex (women/men) was included in the ANOVAs as between-subject factor because the data set was used in prior study addressing sex differences in controlled semantic processing (Wirth et al., 2007). Only Huynh-Feldt corrected ANOVA results are reported.

Post-hoc paired one-tailed t-tests were used to further explore the obtained interactions mainly for the early context effect. Furthermore, context effects were measured by subtracting the map occurrences between related and unrelated words and compared with paired one-tailed t-tests between the abstract and concrete conditions across subjects. (Note that the presence of a significantly different context effect for concrete and abstract words is expected to vield a significant interaction of concreteness and relatedness.) For the interpretation of map occurrences, it is important to note that due to topographic variability, a defined time-window in the ERP of a given subject and experimental condition is not continuously and exclusively labelled with one map. Nonetheless the fitting procedure determines whether a microstate map occurs more often in one experimental condition compared to another. The measured occurrence of a specific microstate map is interpreted to reflect synchronization of neural activation in a functional generator network (Lehmann et al., 1987).

The topographic fitting procedure is a rather global method that is conducted in rather extended time frames. In order to identify the exact onset and offset data points of significant map occurrence differences (in ms following word onset), topographic effects were further assessed with a data-point wise randomization-based topographic testing procedure (Kondakor et al., 1995; Strik et al., 1998). (Note, consistent differences in map assignment should coincide with consistent topographic differences.) This test is based on non-parametric permutation statistics and compares maps that are normalized to their Global Field Power (GFP, Lehmann and Skrandies, 1980) by computing the exact probability that a global topographic difference between experimental conditions is compatible with the null-hypothesis. Only those topographic differences that lasted for  $\geq$  3 consecutive time frames are reported.

In practice, the common one-way factorial TANOVA implemented in the LORETA software (Pascual-Marqui et al., 1999) was applied in the time intervals of fit (as defined above) comparing the experimental conditions of interest, here the unrelated and related conditions within abstract and concrete words. In addition, a twoby-two factorial TANOVA was used to assess unexpected topographic dissimilarities across all experimental conditions. The twoby-two factorial TANOVA is an extension of the existing one-way factorial TANOVA (Kondakor et al., 1995; Strik et al., 1998) and is here described in detail: Assume that electric or magnetic field topographies have been sampled across subjects and several levels of a factor of interest. These topographies can be at a specific time point, an average over some time span or otherwise extracted from the data. To determine the factor's significance, the null-hypothesis that one has to test is whether the mean topography across subjects of each level of the factor (here called level-mean topography) was potentially the same for all levels and thus identical to the grandmean topography across all levels and subjects. Precisely, one would like to know the probability that the observed differences between the level-mean topographies and the overall grand-mean topography could have been observed by chance. This problem can be simplified by first subtracting the overall grand-mean topography from the topographies of each subject at each level. Once this has been done, the null-hypothesis to be tested is how likely the residual level-mean topographies have occurred by chance. The test-statistics to be employed here should thus measure the strength



Fig. 3. Topographic map series of the average-referenced ERP data for the four experimental conditions from 50 to 550 ms every 50 ms. The three wellestablished ERP components of interest, the P1, N1 and N400, are visible (for description see text).

of the remaining level-mean topographies of all levels. A straightforward implementation of such a test-statistics is the sum of the GFP values across these grand-means of each level. The larger this sum of GFP values, the more different some or all of the levelmean topographies were from the overall grand-mean. (Note that for the case of just two conditions, it can be shown that this teststatistics is equivalent to the dissimilarity index (Lehmann, 1987) used in the earlier TANOVA implementations: This dissimilarity was defined as the GFP of the difference topography, which is equivalent to the sum of the GFP of the topographies of the two conditions after subtraction of the mean topographies of both conditions).

Given this test-statistics, the probability of the null-hypothesis can be estimated using the standard randomization procedure: First, the test-statistics is computed in the original dataset. Then, in each subject, the level assignments are randomly shuffled, and the test-statistics is computed based on the randomized data. By repeating the randomization and computation of the test-statistics a large number of times, one obtains a distribution of the teststatistics that is based on the null-hypothesis. The probability that the test-statistics obtained in the measured data is compatible with the null-hypothesis is then given by the percentage of results where the test-statistics obtained in randomized data that was larger or equal to the test-statistics obtained using the correct assignments (Manly, 1997).

This approach can be extended for more complicated analyses. For an analysis with several orthogonal factors, the procedure can simply be repeated for each factor. Also, the same test-statistics and randomization procedure can be used if several independent groups are to be compared; the mere difference here is that the randomization procedure has to affect the group assignment, and groupmean maps have to be summed for the test-statistics. If several factors are present, the interactions of factors can be investigated by constructing new levels that contain the combinations of levels of the factors. For example, if factor 1 has the levels a, b, and c, and factor 2 has the levels X and Y, one would construct 6 levels; aX, aY, bX, bY, cX and cY. Furthermore, when interactions between factors are investigated, one is usually interested in knowing specifically only those effects of the interaction that cannot be explained by the main-effects of the factors alone. One therefore has to remove the main-effects of factors included in the potential interaction from the data before analyzing the interaction of the factors. This is achieved by computing the level-mean topographies for each factor and subtracting these level-mean topographies from the individual data corresponding to the levels. In the example above, one would thus subtract the level-mean map of 1a (factor 1, level a) from the individual data belonging to aX and aY, the level-mean map of 1b (factor 1, level b) from bX and bY, and so on. One can then proceed with testing as described above, using the combinations of levels of the factors to be tested as new levels for the group means. For the current analysis, a matlab-based implementation of these statistics have been used, these tools are available upon request.

