

FEATURE ARTICLE

Sex Differences in Semantic Processing: Event-Related Brain Potentials Distinguish between Lower and Higher Order Semantic Analysis during Word Reading

Behavioral studies suggest that women and men differ in the strategic elaboration of verbally encoded information especially in the absence of external task demand. However, measuring such covert processing requires other than behavioral data. The present study used event-related potentials to compare sexes in lower and higher order semantic processing during the passive reading of semantically related and unrelated word pairs. Women and men showed the same early context effect in the P1-N1 transition period. This finding indicates that the initial lexical-semantic access is similar in men and women. In contrast, sexes differed in higher order semantic processing. Women showed an earlier and longer lasting context effect in the N400 accompanied by larger signal strength in temporal networks similarly recruited by men and women. The results suggest that women spontaneously conduct a deeper semantic analysis. This leads to faster processing of related words in the active neural networks as reflected in a shorter stability of the N400 map in women. Taken together, the findings demonstrate that there is a selective sex difference in the controlled semantic analysis during passive word reading that is not reflected in different functional organization but in the depth of processing.

Keywords: ERP, gender, language processing, N400, P1, semantic integration

Introduction

Current research suggests a sex difference favoring women in certain types of language-based abilities (see for review, Hampson and Kimura 1992; see against Hyde and Linn 1988). Specifically, females seem to have an advantage in episodic memory tasks where verbal processing is required or can be used (Herlitz et al. 1997, 1999; Maitland et al. 2004) as well as in verbal fluency (Herlitz et al. 1997; Maitland et al. 2004). Very little is known, however, about the nature of these sex differences. Global measures of basic memory capacity, overall intellectual capacity, and semantic knowledge do not yield a sex differentiation (Herlitz et al. 1997; Maitland et al. 2004). Behavioral studies have claimed that sexes differ selectively in higher order stages of verbal-based processing. Thus, findings show that females are more likely to engage in the elaborative processing of the meaning of verbal (or verbally encoded) information than males are. This is most evident in tasks that do not advance a specific processing style (Meyers-Levy and Tybout 1989; Meyers-Levy and Maheswaran 1991).

The biological basis for sex differences in cognition remains elusive. It has been hypothesized that women and men differ in the neural organization of language functions, namely, in the lateralization. Most important to our study, some functional magnetic resonance imaging (fMRI) studies have reported

M. Wirth¹, H. Horn¹, T. Koenig¹, M. Stein¹, A. Federspiel¹, B. Meier², C.M. Michel³ and W. Strik¹

¹University Hospital of Psychiatry, Bern, Switzerland, ²Institute of Psychology, University of Bern, Bern, Switzerland and ³Functional Brain Mapping Laboratory, University Hospital and University Medical School, Geneva, Switzerland

reduced asymmetry among females in semantic decision making (e.g., Shaywitz et al. 1995; Pugh et al. 1996; Baxter et al. 2003), whereas other studies show the lack of such a difference (e.g., Frost et al. 1999). In a review paper on fMRI studies, Sommer et al. (2004) found no significant sex difference in language lateralization suggesting that the effect is absent at the level of the general population. However, it has been argued that fMRI measurement could blur lateralization effects due to low temporal resolution. Instead, the exact temporal cascade of language processing may be important in understanding the neurobiological mechanisms involved in language comprehension and in detecting possible sex differences (Ortigue et al. 2005). Only electroencephalogram (EEG) and magnetoencephalogram (MEG) studies can reach this order of temporal resolution necessary because they provide an online monitoring of the millisecond-by-millisecond basis of neural processes independent of overt responses. Moreover, the event-related potential (ERP) to a stimulus can be segmented into a sequence of transient topographic patterns, also referred to as microstates. Similar to the interpretation of ERP waveform components (Donchin et al. 1978), microstates are thought to reflect synchronized activity in functionally interconnected neural networks. These networks are thought to correspond to different global stages in information processing (e.g., Lehmann 1987; Michel et al. 2001 for review), each stage comprising a number of subprocesses that may proceed in parallel.

Whereas sex differentiations in language processing have mainly been reported using functional brain imaging and behavioral methods, only a few ERP studies exist. Some of these studies found sex-specific lateralization differences in word recognition tasks (Walla et al. 2001; Hill et al. 2005; Ortigue et al. 2005). The study of Guillem and Mograss (2005) showed that superior face recognition in females corresponded to a larger old/new effect in the late N400-P600 complex. This effect was attributed to higher elaboration during face encoding. Other ERP studies found a larger amplitude during word reading (from 70 to 1200 ms) (Skrandies et al. 1999) and reduced latencies in the N4 component (Taylor et al. 1990) in women.

When assessing sex differences in language processing, current models of word recognition (e.g., Zwitserlood 1989) have to be considered. Commonly these models distinguish 3 major stages: In the first lexical-semantic access, the word form is extracted and at the same time (or shortly after) semantic and syntactic word features become available. This process is followed by the selection of one or more lexical representations. Finally, the lexical elements are fitted into the higher order meaning representation by means of an (nonautomatic) integration process.

Previous ERP studies have established 2 critical time segments during which different aspects of the lexical-semantic analysis occur. Firstly, activations between 100 and 200 ms after word onset are thought to represent the early and possibly automatic lexical-semantic access in visual word recognition (Sereno et al. 1998; Sereno and Rayner 2003). This view is based on studies that report ERP modulations due to lexical and semantic word features in the time interval, mainly characterized by the P1 (70–110 ms) and N1 (140–200 ms) components. In particular, these are effects of lexicality around 160 ms (Hauk et al. 2006) and word meaning (80–130 ms, Skrandies 1998), word category (100–150 ms, Assadollahi and Rockstroh 2005), emotional valence (100–140 ms, Ortigue et al. 2004), semantic association strength (~100 ms, Pulvermüller et al. 2001), and semantic coherence (~160 ms, Hauk et al. 2006). Consistently, effects of context (i.e., semantic priming effects) were reported in the P1–N1 time interval by 2 independent ERP studies (Sereno et al. 2003; Michel et al. 2004). Sereno et al. (2003) revealed a topographic context effect between 132 and 192 ms, whereas Michel et al. (2004) found a longer occurrence of the P1 topography for semantically related words in a similar time interval. Another study of Rossel et al. (2003) reported a context effect between 120 and 140 ms. Together these studies suggest that the primary semantic access occurs rapidly and is modulated by context.