# LAURA source analysis

Source localizations were estimated and compared in the (early) time period where significant topographic differences between experimental conditions were found. (Note, topographic dissimilarities are indicative of differences in the underlying generator configurations). Sources were estimated using a local autoregressive distributed linear inverse solution (LAURA, Grave de Peralta et al., 2001). A realistic head model based on a standard MRI (MNI brain from the Montreal Neurological Institute) was used by applying the SMAC transformation method (Spinelli et al., 2000), which transforms the MRI to a best-fitting sphere. Then, 3005 solution points were defined in regular distances within the gray



Comparison of context effects between concrete and abstract words

Fig. 4. Result of the global ERP waveform analysis sorted for frontal (f), central (c) and posterior (p) electrode sites. Data-point wise *t*-test comparisons of the context effects (measured by the difference of related minus unrelated conditions) showed significant (P < 0.05, black marks) waveform modulations between abstract and concrete words before 200 ms and in the N400 time period, after 350 ms.

matter and a 3-shell spherical lead field was calculated for this set of solution points and for the 74 scalp electrodes. To identify the principal networks active during the early context effect, the mean LAURA source estimation was calculated from the grand-mean ERP fields of the different conditions across the time of interest. The obtained current density estimates provide only a visualisation of the likely generator configuration in each experimental condition and do not contain information about the signal to noise ratio of the activation. Furthermore, across the time of significant topographic differences, LAURA current density estimates were computed in the individual data and averaged across time. Then, voxelwise two-tailed *t*-tests were calculated on the mean LAURA source estimates, comparing those conditions that were topographically different. Differences in the current source density at P<0.001 are reported.

# Results

# Visual ERP data inspection

The visual inspection of the average-referenced ERP waveform components (Fig. 2) and their corresponding scalp-wide topographies (Fig. 3) allowed the identification of three components of interest: P1 (positive amplitude deflation at posterior electrode sites, maximum at around 120 ms), N1 (negative amplitude deflation at posterior electrode sites, maximum at around 200 ms) and N400 (negative amplitude deflation at central electrode sites and bilateral posterior positivity with an onset at around 350 ms across experimental conditions). Consequently, the time intervals of interest were set to approximately 100-200 ms and 350-600 ms. Importantly, during these time intervals, the ERP data suggested aggravated context effects (i.e., amplitude difference between related and unrelated condition) in abstract words: This was observable for the early context effect in the P1-N1 transition period (around 120-150 ms) as well as the late context effect starting at around 400 ms, depicted in Fig. 2B exemplary for F7 and Pz respectively.

# Global waveform analysis

Data-point wise *t*-tests (see Fig. 4) comparing the difference data sets (related minus unrelated conditions) of abstract and concrete words confirmed the observations mentioned above. Significant modulations were detected for the early context effect; those were distributed over left anterior electrode sites (e.g., F7). In addition, the method identified differences between abstract and concrete words in the late context effects linked to the N400 topography, but also after around 280 ms.

# Descriptive microstate analysis

The descriptive microstate analysis yielded an optimal set of seven microstate maps that explained the collective grand-mean ERP data from 0–600 ms across experimental condition. The global explained variance accounted for by these maps was 92.6%. Fig. 5 shows the microstate maps and their time of occurrence. Whenever possible, maps were labelled according to ERP components that corresponded in topography and time. These were the P1, the N1 and the N400 microstate maps. The microstate analysis detected a slightly different N1 map in related abstract words. In the time period where this particular N1 was observed (156–188ms), the randomi-

# Microstate maps and assignment



Fig. 5. Result of the overall microstate analysis. The upper panel shows the obtained microstate maps that explained the ERP data across experimental conditions. The lower panel depicts the temporal assignment of the microstate maps between 0 to 600 ms for related (R) and unrelated (UR) abstract and concrete words. Context effects in map occurrences were present during the P1–N1 and N400 time intervals.

zation-based topographic test procedure (two-by-two factorial TANOVA) yielded an interaction between context and concreteness that was in trend significant (P=0.07). In unrelated abstract words, the N400 map apparently also occurred roughly from 130 to 150 ms. Because of its early presence before 200 ms and clear-cut separation by intermediating states, this state does not represent an early onset of the functional N400 microstate but rather a topographically identical transition from the P1 to the N1 microstate. The particular map was thereafter termed P1–N1 transition map. In accordance with prior hypotheses and the global waveform analysis, visual inspection of the microstate assignment suggested context and concreteness interactions in the temporal assignment of maps during the P1–N1 transition and N400 time period. These observations were statistically tested.

# Statistical validation of the microstate assignment

# The early context effect

To investigate the context effect in abstract and concrete words, the P1, N1 and the P1–N1 transition map were fitted to the individual ERP data. The time period for fitting was set from 100 to 150 ms, where the P1–N1 transition took place. The obtained map occurrences were subjected to repeated-measurement ANOVAs with the factors concreteness (abstract/concrete) and context (related/unrelated) and the group-factor sex (women/men). There were no significant effects in the P1 and N1 map occurrences. For the P1-N1 transition map occurrence, a significant main effect of context [F (1,18)=6.37; P<0.05] and a significant interaction of context and concreteness [F(1,18)=4.70; P<0.05] were obtained (Fig. 6, left side). No sex effects were found. Post-hoc t-tests indicated that related and unrelated condition differed significantly only in abstract words ( $t_{df=19} = -2.64$ , P < 0.01) but not in the concrete words ( $t_{df=19}=0.0$ , P=0.5). Accordingly the size of the context effect (related minus unrelated condition) was stronger in abstract than in concrete words ( $t_{df=19}=2.23$ , P<0.05). Moreover, the occurrences of the P1-N1 transition map in the related abstract condition did not differ significantly from concrete words (both P's>0.1). Post-hoc randomization-based topographic testing in the time interval of fit (100-150 ms) indicated that the topographic context effect occurred exactly from 116 to 140 ms in abstract words, while there was no statistical evidence for topographic context effects during this time range in concrete words.