The electrophysiological correlate sensitive to higher order lexical-semantic integration is the N400 component (Stuss et al. 1988; Holcomb 1993; Chwilla et al. 1995; Kutas and Federmeier 2000). Emerging at 350–600 ms after stimulus presentation, the N400 depends mainly upon temporal lobe brain structures. The N400 amplitude is attenuated at final words in sentences (e.g., Kutas and Hillyard 1980), word pairs, and even word lists (e.g., Bentin 1987; Weisbrod et al. 1999) when these final words are related to the prior context. This so called N400 context effect (here referred to as N400 effect) is reliably obtained in active (overt response) and passive (without overt response) paradigms (Brown et al. 2000), and it is thought to index the ease with which the word representation fits the context. This integration process is enhanced when subjects actively engage in deep semantic analysis (Bentin et al. 1993). As such, the N400 effect is stronger when word meaning is closely attended (McCarthy and Nobre 1993), and controlled mechanisms (e.g., strategies) of language processing are encouraged (e.g., semantic expectancy and semantic matching; for review, see Kutas and Federmeier 2000).

Based on the reviewed literature, the present study followed 2 aims: First, we wanted to compare women and men in lower and higher order semantic processing. Higher order word recognition is thought to build on the outcome of lower level processes. Therefore, sex differences in higher order word comprehension may result from variations occurring earlier in the processing stream, for example, in the early lexical-semantic access. To address this point, we chose a single word context paradigm. This paradigm yields context effects on “early” (<200 ms) and “late” (>350 ms) activations in the ERP of visually presented words (Michel et al. 2004) and shares core feature with semantic tasks known to detect sex effects (Ullman et al. 2002; Baxter et al. 2003). We expected females to process the verbal information more comprehensively and incorporate the words’ meanings to a larger extent. This should be reflected in latency and duration of the N400 effect and possibly in the earlier context effect in the P1–N1 time window. Second, we

aimed to explore sex-specific lateralization effects during low-demanding word recognition. Therefore, the task at hand was conducted passively (without overt response), and the subjects were kept unaware of the experimental conditions.

Contrary to waveform analysis at selected electrode sites, we applied a topographic analysis of the ERP data. With this procedure, the topographic configuration of the electric field can be analyzed at each point in time using the information of all measured electrodes simultaneously. This has several advantages: Firstly, the results do not depend on the choice of active and reference electrodes to be used and are therefore more objective. Second, by separating changes in amplitude (assessed by Global Field Power [GFP]; Lehmann and Skrandies 1980) from changes in topography (as assessed by topographic testing), changes in source strength can be separated from changes in source configuration. This makes the interpretation of an ERP effect more elaborate and precise. An ERP waveform at a given electrode can be composed from signals caused by sources at various locations. Identifying a change in amplitude at that electrode may thus result from either a change of source strength or distribution. Using topographic ERP methods, we therefore expected to resolve some of these possible ambiguities. In this study, we will therefore refer to ERP components as specific scalp topographies within a period of time.

There are a number of factors that may lead to differences in the results of topographic and waveform analyses. These factors include the choice of the recording reference, eventual normalization for global map amplitude (GFP), and eventual corrections for testing across multiple electrodes. Because the analyses presented here do not depend on the chosen reference, and because the statistics employed here are global and need no correction for multiple testing, the results presented here are not biased by a priori choices.

Materials and Methods

Subjects

Twenty-two paid subjects participated in the study and gave their written consent to the procedure. Two EEG data sets were rejected because of defective EEG recordings. In the final set, the data of 10 females (mean age = 24.03, standard deviation [SD] = 1.51) and 10 males (mean age = 25.11, SD = 3.33) were included. Fifteen subjects were university students and 5 had a university degree. All participants were right handed, had normal or corrected-to-normal vision, and reported to be free of medication. The study was approved by the Ethics committee of the Canton of Bern.

Stimuli

The stimulus material consisted of 180 noun-noun German word pairs varying in the relatedness of the visually present letter strings (index word-terminal word combinations). The terminal word was either preceded by a semantically related, indirectly related, or unrelated index word. In the initial item-selection process, concrete and abstract words were selected from the lists published in Hager and Hasselhorn (1994) or were translated from the MRC psycholinguistic database (Coltheart 1981). Following 2 word pair sets with 110 abstract and 110 concrete word pairs were composed so that each set contained 40 unrelated, 30 indirectly related, and 40 directly related word pair combinations. Sixty psychology students of the University of Bern rated the association strength of the word pairs on a scale from 1 to 5 (1 = not associated, 5 = very strong associated). Word pairs were then ranked from the lowest to the highest mean rating value separately for the concrete and the abstract set. All indirectly related concrete and abstract word pairs were rated as “weakly associated” and included in the final stimulus set. Additionally, the 30 lowest rated unrelated and the 30 highest rated related abstract and concrete word pairs were added to the final set.

The chosen 180 word pairs (60 related, 60 indirectly related, and 60 unrelated) were randomly ordered; the sequence remained constant for all presentations. Related and unrelated words were equated for word length and frequency with the following mean word lengths: index word (related: mean = 5.6, SD = 1.3; unrelated: mean = 5.9, SD = 1.5) and terminal word (related: mean = 6.1, SD = 1.4; unrelated: mean = 6.0, SD = 1.5). The logarithmic frequency classes were taken from the Leipzig Wortschatz Datenbank (<http://www.wortschatz.uni-leipzig.de>) where frequency values range from 0 (=high frequency) to 25 (=low frequency). The following mean word frequencies were calculated: index word (related: mean = 11.1, SD = 2.3; unrelated condition: mean = 12.2, SD = 2.7) and terminal word (related: mean = 11.5, SD = 2.1; unrelated: mean = 12.4, SD = 2.2).

Procedure

The testing took place at the Department of Psychiatric Neurophysiology, University Hospital of Psychiatry, Bern. After electrode placement, participants were seated in an electrically shielded and dimly lit room in front of a computer screen. The experimental session lasted 20 min. The design of the experiment is illustrated in Figure 1. Index and terminal words were presented sequentially (white on black), each word for 935 ms, in the center of the computer screen. During the intertrial interval (from word pair offset to the next word pair onset) of 1870 ms, a fixation point remained present. Subjects were instructed to read the words silently; they were not informed of their semantic relation. To control for attention, 30 blue squares were randomly mixed between the word pairs, and subjects were asked to press a button when the blue square appeared. The indirectly related word pairs did not constitute a homogenous and discrete experimental category and served as filler words. They were added to the stimulus material in order to not force the subject's attention on the experimental manipulation and thus to minimize the employment of task strategies. The squares and the indirectly related word pairs were not included in the ERP analysis.