For abstract words, the localization of active generators was further estimated during the time period of topographic differences (116–140 ms). Fig. 7A shows the LAURA inverse solutions of the grand-mean ERPs of the related and unrelated condition. In both conditions, the inverse solution showed similar maximal electrical activity in bilateral occipital brain regions and somewhat leftlateralized temporal generators including the posterior part of the middle and superior temporal cortex. Voxel-wise two-tailed paired *t*-tests comparing individual LAURA current density estimates for related and unrelated abstract word ERPs indicated significant differences (P<0.001) in the left-lateralized prefrontal cortex in close proximity to the middle frontal cortex and the triangular part

# Mean occurrences of microstate maps



Fig. 6. Result of the topographic fitting procedure. The graphs depict the mean occurrences (in milliseconds [ms], bars indicate standard error of the mean) of the P1–N1 transition map and N400 map over the time interval of fit across experimental conditions. Paired *t*-tests confirmed that context effects (difference [D] between related (R) and unrelated (UR) p conditions) were significant larger (asterisks) for abstract (D<sub>ab</sub>) than concrete (D<sub>co</sub>) words in the respective map occurrences.

# A: Source activity 116 – 140ms Abstract words



# B: Mean Difference 116 – 140ms Abstract words



Fig. 7. LAURA source localization of the early context effect in abstract words. (A) Mean LAURA source estimation of the grand-mean ERP data between 116–140 ms indicated similar activity in occipital and posterior middle and superior temporal brain areas with slightly left-lateralized maximum for related and unrelated abstract words. (B) Mean LAURA source image of the paired-statistical comparison of related and unrelated words over the time period of topographic difference (116–140 ms). Related abstract words induced higher activity ( $t_{df=19}>3.88$ , P<0.001) in the left inferior prefrontal cortex.

of the inferior frontal cortex (Fig. 7B). In these voxels, current density was higher in related abstract words.

# The late context effect

To investigate late context effects in abstract and concrete words, the N400 map and the subsequent microstate map were fitted to the individual ERP data across experimental conditions. The time interval of fit was set from 460–560 ms, in the time range where the shift from the N400 to subsequent map occurred. The obtained map occurrences were subjected to a repeated-measurement ANOVA with the factors concreteness (abstract/concrete) and context (related/unrelated) and the group-factor sex (women/men). The ANOVA yielded a significant main effect of context [F (1,18)=16.17; P<0.01] and a significant interaction of concreteness and context [F (1,18)=5.15; P<0.05]. Furthermore there was a significant main effect of sex [F (1,18)=5.91; P<0.05] and the significant interaction between sex and concreteness [F (1,18)=5.43; P<0.05]. The trend of significance in the triple interaction between sex × concreteness × context [F (1,18)=3.78; P<0.07] indicated that the concreteness-dependent differences in

context effects were modulated by sex. Post-hoc t-tests showed significant context effects in abstract ( $t_{df=19}=3.79$ , P<0.01) and concrete words ( $t_{df=19}=1.83$ , P<0.05). Importantly though, the size of the context effect (related minus unrelated condition) was stronger in abstract than in concrete words ( $t_{df=19}=2.21, P<0.05$ ). Results are depicted in Fig. 4, right side. Correspondingly, randomization-based topographic testing detected significant topographic differences in abstract words within the time range of fit (460-560 ms), namely between 492 to 568ms and, in addition, somewhat earlier from 444 to 468ms. In concrete words a temporally-reduced context effect occurred from 512 to 524 ms. In addition, the microstate analysis suggested subtle differences in the N400 microstate onsets across experimental conditions. Therefore additional topographic fitting was conducted between 340-400 ms. The repeated measures ANOVA with the factors concreteness, context and sex showed a significant main effect of concreteness [F (1,18)=15.75; P<0.01]. Most importantly though, there were no significant effects for the factor context (P=0.1) and the interaction between context and concreteness (P=3). The result linked concreteness-evoked modulations to the N400 microstate offsets.

# Discussion

The present ERP study demonstrates a concreteness-dependent modulation of the early context effect that indicates its sensitivity to semantic processing. Further, the early context effect in abstract words corresponds to activity in predominately left-lateralized temporo-parietal and -prefrontal brain structures known to subserve lexico-semantic retrieval. Specifically, we observed an elevation of neural activity in the left prefrontal cortex for related compared to unrelated abstract words. Below we argue that the result reflects automatic feedforward processing of context-related information to higher-order brain areas. Together these results provide evidence for a semantic foundation of early context effects previously found in visual words (Michel et al., 2004b; Wirth et al., 2007). Additional we replicate concreteness effects in the N400 component.

# The early context effect

The findings of the ERP waveform, topographic and source analyses converge on the view that the early context effect emerges from the retrieval of verbal semantics. In a first step, this interpretation was supported by concreteness-evoked modulations of ERP context effects. Measured in the difference data of related and unrelated conditions between abstract and concrete words, these modulations occurred during the P1-N1 time period (~ 100-200 ms); the time-window previously shown to be sensitive to semantic effects (see Sereno and Rayner, 2003, for review). The topographic microstate analysis further linked the observed waveform changes to differences in the occurrences of the P1-N1 transition map, i.e., the map mediating the transition between the well-established and pre-dominant P1 and N1 microstates (Brem et al., 2006). In terms of its topographic distribution, the P1-N1 transition was identical to the N400 microstate map and might engage a similar generator network. This assumption needs however careful consideration because indistinguishable scalp-wide topographic patterns may correspond to dissimilar generator populations (Kavanagh et al., 1978). Yet, the P1-N1 transition does not represent an early N400 microstate but a separate state due to its presence well before 200 ms and unequivocal separation by intermediating states.