Data Acquisition

The EEG was recorded from 74 electrodes, positioned in an electrode cap according to the extended 10–20 system. Two additional electrodes recorded vertical eye movements. Impedances were kept below 25 kOhms. Cz served as recording reference; the ground electrode was placed on the lateral neck of the subject. Recording was done with a BrainScope Amplifier. The EEG was online band-pass filtered from 0.5 to 70 Hz and digitized at 250-Hz sampling rate. Artifact rejection was conducted in a 2-step procedure: First an independent component analysis (ICA) was applied, and ICA components that clearly accounted for vertical and horizontal eye movements were removed from the EEG without topographic distortion (Jung et al. 2001). The EEG data were then recalculated to common average reference and inspected for remaining artifacts. Epochs with voltage exceeding $\pm 100 \mu\text{V}$ or below

$0.50 \mu\text{V}$ for 100 ms at any electrode site were discarded. If needed, bad electrodes were replaced by linear interpolation between their neighboring electrodes. The data were band-pass filtered at 1.0 Hz (12 db/oct)–12.0 Hz (24 db/oct). The continuous EEG was segmented into epochs of 600 ms starting with the onset of the terminal word. Individual averages and finally grand-mean averages were computed for each experimental condition.

ERP Analysis

The ERP data of related and unrelated terminal words were analyzed in a 2-step procedure: In reference to traditional N400 analyses, we first analyzed the N400 effect in the difference ERP between unrelated and related condition. To include all measured electrodes, we chose a topographic analysis approach. ERP difference effects blur underlying electrophysiological mechanisms. To overcome this limitation and to replicate the topographic P1 effect described by Michel et al. (2004), we subsequently analyzed the nondifference ERPs in a global analysis for changes in GFP and topographic microstates. Finally, selected microstate maps were localized to the corresponding neural generators.

Analysis of the N400 Effect

In the current study, the N400 effect was analyzed in the topographic configuration and temporal presence of the N400 difference map simultaneously containing the information at all measured electrode sites. Sex-specific changes of the N400 effect were assessed in the following way: First, we identified the data point where the N400 effect was largest. That is, the data point of maximal GFP in the grand-mean difference ERP (unrelated minus related condition) for men and women, respectively. The topography of the N400 difference maps at the respective data points was then compared between women and men using a randomization-based topographic test procedure (Strik et al. 1998; Pascual-Marqui et al. 1999). This nonparametric permutation statistics was conducted on normalized maps ($\text{GFP} = 1$) and computed the exact probability that a global topographic difference between subject groups is compatible with the null hypothesis. Significant changes in the topographic configurations were interpreted as changes in the active neural generator population (Lehmann 1987). To identify whether the N400 effect was differently distributed across time, a strength-independent topographic component recognition (TCR) (Brandeis et al. 1992) was applied to the individual ERPs using the group-mean N400 difference maps. That is, the spatial correlation between the group-specific N400 difference map and the moment-by-moment topography of the N400 effect was computed for each subject. In this analysis, spatial correlation coefficients of 1 indicate maximal map similarity and spatial correlations of -1 inverted maps. The individual moment-by-moment correlation coefficients were then averaged in 5 consecutive time periods of 40 ms duration in a time window from 400 to 600 ms. These individual mean correlation

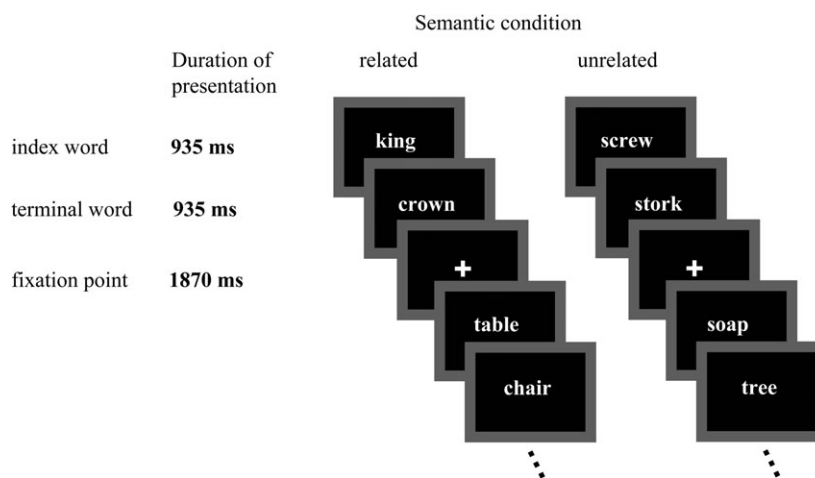


Figure 1. Schematic illustration of the noun–noun reading task. Terminal words were preceded by related or unrelated index words. Subjects were instructed to read the words silently, no overt response was required. Only conditions analyzed in this paper are illustrated.

coefficients were subjected to a repeated measure analysis of variance (ANOVA) with time period as within-subject factor and sex as between-subject factors. Unpaired *t*-tests were performed for post hoc testing.

Global ERP Analysis

Amplitude analysis. Changes in the strength of the global electric field were assessed with the GFP (Lehmann and Skrandies 1980). The GFP corresponds to the spatial SD of the scalp electric field and is computed (for average referenced data) as the square root of the mean of the squared value recorded at each electrode site. It yields larger values for stronger electric fields. First, the GFP was calculated for the individual average ERPs of each semantic condition. Next, GFP values for related and unrelated conditions were compared between men and women, respectively, using data point-wise *t*-tests. A GFP modulation was considered significant if the 0.05 alpha criterion was exceeded for at least 5 consecutive data points (>20 ms at 250-Hz digitization rate) (Picton et al. 2000). It should be noted that a significant change in the GFP simply signals a modulation in the amount of neural synchronization neither including nor excluding topographic modulations in the global electric field.

Microstate analysis and topographic fitting procedure. Changes in the topographic time course of the scalp electric field were assessed with a strength-independent microstate analysis (Pascual-Marqui et al. 1995). With this method, the grand-mean ERPs of all experimental conditions were segmented into time periods with stable scalp topographies, here referred to as microstates. Practically, a spatial *k*-mean cluster analysis was performed using the 4 normalized grand-mean ERPs (related/unrelated condition for men and women). The procedure extracted the most dominant scalp topographies over time, here referred to as microstate maps or maps. The temporal extend of the microstates in the grand-mean ERPs was established, based on a "best fit criterion" with smoothing and the temporal criterion that microstate maps must be observed for at least 5 consecutive data points. The optimal number of microstate maps was determined with a modified cross-validation criterion (Pascual-Marqui et al. 1995).

A topographic fitting procedure (described in detail, Michel et al. 1999, 2001) was applied to statistically analyze observed latency effects, that is, changes in the time when one microstate terminates and the next one begins. To claim that there is a difference in microstate latencies, it is reasonable to show that in the transition period the topography of the earlier microstate predominates in one condition and the topography of the following microstate is rarely observed, whereas in the other condition, the topography of the following microstate is predominant and the topography of the earlier microstate is relatively rare. This is what is done with the competitive topographic labeling procedure that determines within a given time window, during how many time frames a given microstate map fits the individual ERP data better than the other microstate map. Therefore, 2 microstate maps are chosen for fitting and are thus differentiated from each other.

In practice, those microstate maps displaying context effects in the latency within early (<200 ms) and late (>350 ms) time segments were selected from the overall microstate analysis and fitted into the individual subject ERPs. The TCR (Brandeis et al. 1992) was used to compare the selected microstate maps with the moment-by-moment scalp topography in each subject. In the competitive labeling procedure, the maps were then labeled to the given topography with which they correlated most. It is important to note that the specific time period in the ERP of a given subject and stimulus condition is not continuously and exclusively labeled with one microstate map. Nevertheless, the fitting procedure detects whether a microstate map appears more often in one experimental condition compared with another. The total amount of occurrence of the maps (in time frames) was extracted from the ERPs across subjects and experimental condition. The values were subjected to a repeated measurement ANOVA with relatedness (related/unrelated) as within-subject factors and sex group as between-subject factor. Post hoc *t*-tests were used to explain significant interactions. Because the topographic fitting procedure is applied within an extended time interval, the exact temporal onset and offset (in ms) of significant topographic effects was determined with the

randomization-based topographic testing described earlier in this section (Strik et al. 1998; Pascual-Marqui et al. 1999). Using the same procedure, the time periods not initially selected for detailed analysis were also explored statistically.

LAURA source estimation. In those microstates where significant latency effects due to relatedness were observed, the 3-dimensional distribution of the active neuronal generator sources was computed using local auto-regressive average (LAURA) (Grave de Peralta et al. 2001). Belonging to the class of distributed inverse solutions, LAURA computes the current density values (A/m²) for each voxel from the scalp-recorded voltages without a priori assumptions on number and location of the active sources. LAURA uses a realistic head model with a solution space of 4024 nodes, selected from a 6 × 6 × 6 mm grid equally distributed within the gray matter of the average brain provided by the Montreal Neurological Institute. The source estimations provided in this article offer a visualization of the most-likely underlying sources of selected microstate maps and do not represent a statistical analysis.

Results

Visual inspection of the measured ERP waveforms (Fig. 2A) suggested early and late context effects in both subject groups. An amplitude difference between related and unrelated words occurred in the P1–N1 transition period (around 120–150 ms). In addition, the well-known N400 effect was observed as an amplitude reduction for related compared with unrelated words around 400–600 ms at left parietal electrode sites (e.g., Pz, P1, P3) depicted in Figure 2B. This N400 effect seemed to start earlier and persist longer in women compared with men (Fig. 2B).

Figure 3 gives an overview of the topographic patterns observed in the ERPs of semantic conditions between 100 and 600 ms for women (Fig. 3, rows 1, 2) and men (Fig. 3, rows 4, 5). Both subject groups showed a similar topographic distribution. In addition, Figure 3 shows the N400 difference maps (unrelated minus related condition) with *t* values indicating the site of significant effects. Visual inspection suggested that the N400 effect was similarly distributed over left parietal electrode sites in women (Fig. 3, row 3) and men (Fig. 3, row 6); it occurred however earlier and longer in women. This observation was tested in a topographic analysis of the N400 effect based on the normalized group-mean N400 difference maps (see Materials and Methods).

Analysis of the N400 Effect

Figure 4A shows the normalized N400 difference maps for women and men. The N400 difference maps did not differ significantly ($P = 0.4$), confirming that women and men showed a left parietal distribution of the N400 effect on the scalp surface. The presence of the N400 difference map was determined by calculating the spatial correlation between the difference topography and the group-mean N400 difference map for each subject at each point in time. The result is depicted in the graph of Figure 4B. The repeated measures ANOVA on the mean spatial correlation within 5 consecutive time periods (each 40 ms, between 400 and 600 ms) identified a main effect of time period ($F_{3,8,69,3} = 2.66$, $P < 0.05$) and a strong interaction between time period and sex ($F_{3,8,69,3} = 6.41$, $P < 0.001$). Post hoc *t*-test confirmed higher spatial correlation for women in the first 120 ms between 400–440 ms ($P < 0.01$), 440–480 ms ($P < 0.05$), and 480–520 ms ($P < 0.05$). For males, spatial correlation was higher between 560 and 600 ms ($P < 0.05$). These results support the observation that