Most importantly, the occurrence of the P1-N1 transition state was shortened in related compared to unrelated abstract words and statistically non-differentiable from concrete words. The precise concreteness-specific changes coincide with behavioural findings (e.g., Schwanenflugel and Stowe, 1989) and the given conceptualization that abstract and concrete words vary in contextual accessibility and structure of the jointly recruited verbal semantic system (Brandsford and McCarrell, 1974; Kieras, 1978). Specifically, the pronounced context effect in the P1-N1 transition of abstract words indicates that semantic retrieval is affected via the externally-presented related context — the established outcome of semantic priming. In concrete words, on the other hand, the context effect was reduced in the way that the P1-N1 transition was comparably shortened for related and unrelated words. The result reflects diminished influence of external context in correspondence with the view that concrete words trigger per se richer access to internally-stored and extensively-linked representations (Schwanenflugel et al., 1988; Schwanenflugel and Shoben, 1983; Schwanenflugel and Stowe, 1989). In other words, the P1-N1 transition was reduced with facilitated conceptual access. Early ERP components may be affected by physical (e.g., brightness, size, length) as well as lexical (frequency) changes in the stimulus material (e.g., Brem et al., 2006; Hauk and Pulvermuller, 2004; Maurer et al., 2005). To control for these possible confounding variables, our stimulus material was matched for the relevant word features. Although overall and letter-specific brightness values did not differ significantly between the evaluated factors of interest, this procedure does not entirely rule out the possibility that subtle brightness changes nevertheless contributed to the measured ERP effects. In addition, care was taken to minimize lexical-semantic expectations thus reducing potential influences of intralexical priming. On the basis of the above arguments, we attribute the obtained modulation of the early context effect to the concreteness factor, in particular, to known differences in structure of and accessibility to verbal semantics in abstract and concrete words.

Data-point wise topographic testing determined that the early topographic context effect occurred exactly from 116 to 140 ms following word onset in abstract words. This effect corresponds in time to electro-/magneto-physiological context effects previously published for visually (Michel et al., 2004b; Rossell et al., 2003; Sereno et al., 2003) and acoustically presented (Shtyrov and Pulvermuller, 2007) words. In some of these studies, by contrast, early context effects were associated with the P1 and N1 topographies (Michel et al., 2004b; Sereno et al., 2003, respectively). Instead, here the context effect was tied to the P1–N1 transition map that proved sensitive to semantic differences. Preliminary, the state will thus be termed early semantic state (ESS), however more research is needed to explore the topographic divergence.

In line with our hypotheses, the estimation of neural sources underlying the early context effect (i.e., the topographic difference) in abstract words indicated activity in the temporo-prefrontal semantic retrieval system (see Vigneau et al., 2006, for review). This functional network is likewise recruited during early context integration in acoustically presented words (Shtyrov and Pulvermuller, 2007). It therefore appears that early semantic processing comprises access to supramodal semantic structures. In detail, the slightly left-lateralized posterior middle and superior temporal generators correspond to cortical regions repeatedly associated with lexico-semantic retrieval (Jobard et al., 2003) and have been found to be activated in abstract as well as concrete words (e.g., Binder et al., 2005; Kiehl et al., 1999; Noppeney and Price, 2004). Moreover, the statistical comparison of source estimates indicated changes in neural activity between related and unrelated abstract words in the inferior part of the left prefrontal cortex (PFC). In principle, the presence of a contextual modulation in the left PFC is in agreement with neuroimaging findings (Copland et al., 2003; Kotz et al., 2002; Matsumoto et al., 2005) and the hypothesis that this cortical region subserves semantic processing (e.g., Friederici, 2004). In the present data, however, the PFC activation was increased for primed (i.e., related) abstract words. This somewhat unexpected outcome has been demonstrated for repeated (e.g., Marinkovic et al., 2003) as well as related (Kotz et al., 2002; Rossell et al., 2003) verbal stimuli using MEG and functional neuroimaging respectively. The finding can be interpreted as a direct consequence of semantic priming using the framework of

spreading activation (Collins and Loftus, 1975; Posner and Snyder, 1975). The model postulates that the neural activation spread scattering from temporal brain structures (Miyashita, 2004) is facilitated in related compared to unrelated words. Assuming that early context effects are triggered by automatic processes (Shtyrov and Pulvermuller, 2007; Wirth et al., 2007) the elevation in the left PFC activity for related words might thus reflect a superior activation spread that projects information to higher-order prefrontal areas (see Marinkovic et al., 2003 for a similar interpretation) at early latencies (Foxe and Simpson, 2002). This automatic feedforward activation flow - observed in a more continuous transition from the P1 to the N1 microstates on the scalp surface - might arguably underlie early context integration (Shtyrov and Pulvermuller, 2007) and the rapid reading performance measured in eyemovement studies (around 300 words per minute, Sereno and Rayner, 2003). In our study, frontal activity was only identified in the statistical comparison of the related and unrelated conditions potentially due to the rather low current density of the frontal generator in comparison to occipito-temporal sources (Michel et al., 2004a). Contrary to earlier neuroimaging findings (Kotz et al., 2002; Rossell et al., 2003) neural activity was not enhanced in temporal generators in response to related word.

In general, the merging results of the different ERP analyses enable the conclusion that the early context effect reflects semantic processing. This finding manifests the applicability of the effect – if well controlled – as an ERP marker of initial and automatic retrieval processes in semantic memory. Because our main research quest was concerned with the semantic origin of the early context effect, statistical analyses were restricted to the comparison of early context effects in abstract and concrete words. Interestingly, Sysoeva et al. (2007) also demonstrated early ERP modulations between 40–100 ms post word onset in the direct contrast of abstract and concrete words employing an implicit task. Our results converge with the study outcomes of Sysoeva et al. (2007) towards the view that retrieval of concreteness-specific semantic word attributes occurs early and automatically during word processing.