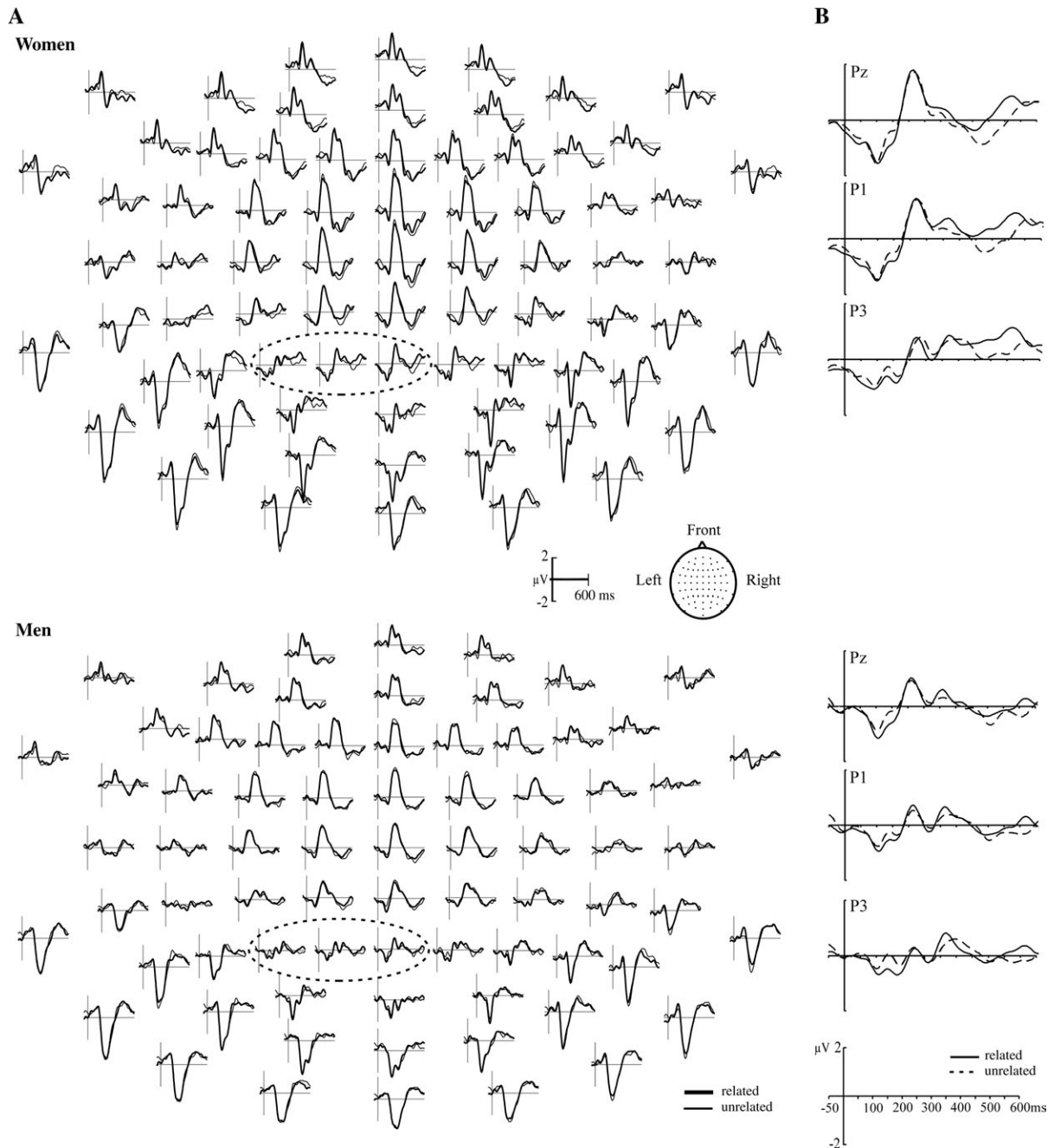


Figure 2. Average reference ERP waveforms for related and unrelated terminal words for women (upper panel) and men (lower panel). (A) ERP signals at 74 scalp electrodes for related (bold line) and unrelated (thin line) words. (B) Selected ERP curves at left parietal electrodes (Pz, P1, P3) for related (solid line) and unrelated (dashed line) words. Amplitude differences occurred in the P1–N1 transition period (around 120–150 ms) and around 400–600 ms in the N400 time interval. Noticeable, the N400 effect started earlier and lasted longer in women.

the N400 effect occurred earlier and lasted longer in women compared with men.

The ERP waveform analysis at one selected electrode (Pz) showed consistent results. The mean amplitude was computed in the 5 consecutive periods (each 40 ms, between 400 and 600 ms) in the difference waves (unrelated–related) at Pz. The repeated measures ANOVA with time interval as within-subject factor and sex as between-subject factor showed a significant interaction of sex \times time interval ($F_{4,0,72,0} = 3.2, P < 0.05$). Post hoc *t*-tests confirmed that women showed a stronger N400 effect between 400–440 ms ($P < 0.05$) and 440–480 ms ($P <$

0.05), whereas men showed a stronger N400 effect between 560 and 600 ms ($P < 0.05$). There was no significant difference between 480 and 520 ms ($P = 0.15$).

Global ERP Analysis

In females compared with males, the GFP analysis indicated significantly larger GFP amplitudes in the early N400 time frame for related (400–476 ms) and unrelated words (400–474 ms) (not depicted). The microstate analysis detected 6 maps, each remaining stable for a specific time in the grand-mean ERPs. An overview is given in Figure 5A. The P1 and N400 microstate

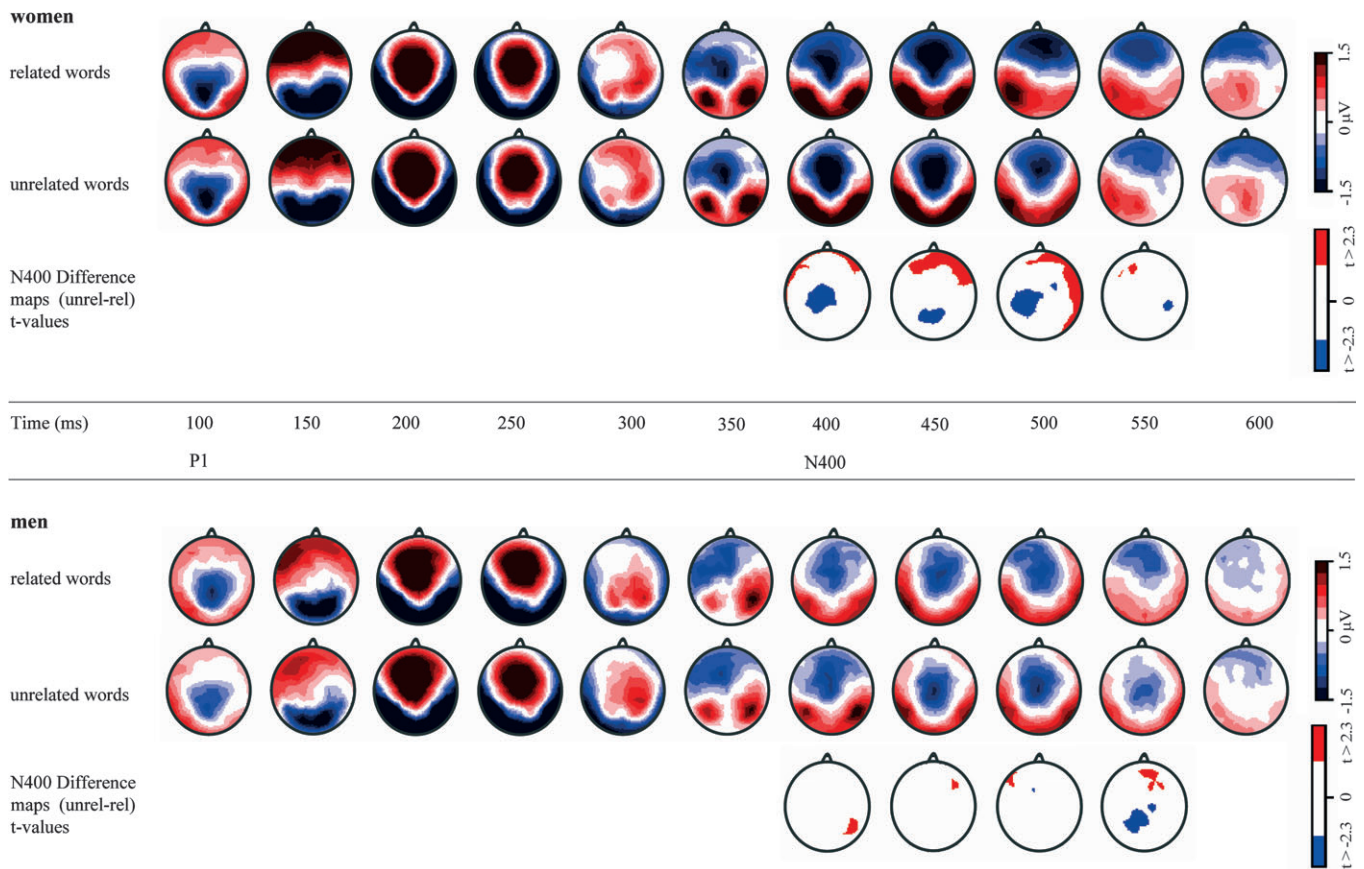


Figure 3. Topographic map series observed for related and unrelated words between 100 and 600 ms after word onset every 50 ms for women (rows 1, 2) and men (rows 4, 5). Rows 3 and 6 depict the scalp distribution of significant ERP modulations in the N400 time period between unrelated and related condition (colored t values correspond to $P < 0.05$).

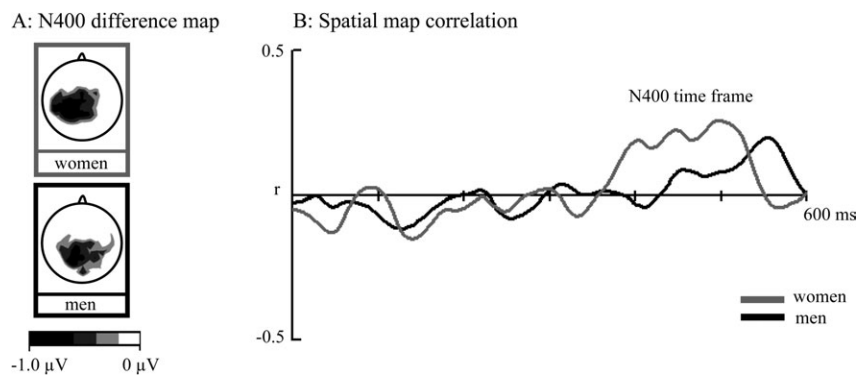


Figure 4. Results of the N400 effect analysis. (A) The statistically nondifferentiable N400 difference maps for women (gray frame) and men (black frame). (B) Mean spatial correlation of the N400 difference map and the moment-by-moment difference topography in women (gray) and men (black). Positive spatial correlation indicates map similarity between the N400 difference map and the given difference topography. Higher map similarity occurs earlier and persists longer in women indicative of an earlier and longer lasting N400 effect in this group.

maps were named in reference to the well-known ERP components because they were compatible with the respective component in topography and temporal occurrence (see also Fig. 3). Microstate maps and respective LAURA source analysis are shown in Figure 5B. For the P1 map, the strongest active sources were found in the left occipitotemporal cortex. The N400 map was explained by bilateral temporal sources. Both microstates displayed offset-latency differences. That is, the P1 map appeared to persist longer for related words in both groups. By contrast, the presence of the N400 map seemed to

be prominently reduced for related words in females only. These observations were tested with the topographic fitting procedure (see Materials and Methods). The total amount of occurrence (in time frames) of the P1 and N400 maps was quantified in the individual ERPs (P1 and N1 microstate map between 80 and 180 ms, N400 and late positive component [LPC] microstate map between 400 and 560 ms). The values were subjected to repeated measure ANOVAs with relatedness as within-subject factor and sex as between-subject factor. The results are shown in Figure 5C. For the P1 map, the ANOVA

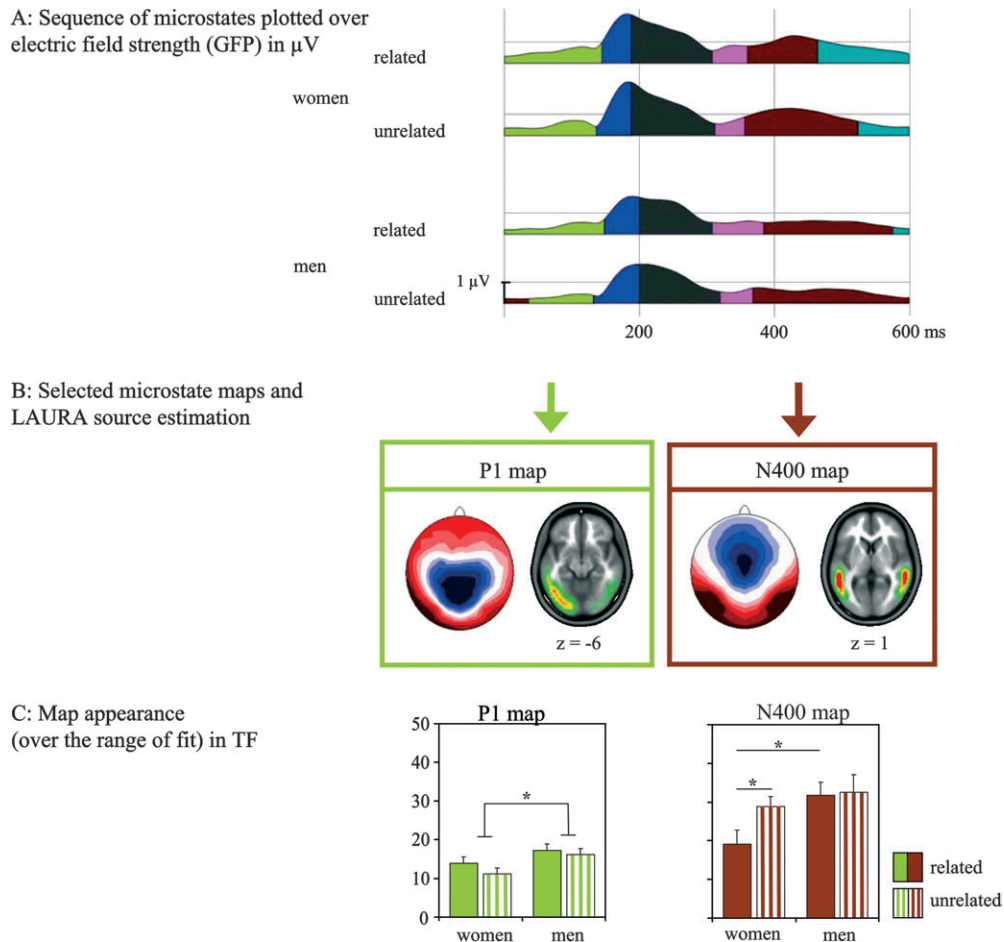


Figure 5. Result of the global ERP analysis. (A) Overview over the appearance of the 6 topographic microstate maps plotted over the mean GFP in women and men for related and unrelated words. (B) Depicted are the P1 map (green) and the N400 map (brown) with the corresponding LAURA source estimation. The P1 topography was explained by activity mainly in the left occipitotemporal brain area; the N400 topography by sources in the bilateral temporal lobes. (C) The occurrence of the P1 and N400 maps for related (full) and unrelated (striped) words in the time range of fit (in time frames [TF]). The P1 map appeared significantly (asterisk) more for related compared for unrelated words independent of subject group. The N400 map occurred significantly less for related words in the female group selectively.