# The late context effect

The presence of concreteness-evoked modulations of the N400 context effect is in line with previous findings in active sentence (Holcomb et al., 1999; West and Holcomb, 2000) and single-word (Swaab et al., 2002) context paradigms similar to our design. As such our result supports the established assumptions that the N400 reflects activity in the semantic system (Kutas and Federmeier, 2000). Contrary to our findings, however, Holcomb et al. (1999) report an amplified N400 context effect for concrete compared to abstract words. Because the current experiment does not enable to determine the nature of these differences further research on the N400 component is required. We

would nevertheless like to point out that the N400 and the N400 context effect are influenced by the degree of attention directed to semantics (Bentin et al., 1993; Chwilla et al., 1995; McCarthy and Nobre, 1993), which may encourage additional semantic and non-semantic operations. Therefore inconsistencies are reasonable in the precise interactions obtained in our passive (low-demand) compared to the active (high-demand) paradigm employed by Holcomb et al. (1999). Also, in agreement with a prior study (Koenig et al., 1998) we report evidence for concreteness effects starting at around 280 ms post word onset.

# Overall discussion

The current study suggests that functionally-distinct (automatic/ controlled) semantic processes can be traced by temporally-segregated electrophysiological markers (early/late ERP context effects, respectively) in this passive context paradigm. Still, one might argue, that controlled semantic processes apparently underlying the N400 context effect (e.g., Chwilla et al., 1995; Friederici, 2004) are minimized during low-demanding silent reading. However, there is evidence for the involvement of controlled semantic functions even in passive reading: In such tasks, Brown et al. (2000) showed that semantic integration (i.e., semantic matching) primarily generates the N400 context effect, while the size of the effect is proportionally related to the effort assigned to semantic operations (Wirth et al., 2007).

In addition, there are three preliminary observations that lead us to propose that early (automatic) and late (controlled) semantic processes activate partly overlapping semantic network structures: First, early as well as late context effects were enhanced in abstract compared to concrete words. Second, the early semantic state (ESS) as well as the N400 microstate displayed comparable topographic patterns and, third, the temporo-prefrontal sources active during early semantic retrieval approximately overlap with those brain regions involved in late semantic processing (Marinkovic et al., 2003). It therefore seems that certain representational network structures are re-accessed during different stages in word comprehension. Consequently, one could assume a possible functional link between early and late semantic analysis. For example, superior early semantic access in related words (here observed in a temporally-reduced ESS occurrence) might facilitate later controlled semantic processing (measured in a shorter occurrence of the N400 microstate). However, post-hoc analysis did not yield significant correlations. This might be attributed to existing sex differences in late semantic analysis during passive reading (Wirth et al., 2007).

# Conclusion

The present study demonstrates the sensitivity of the early context effect to differences in the structure of and accessibility to verbal semantics. This is indicated by a topographic difference in the P1–N1 transition period that occurred selectively in abstract words. Moreover, the early context effect corresponded to activation in left-lateralized temporo-prefrontal brain regions critical to semantic retrieval. In particular, we found higher activation in the left inferior prefrontal cortex for related compared to unrelated abstract words in addition to temporo-parietal generators similarly activated in both conditions. Taken together, the findings provide evidence that the early context effect reflects processes in verbal semantic memory.

## Acknowledgments

We thankfully appreciate the valuable comments of Prof. Dr. C.M. Michel and the help of N.H. Berger, Y. Fontana, Ch. Hug, Dr. U. Raub, X. Zhang in data analysis and/or data acquisition. The Cartool software (http://brainmapping.unige.ch/Cartool.php) has been programmed by Denis Brunet, from the Functional Brain Mapping Laboratory, Geneva, Switzerland, and is supported by the Center for Biomedical Imaging (CIBM) of Geneva and Lausanne. This study was in part financed by a Swiss National Science Foundation grant (3200BO-10082).

# References

- Baschek, I.L., Bredenkamp, J., Oehrle, B., Wippich, W., 1977. Bestimmung der Bildhaftigkeit (I), Konkretheit (C) und der Bedeutungshaltigkeit (m') von 800 Substantiven. Z. Exp. Angew. Psychol. 24, 353–396.
- Bentin, S., Kutas, M., Hillyard, S.A., 1993. Electrophysiological evidence for task effects on semantic priming in auditory word processing. Psychophysiology 30, 161–169.
- Binder, J.R., Westbury, C.F., McKiernan, K.A., Possing, E.T., Medler, D.A., 2005. Distinct brain systems for processing concrete and abstract concepts. J. Cogn. Neurosci. 17, 905–917.
- Brandeis, D., Naylor, H., Halliday, R., Callaway, E., Yano, L., 1992. Scopolamine effects on visual information processing, attention, and event-related potential map latencies. Psychophysiology 29, 315–336.
- Brandeis, D., Vitacco, D., Steinhausen, H.C., 1994. Mapping brain electric micro-states in dyslexic children during reading. Acta Paedopsychiatr. 56, 239–247.
- Brandsford, J.D., McCarrell, N.S., 1974. A sketch of a cognitive approach to comprehension: Some thoughts about understanding what it means to comprehend. In: Weimer, W., Palermo, D. (Eds.), Cognition and the Symbolic Processes. Erlbaum, Hilsdale, NJ, pp. 189–229.
- Brem, S., Bucher, K., Halder, P., Summers, P., Dietrich, T., Martin, E., Brandeis, D., 2006. Evidence for developmental changes in the visual word processing network beyond adolescence. Neuroimage. 29, 822–837.
- Bressler, S.L., Kelso, J.A., 2001. Cortical coordination dynamics and cognition. Trends Cogn. Sci. 5, 26–36.
- Brown, C.M., Hagoort, P., Chwilla, D.J., 2000. An event-related brain potential analysis of visual word priming effects. Brain Lang. 72, 158–190.
- Chwilla, D.J., Brown, C.M., Hagoort, P., 1995. The N400 as a function of the level of processing. Psychophysiology 32, 274–285.
- Collins, A.M., Loftus, E.F., 1975. A spreading-activation theory of semantic processing. Psychol. Rev. 82, 407–428.
- Coltheart, M., 1981. The MRC psycholinguistic database. Q. J. Exp. Psychol. 33, 497–505.
- Copland, D.A., de Zubicaray, G.I., McMahon, K., Wilson, S.J., Eastburn, M., Chenery, H.J., 2003. Brain activity during automatic semantic priming revealed by event-related functional magnetic resonance imaging. NeuroImage 20, 302–310.
- Copland, D.A., de Zubicaray, G.I., McMahon, K., Eastburn, M., 2007. Neural correlates of semantic priming for ambiguous words: an eventrelated fMRI study. Brain Res. 1131, 163–172.
- De Santis, L., Clarke, S., Murray, M.M., 2007. Automatic and intrinsic auditory "what" and "where" processing in humans revealed by electrical neuroimaging. Cereb. Cortex 17, 9–17.
- DeGroot, A.M.B., 1984. Primed lexical-decision: combined effects of theproportion of related prime-target pairs and the stimulus-onsetasynchrony of prime and target. Q. J. Exp. Psychol. 36, 253–280.
- Fingelkurts, A.A., Fingelkurts, A.A., 2004. Making complexity simpler: multivariability and metastability in the brain. Int. J. Neurosci. 114, 843–862.