indicated a significant effect of semantic condition ($F_{1,18} = 4.42$, $P \leq 0.05$), indicating that the P1 topography appeared significantly more often in the related condition (asterisk in Fig. 5C). Most importantly, there was no significant interaction between semantic relatedness and subject group ($P = 0.6$), confirming that comparable context effects were observed for men and women. Topographic testing between related and unrelated condition revealed that the context effect lasted exactly from 132 to 144 ms. The ANOVA on the N400 map occurrence showed a significant effect of semantic condition ($F_{1,18} = 6.29$, $P < 0.05$) and a significant interaction between sex and semantic condition ($F_{1,18} = 4.54$, $P < 0.05$). Post hoc comparisons confirmed that the N400 map was significantly less often observed for related compared with unrelated words in females ($P < 0.01$) but not in males ($P = 0.39$); depicted with asterisks in Figure 5C. Furthermore, females differed from males in the related condition only ($P < 0.05$). Topographic testing further specified that the N400 context effect lasted in the female group exactly from 424 to 532 ms. No other topographic effects were found between relatedness conditions in the remaining time periods for men and women.

Conventional ANOVAs on the mean amplitudes between 120–150 ms and 400–600 ms using the within-subject factors

electrodes (74) and semantic condition (related/unrelated) and the between-subject factor sex (women/men) showed in general the same results; that is a significant electrode \times relatedness interaction ($F_{9,8,177.2} = 3.6$, $P < 0.001$, $F_{8,5,152.5} = 4.6$, $P < 0.001$, respectively). There was no significant interaction between electrode \times relatedness \times sex in the time period 400–600 ms ($P = 0.3$).

Discussion

This ERP study compared early and late stages of semantic processing in passive word pair reading in men and women. The early access to lexical-semantic information is thought to occur within 100–200 ms post word onset (Sereno et al. 1998; Hauk et al. 2006), whereas late ERP activations (>350 ms) are sensitive to post-lexical semantic processes (e.g., Holcomb 1993). The present study provides evidence that women and men differ selectively in the latency and duration of the N400 effect in similarly activated networks. This leads to the conclusion that sexes differ in the depth of higher order semantic elaboration and integration.

In reference to other N400 studies, the N400 effect was identified in the difference ERP across semantic conditions.

However, we conducted a topographic analysis of the N400 effect (see also, Brandeis et al. 1994). Thus, in contrast to the waveform analysis at preselected electrodes, the global scalp electric field configuration was considered that possibly can contribute to a better comparison of the N400 effect across different studies and task designs. In the present ERP data, the N400 difference map displayed a left-lateralized parietal negativity in both subject groups. At parietal electrode sites, this resembles a reduction of the N400 amplitude for related compared with unrelated words, reflecting the well-known N400 effect (Kutas and Federmeier 2000). The fact that sexes did not differ in the spatial configuration of the N400 difference map indicates that the N400 effect was comparably distributed over the left parietal scalp surface in women and men. However, the N400 difference map occurred earlier and had a longer duration in females. In other words, women showed an earlier and persistent N400 effect. According to previous findings, the N400 effect is enhanced when subjects direct their attention to semantic word attributes (Bentin et al. 1993). Thus, our result suggests that women engage more extensively in semantic processing during passive word reading. The presence of a N400 difference map in men, even though if late and reduced, supports the idea, that the integration process constitutes a mandatory operation, which is however intensified when semantic relation is attended (Fodor 1983; Holcomb 1993).

It should be considered that ERP difference effects blur the underlying electrophysiological mechanisms, which has been a matter of debate in the N400 research. To overcome this limitation, we conducted a topographic analysis in the non-difference ERPs.

The microstate analysis identified the same sequence of transient topographic microstates in the nondifference ERPs. Because each microstate is assumed to reflect synchronized activity of neurons in a functionally interrelated network, the present finding indicates that men and women perform comparable global computational steps during visual word processing. Moreover, a similar context effect was found in men and women in the P1–N1 transition period (132–144 ms post word onset). The observation of an early context effect is in line with recent ERP findings (Michel et al. 2004). Employing a sentential paradigm Sereno et al. (2003) reported a context effect between 132 and 192 ms that was topographically attributed to the N1 component. However, the temporal and topographical dissimilarities between our and Sereno's findings might be explained by differences between sentential and single word context. One might query the idea that semantic effects occur this early during word recognition. Specifically, because there are ERP studies reporting orthographic effects between 150 and 200 ms (Cohen et al. 2000; Holcomb and Grainger 2006). Traditionally, these effects were assumed to precede semantic activations, thus they apparently support word recognition models that place the lexical-semantic access only after 350 ms (Pyllkanen and Marantz 2003). However, recent research has shown that the information processing in the visual system is more rapid than it was before believed to be. Thus, neural activity occurs between 50 and 80 ms post stimulus onset within a widespread system of sensory, parietal, and prefrontal areas (Foxe and Simpson 2002). Moreover, other findings suggest that selective word features can be extracted simultaneously (Hauk et al. 2006). Taking these studies into account, it is very likely that semantic information is retrieved within the first 200-ms post visual word onset (for review, see

Sereno and Rayner 2003). Besides differences in task design, there might be various reasons however why early semantic effects are still rarely described. Hauk et al. (2006) quotes "... most studies only looked at one or two word parameters at a time ..." and "... early effects might be smaller in amplitude, such that they were either overlooked or not detectable due to a lack of sensitivity of the methods ...". Given the recent evidence for early semantic activations and the detection of similar context effects (Michel et al. 2004), our findings suggest a contextual influence on lower order semantic activation in visual word recognition that is similar in men and women.

In agreement with findings of Michel et al. (2004), we could show that the P1 topography terminated later for related words in the P1–N1 transition period. Replicating earlier ERP studies, the P1 map showed a bilateral occipital positivity that is reflected in positive peaks at lateral occipital electrode sites (Curran et al. 1993; for detailed comparison, see Foxe et al. 2005). The fact that the stability of the P1 topography is observed from the beginning of the analysis period until about 140 ms indicates that the generators that predominate in the ERP (and are most likely to be visual) remain apparently stable. Other processes that start during this period may cause more subtle effects that are not accounted for well in an overall description of the data. Importantly, women and men showed a statistically nondifferentiable P1 topography that corresponded predominantly to neural activity in the left occipital-temporal brain areas, also found by Michel et al. (2004). Being part of the visual ventral "what" processing stream, this brain region shows repeated activation during word processing, which has led to the description of a specialized word recognition system (Fiebach et al. 2002). Thus, the topographic P1 effect can be interpreted as reflecting sustained neural activation within these neural networks, possibly suggesting early elaboration or integration mechanisms in the lexical-semantic access for related words. A temporal model of word recognition that considers the early context effect further emphasizes the prevalent view that the N400 comprises post-lexical semantic processes. In this line of reasoning, the observed similarity in the early context effect and the lack of a topographic difference indicate that men and women similarly encode prior context and the individual words' meanings during word reading.

After around 400 ms post word onset, a topographically identical N400 map occurred in the processing of related and unrelated words for both groups. This N400 map was characterized by a central negativity and bilateral temporal positivity, which has been described previously in a context paradigm (Michel et al. 2004). The occurrence of an indifferentiable and nonlateralized N400 map suggests the lack of a generalized sex-related lateralization effect. It rather seems that only specific language tasks evoke sex differences in the lateralization. Those might be "frontal lobe" tasks with higher processing demands as suggested by the position emission tomography study of Eposito et al. (1996).

In contrast to a similar spatial distribution, a sex-related difference was observed in the stability of the N400 map that was reduced for related words in women. This effect led to a prominent topographic difference in the ERP between related and unrelated words that accounted for the reduced latency and longer duration of the N400 effect in the female group. Accordingly, the late and short N400 effect in men was explained by a small and delayed (yet insignificant) difference

in the persistence of the N400 map. Thus with the help of the topographic analysis, we could show that in passive noun-noun reading, the N400 effect is the result of an earlier shift from the N400 to the subsequent LPC topography. In consequence, this finding suggests that prior context specifically modulates the temporal stability of neural activity in task-relevant networks. In particular, processing seems to be speeded up for related words in the active bilateral temporal networks known to be critically involved in semantic processing (e.g., St George et al. 1999; Kotz et al. 2002; Baxter et al. 2003; Giesbrecht et al. 2004). This effect was most evident in women suggesting that they actively engage in semantic elaboration and integration. The conclusion is strengthened by the observed differences in the global signal strength. In contrast to other studies that report broadly enlarged GFP amplitude for women (Skrandies et al. 1999), we specifically observed a GFP increase in the N400 time period in the female group. The N400 amplitude at single electrode level is enhanced by the degree of semantic elaboration a given word undergoes in task processing (e.g., Bentin et al. 1993). Consistently, the enhanced GFP could reflect more elaboration during higher order semantic analysis. In order to reinforce the functional relation between electric signal strength (GFP amplitude) and the N400 effect, the GFP amplitude was correlated with the latency of the N400 effect in a post hoc analysis. Indeed, the mean GFP between 400 and 500 ms averaged over related and unrelated condition correlated significantly and negatively with the latency of the positive spatial correlation peak in women only ($r = -0.78$, $P = 0.008$); note, positive spatial correlation indicated similarity of the N400 difference map and a given difference topography. Hence, in females, higher signal strength in the N400 time period was indeed followed by a faster modulation in the processing of related words. This result shows that the elaborate semantic analysis leads to faster integration of related words in women.

Taken together, the present ERP results support previous behavioral studies which showed that sexes differ in the threshold for elaborative processing in high-order language-related functions (Krugman 1966; DePaulo et al. 1979; Meyers-Levy and Sternthal 1991). In particular, our results can be linked to the "levels of processing" framework (Craik and Lockhart 1972; Jacoby and Craik 1979). In the absence of external task demands, men conduct a "shallow" semantic analysis in the way that they neglect the semantic relation of the verbal sequence. In contrast, for women the elaboration threshold was exceeded. They conducted a "deep" semantic analysis apparently directing more attention to the lexical-semantic "neighbors" (e.g., concepts), while processing the words as if to form an episodic trace. Presumably, this strategic elaboration leads to better episodic memory performance as reported by Guillem and Mograss (2005).

Neurophysiologically, the described sex difference could be associated with prefrontal brain areas involved in higher order operations in semantic memory conceptual space. It is well established that semantic association modulates the blood oxygen level-dependent response in the left inferior frontal gyrus (IFG) (Giesbrecht et al. 2004). Although we did not detect this specific prefrontal generator in the N400 map, the IFG is involved in the N400 generation especially in strategic semantic processing (Friederici 2004). Thus, it is possible that a strategic selection or elaboration mechanism guided by the left IFG contributes to the sex-related variation in the occurrence and duration of the N400 effect. Consistently, studies have reported

a female advantage in verbal generation (Maitland et al. 2004), known to engage the left IFG (Klein et al. 1995). And Schirmer et al. (2004) previously reported a gender difference in the IFG activation during emotional speech perception. This aspect should be subject to future research and might require both fMRI and EEG methods.

Finally, we want to emphasize that passive paradigms in combination with ERP techniques are beneficial in exploring temporal dynamics of language processing possibly subject to sex differences. At the same time, one should carefully consider sex effects when investigating cognitive functions especially when using designs that do not strongly advance a specific processing strategy. Assuming that women and men can both flexibly adapt specific processing strategies, sex differences could be absent in active response paradigms. This would explain the infrequent report of sex-related differences in these paradigms. However, the issue was not addressed in the present study and would require the explicit comparison of active and passive tasks.

Conclusion

In summary, the results of the present ERP study confirm and extend behavioral studies concerning sex differences in higher order language functions. ERP techniques elucidated the time course of visual word processing in a passive context paradigm. Men and women encode semantic information similarly. This was indicated by a comparable context effect in the P1-N1 transition period that was associated with a sustained persistence of the P1 map for related words. In the N400 time period, women showed enhanced electric field strength and a reduced stability of the N400 map for related words compared with men. These results suggest that sexes differ in the controlled processing of meaning and—in consequence—in the use of the message content in passive word reading.

Notes

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Address correspondence to Dr Helge Horn, University Hospital of Psychiatry, Bolligenstrasse 111, CH-3000 Bern 60, Switzerland. Email: horn@puk.unibe.ch.

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