Fodor, J.A., 1983. The Modularity of Mind. MIT Press, Cambridge, MA.

- Foxe, J.J., Simpson, G.V., 2002. Flow of activation from V1 to frontal cortex in humans. A framework for defining "early" visual processing. Exp. Brain Res. 142, 139–150.
- Friederici, A.D., 2004. Event-related brain potential studies in language. Curr. Neurol. Neurosci. Rep. 4, 466–470.

- Frishkoff, G.A., Tucker, D.M., Davey, C., Scherg, M., 2004. Frontal and posterior sources of event-related potentials in semantic comprehension. Brain Res. Cogn. Brain Res. 20, 329–354.
- Friston, K.J., 1997. Transients, metastability, and neuronal dynamics. NeuroImage 5, 164–171.
- Giesbrecht, B., Camblin, C.C., Swaab, T.Y., 2004. Separable effects of semantic priming and imageability on word processing in human cortex. Cereb. Cortex 14, 521–529.
- Giffard, B., Desgranges, B., Nore-Mary, F., Lalevee, C., de la Sayette, V., Pasquier, F., Eustache, F., 2001. The nature of semantic memory deficits in Alzheimer's disease: new insights from hyperpriming effects. Brain 124, 1522–1532.
- Gotman, J., Ives, J.R., Gloor, P., 1981. Frequency content of EEG and EMG at seizure onset: possibility of removal of EMG artefact by digital filtering. Electroencephalogr. Clin. Neurophysiol. 52, 626–639.
- Grave de Peralta, M.R., Gonzalez, A.S., Lantz, G., Michel, C.M., Landis, T., 2001. Noninvasive localization of electromagnetic epileptic activity. I. Method descriptions and simulations. Brain Topogr. 14, 131–137.
- Hager, W., Hasselhorn, M., 1994. Handbuch Deutschsprachiger Wortnormen. Hogrefe, Göttingen.
- Halgren, E., Baudena, P., Heit, G., Clarke, J.M., Marinkovic, K., Clarke, M., 1994. Spatio-temporal stages in face and word processing. I. Depthrecorded potentials in the human occipital, temporal and parietal lobes. J. Physiol. (Paris) 88, 1–50.
- Hauk, O., Davis, M.H., Ford, M., Pulvermuller, F., Marslen-Wilson, W.D., 2006. The time course of visual word recognition as revealed by linear regression analysis of ERP data. NeuroImage 30, 1383–1400.
- Hauk, O., Pulvermuller, F., 2004. Effects of word length and frequency on the human event-related potential. Clin. Neurophysiol. 115, 1090–1103.
- Helenius, P., Salmelin, R., Service, E., Connolly, J.F., 1998. Distinct time courses of word and context comprehension in the left temporal cortex. Brain 121, 1133–1142.
- Holcomb, P.J., Kounios, J., Anderson, J.E., West, W.C., 1999. Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electrophysiological investigation. J. Exp. Psychol. Learn. Mem. Cogn. 25, 721–742.
- Jobard, G., Crivello, F., Tzourio-Mazoyer, N., 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. NeuroImage 20, 693–712.
- Kavanagh, R.N., Darcey, T.M., Lehmann, D., Fender, D.H., 1978. Evaluation of methods for three-dimensional localization of electrical sources in the human brain. IEEE Trans. Biomed. Eng. 25, 421–429.
- Khateb, A., Michel, C.M., Pegna, A.J., O'Dochartaigh, S.D., Landis, T., Annoni, J.M., 2003. Processing of semantic categorical and associative relations: an ERP mapping study. Int. J. Psychophysiol. 49, 41–55.
- Kiehl, K.A., Liddle, P.F., Smith, A.M., Mendrek, A., Forster, B.B., Hare, R.D., 1999. Neural pathways involved in the processing of concrete and abstract words. Hum. Brain Mapp. 7, 225–233.
- Kieras, D., 1978. Beyond pictures and words: alternative information processing models for imagery effects in verbal memory. Psychol. Bull. 85, 532–554.
- Koenig, T., Kochi, K., Lehmann, D., 1998. Event-related electric microstates of the brain differ between words with visual and abstract meaning. Electroencephalogr. Clin. Neurophysiol. 106, 535–546.
- Kondakor, I., Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1995. Event-related potential map differences depend on the prestimulus microstates. J. Med. Eng. Technol. 19, 66–69.
- Kotz, S.A., Cappa, S.F., von Cramon, D.Y., Friederici, A.D., 2002. Modulation of the lexical-semantic network by auditory semantic priming: an eventrelated functional MRI study. NeuroImage 17, 1761–1772.
- Kounios, J., Holcomb, P.J., 1994. Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. J. Exp. Psychol. Learn. Mem. Cogn. 20, 804–823.
- Kuperberg, G.R., Deckersbach, T., Holt, D.J., Goff, D., West, W.C., 2007. Increased temporal and prefrontal activity in response to semantic associations in schizophrenia. Arch. Gen. Psychiatry 64, 138–151.

- Kutas, M., Hillyard, S.A., 1980. Reading senseless sentences: brain potentials reflect semantic incongruity. Science 207, 203–205.
- Kutas, M., Federmeier, K.D., 2000. Electrophysiology reveals semantic memory use in language comprehension. Trends Cogn. Sci. 4, 463–470.
- Lehmann, D., 1987. Principles of spatial analysis. In: Gevins, A.S., Rémond, A. (Eds.), Handbook of Electroencephalography and Clinical Neurophysiology, vol.1. Elsevier, Amsterdam, pp. 309–354.
- Lehmann, D., Skrandies, W., 1980. Reference-free identification of components of checkerboard-evoked multichannel potential fields. Electroencephalogr. Clin. Neurophysiol. 48, 609–621.
- Lehmann, D., Ozaki, H., Pal, I., 1987. EEG alpha map series: brain microstates by space-oriented adaptive segmentation. Electroencephalogr. Clin. Neurophysiol. 67, 271–288.
- Manly, B.F.J., 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd ed. Chapman & Hall, London, UK.
- Marinkovic, K., Dhond, R.P., Dale, A.M., Glessner, M., Carr, V., Halgren, E., 2003. Spatiotemporal dynamics of modality-specific and supramodal word processing. Neuron 38, 487–497.
- Matsumoto, A., Iidaka, T., Haneda, K., Okada, T., Sadato, N., 2005. Linking semantic priming effect in functional MRI and event-related potentials. NeuroImage 24, 624–634.
- Maurer, U., Brem, S., Bucher, K., Brandeis, D., 2005. Emerging neurophysiological specialization for letter strings. J. Cogn. Neurosci. 17, 1532–1552.
- McCarthy, G., Nobre, A.C., 1993. Modulation of semantic processing by spatial selective attention. Electroencephalogr. Clin. Neurophysiol. 88, 210–219.
- Meyer, D.E., Schvaneveldt, R.W., 1971. Facilitation in recognizing pairs of words: evidence of a dependence between retrieval operations. J. Exp. Psychol. 90, 227–234.
- Michel, C.M., Seeck, M., Landis, T., 1999. Spatiotemporal dynamics of human cognition. News Physiol. Sci. 14, 206–214.
- Michel, C.M., Thut, G., Morand, S., Khateb, A., Pegna, A.J., Grave de Peralta, R., Gonzalez, S., Seeck, M., Landis, T., 2001. Electric source imaging of human brain functions. Brain Res. Brain Res. Rev. 36, 108–118.
- Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R., 2004a. EEG source imaging. Clin. Neurophysiol. 115, 2195–2222.
- Michel, C.M., Seeck, M., Murray, M.M., 2004b. The speed of visual cognition. Suppl. Clin. Neurophysiol. 57, 617–627.
- Miyashita, Y., 2004. Cognitive memory: cellular and network machineries and their top-down control. Science 306, 435–440.
- Moss, H.E., Tyler, L.K., 1995. Investigating semantic memory impairments: the contribution of semantic priming. Memory 3, 359–395.
- Mummery, C.J., Shallice, T., Price, C.J., 1999. Dual-process model in semantic priming: a functional imaging perspective. NeuroImage 9, 516–525.
- Murray, M.M., Michel, C.M., Grave, d.P., Ortigue, S., Brunet, D., Gonzalez, A.S., Schnider, A., 2004. Rapid discrimination of visual and multisensory memories revealed by electrical neuroimaging. NeuroImage 21, 125–135.
- Murray, M.M., Camen, C., Gonzalez Andino, S.L., Bovet, P., Clarke, S., 2006. Rapid brain discrimination of sounds of objects. J. Neurosci. 26, 1293–1302.
- Neely, J.H., 1977. Semantic priming and retrieval from lexical memory: roles of inhibitionless spreading activation and limited capacity attention. J. Exp. Psychol. Gen. 106, 226–254.
- Neely, J.H., 1991. Semantic priming effects in visual word recognition: a selective review of current findings and theories. In: Besner, D., Humphreys, G.W. (Eds.), Basic Processes in Reading: Visual word Recognition. Erlbaum, Hillsdale, NJ, pp. 264–336.
- Neely, J.H., Keefe, D.E., Ross, K.L., 1989. Semantic priming in the lexical decision task: roles of prospective prime-generated expectancies and retrospective semantic matching. J. Exp. Psychol. Learn. Mem. Cogn. 15, 1003–1019.
- Noppeney, U., Price, C.J., 2004. Retrieval of abstract semantics. Neuro-Image 22, 164–170.

- O'Donnell, R.D., Berkhout, J., Adey, W.R., 1974. Contamination of scalp EEG spectrum during contraction of cranio-facial muscles. Electroencephalogr. Clin. Neurophysiol. 37, 145–151.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.
- Ortigue, S., Michel, C.M., Murray, M.M., Mohr, C., Carbonnel, S., Landis, T., 2004. Electrical neuroimaging reveals early generator modulation to emotional words. NeuroImage 21, 1242–1251.
- Paivio, A., 1971. Imagery and Verbal Processes. Holt, Rinehart and Winston, New York.
- Paivio, A., 1986. Mental Representations: A Dual Coding Approach. Oxford University Press, New York.
- Paivio, A., 1991. Dual coding theory: retrospect and current status. Can. J. Psychol. 45, 255–287.
- Pascual-Marqui, R.D., Michel, C.M., Lehmann, D., 1995. Segmentation of brain electrical activity into microstates: model estimation and validation. IEEE Trans. Biomed. Eng. 42, 658–665.
- Pascual-Marqui, R.D., Lehmann, D., Koenig, T., Kochi, K., Merlo, M.C., Hell, D., Koukkou, M., 1999. Low resolution brain electromagnetic tomography (LORETA) functional imaging in acute, neuroleptic-naive, first-episode, productive schizophrenia. Psychiatry Res. 90, 169–179.
- Posner, M.I., Snyder, C.R.R., 1975. Attention and cognitive control. In: Solso, R.L. (Ed.), Information Processing and Cognition: The Loyola Symposium. Erlbaum, Hillsdale, NJ, pp. 55–85.
- Price, C.J., 2000. The anatomy of language: contributions from functional neuroimaging. J. Anat. 197, 335–359.
- Pulvermuller, F., Assadollahi, R., Elbert, T., 2001. Neuromagnetic evidence for early semantic access in word recognition. Eur. J. Neurosci. 13, 201–205.
- Pylkkanen, L., Marantz, A., 2003. Tracking the time course of word recognition with MEG. Trends Cogn. Sci. 7, 187–189.
- Rissman, J., Eliassen, J.C., Blumstein, S.E., 2003. An event-related FMRI investigation of implicit semantic priming. J. Cogn. Neurosci. 15, 1160–1175.
- Rossell, S.L., Price, C.J., Nobre, A.C., 2003. The anatomy and time course of semantic priming investigated by fMRI and ERPs. Neuropsychologia 41, 550–564.
- Salmelin, R., Kujala, J., 2006. Neural representation of language: activation versus long-range connectivity. Trends Cogn. Sci. 10, 519–525.
- Schwanenflugel, P.J., Shoben, E., 1983. Differential context effects in the comprehension of abstract and concrete verbal materials. J. Exp. Psychol. Learn. Mem. Cogn. 9, 82–102.
- Schwanenflugel, P.J., Stowe, R.W., 1989. Context availability and the processing of abstract and concrete words in sentences. Reading Research Quarterly 24, 114–126.
- Schwanenflugel, P.J., Harnishfeger, K.K., Stowe, R.W., 1988. Context availability and lexical decisions for abstract and concrete words. J. Mem. Lang. 27, 499–520.
- Sereno, S.C., Rayner, K., 2003. Measuring word recognition in reading: eye movements and event-related potentials. Trends Cogn. Sci. 7, 489–493.
- Sereno, S.C., Brewer, C.C., O'Donnell, P.J., 2003. Context effects in word recognition: evidence for early interactive processing. Psychol. Sci. 14, 328–333.
- Shtyrov, Y., Pulvermuller, F., 2007. Early MEG activation dynamics in the left temporal and inferior frontal cortex reflect semantic context integration. J. Cogn. Neurosci. 19, 1633–1642.
- Skrandies, W., 1998. Evoked potential correlates of semantic meaning—a brain mapping study. Brain Res. Cogn. Brain Res. 6, 173–183.
- Spinelli, L., Andino, S.G., Lantz, G., Seeck, M., Michel, C.M., 2000. Electromagnetic inverse solutions in anatomically constrained spherical head models. Brain Topogr. 13, 115–125.
- Stein, M., Dierks, T., Brandeis, D., Wirth, M., Strik, W., Koenig, T., 2006. Plasticity in the adult language system: a longitudinal electrophysiological study on second language learning. NeuroImage 33, 774–783.
- Strik, W.K., Fallgatter, A.J., Brandeis, D., Pascual-Marqui, R.D., 1998. Three-dimensional tomography of event-related potentials during response inhibition: evidence for phasic frontal lobe activation. Electroencephalogr. Clin. Neurophysiol. 108, 406–413.

- Swaab, T.Y., Baynes, K., Knight, R.T., 2002. Separable effects of priming and imageability on word processing: an ERP study. Brain Res. Cogn. Brain Res. 15, 99–103.
- Sysoeva, O.V., Ilyuchenok, I.R., Ivanitsky, A.M., 2007. Rapid and slow brain systems of abstract and concrete words differentiation. Int. J. Psychophysiol. 65, 272–283.
- Tran, Y., Craig, A., Boord, P., Craig, D., 2004. Using independent component analysis to remove artifact from electroencephalographic measured during stuttered speech. Med. Biol. Eng. Comput. 42, 627–633.
- Varela, F., Lachaux, J.P., Rodriguez, E., Martinerie, J., 2001. The brainweb: phase synchronization and large-scale integration. Nat. Rev. Neurosci. 2, 229–239.
- Vigneau, M., Beaucousin, V., Herve, P.Y., Duffau, H., Crivello, F., Houde, O., Mazoyer, B., Tzourio-Mazoyer, N., 2006. Meta-analyzing left hemi-

sphere language areas: phonology, semantics, and sentence processing. NeuroImage 30, 1414–1432.

- Weisbrod, M., Kiefer, M., Winkler, S., Maier, S., Hill, H., Roesch-Ely, D., Spitzer, M., 1999. Electrophysiological correlates of direct versus indirect semantic priming in normal volunteers. Brain Res. Cogn. Brain Res. 8, 289–298.
- West, W.C., Holcomb, P.J., 2000. Imaginal, semantic, and surface-level processing of concrete and abstract words: an electrophysiological investigation. J. Cogn. Neurosci. 12, 1024–1037.
- Wirth, M., Horn, H., Koenig, T., Stein, M., Federspiel, A., Meier, B., Michel, C., Strik, W., 2007. Sex differences in semantic processing: event-related brain potentials distinguish between lower and higher order semantic analysis during word reading. Cereb. Cortex 17, 1987–1997.