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Increased neuronal communication accompanying sentence comprehension

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Abstract

The main purpose of this study was to examine large-scale oscillatory activity and frequency-related neuronal synchronization during the comprehension of English spoken sentences of different complexity. Therefore, EEG coherence during the processing of subject–subject (SS)- and more complex subject–object (SO)-relatives was computed using an adaptive fitting approach of bivariate auto-regressive moving average (ARMA) models which enabled the continuous calculation of coherence in the course of sentence processing with a high frequency resolution according to the dynamic changes of the EEG signals.

Coherence differences between sentence types were observed in the theta (4–7 Hz), beta-1 (13–18 Hz) and gamma (30–34 Hz) frequency ranges, though emerging during the processing of different parts of these sentences: gamma differences were evident mainly during the relative clause while theta and beta-1 differed significantly following the end of the relative clause. These findings reveal no simple one to one map between EEG frequencies and cognitive operations necessary for sentence comprehension. Instead, they indicate a complex interplay and dynamic interaction between different EEG frequencies and verbal working memory, episodic memory, attention, morpho-syntactic and semantic–pragmatic analyses, which though distinct often co-occur.

Keywords: EEG coherence; Sentence processing; Language; Working memory; Theta; Gamma; Large-scale synchronization; Oscillation

1. Introduction

During the course of a sentence, the language system must perform a series of analytic and integrative functions including auditory perception, phonological analysis, lexical access, morpho-syntactic, prosodic, semantic and pragmatic analyses in order to arrive at some meaning. Forming a coherent percept requires both serial and parallel integration across different aspects of language together with more general cognitive components. This so-called binding problem for language is a matter of intense debate. Little is known about how the human brain copes with these requirements of the language system and how it integrates the activity of different neuronal resources involved in the different aspects of sentence processing.

Over the past 20 years this neurophysiological binding problem has been theoretically addressed and empirically investigated within cognitive domains such as visual object perception (e.g., Singer, 2002; for review), focusing mainly on the ways in which the brain integrates signals, separated in space and time, to yield a unified sensory experience. According to the temporal correlation hypothesis, binding

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occurs in the temporal domain by virtue of neurons synchronizing their discharges (Singer, 2002). Synchronization phenomena, frequently found within small frequency ranges of the neuronal signals investigated, are being increasingly recognized as a key feature for establishing communication between different brain regions (Singer, 1999).

The neurophysiological binding problem within language–specifically sentence processing–has rarely been addressed even though determining mechanisms of neuronal integration in language is a key question within Cognitive Neuroscience. Only a handful of studies have investigated the role that brain oscillations in different frequency bands may play in sentence processing (Bastiaansen and Hagoort, 2003; Braeutigam et al., 2001; Roehm et al., 2001); these investigated power changes during sentence reading. Only a few EEG studies have investigated neuronal synchronization processes accompanying online sentence processing in the visual (Haarmann et al., 2002) and auditory domain (Mueller et al., 1997b; Weiss and Mueller, 2003; Weiss et al., 2001, 2002). Almost all of the EEG studies aimed at providing information about the neurophysiological mechanisms accompanying sentence processing used event-related brain potentials (ERPs) (e.g., Brown and Hagoort, 1999; Kutas, 1997, for review). Even though the analysis of ERPs provides data with exquisite temporal resolution, it is of limited value for studying the processes involved in large-scale synchronization of different brain areas over several milliseconds or seconds. By contrast, fMRI data collected during sentence processing reveals activation in various brain areas such as left frontal and temporo-parietal as well as right hemispheric regions but with a temporal resolution that is not high enough to investigate certain syntactic processes that take place on the order of milliseconds (e.g., Just et al., 1996; Sakai et al., 2001, for review). In any case, these data do not by themselves reveal much, if anything, about the functional organization of information within regions or the cooperation across activated regions during the comprehension act (though see initial attempts assessing temporal correlation of specific prefrontal regions during sentence comprehension task, Homae et al., 2003).

To date, neuronal interaction has been inferred primarily from analyses of electrophysiological recordings. A number of different mathematical approaches exist for extracting information on frequency-based cooperation between neuronal structures during various cognitive tasks in healthy humans (e.g., Bressler and Kelso, 2001; Nikolaev et al., 2001; Varela et al., 2001; Schack and Weiss, 2003, 2005). One well-known algorithm for assessing neuronal interaction or coupling during language processing is the computation of EEG coherence (e.g., Weiss and Mueller, 2003, for review). Coherence (C) at a frequency (w) for two signals x and y is derived from the smoothed cross-spectrum amplitude $|Gxy(w)|$ and the two corresponding smoothed power spectra, $Gxx(w)$ and $Gyy(w)$, $C^2xy(w)=|Gxy(w)|^2/Gxx(w)Gyy(w)$. The coherence function provides a measure of the linear synchronization between two signals as a function of frequency (Nunez et al., 1997; Petsche and Etlinger, 1998; Rappelsberger, 1998); it is very useful when synchronization is limited to some particular frequency bands, as it is typically the case in EEG signals.

In the current study we investigated the dynamic pattern of EEG coherence during sentence processing in order to gather information about frequency-related transient neuronal co-operation of brain oscillations correlated with syntactic analysis and verbal working memory processes. We investigated EEG coherence coincident with the processing of English subject–subject (SS)- and subject–object (SO)-relative sentences. In SS-relative sentences, such as *The fireman who speedily rescued the cop sued the city over working conditions*, the subject of the main clause (The fireman) is also the subject and agent of the relative clause. Such sentences have consistently been found to be easier to process than SO-relatives, in which the subject of the main clause is the object and patient of the relative clause (e.g., *The fireman who the cop speedily rescued sued the city over working conditions*). Children find it easier to comprehend subject relatives than object relatives (e.g., Tavakolian, 1981) as do young adults (e.g., King and Just, 1991) and patients with aphasia, probable Alzheimer disease or fronto-temporal dementia (e.g., Cooke et al., 2003; Grossman et al., 2003). This greater processing difficulty has been attributed by several researchers to the greater working memory (WM) demands of SO-sentences for which the main clause noun phrase (NP; The fireman) has to be maintained in memory over longer stretches of time until its role becomes clear and processing can resume. Another potentially difficult aspect of SO-relatives compared to SS-relatives is that the grammatical role played by the main clause NP in the former changes in the course of sentence processing.

In behavioral studies with sentence materials similar to those we used in our study, SO-sentences were associated not only with more comprehension errors but also slower word-by-word reading times at and just following the end of the relative clause, predominantly at the main clause verb (King and Just, 1991). Similar results have been observed in French (Holmes and O'Regan, 1981), German (e.g., Schriefers et al., 1995), Dutch (Mak et al., 2002) and Japanese (Miyamoto and Nakamura, 2003) but not in Chinese (Hsiao and Gibson, 2003). Across almost all the studies, reading time data show no evidence for a processing difference (e.g., greater WM load) until the end of the relative clause, just at that point when the load may begin to decrease.

In contrast, ERP measurements reveal a neural processing difference between subject and object relatives much earlier in the sentence, specifically shortly after the reader encounters the relative clause. King and Kutas (1995), for example, recorded a greater left fronto-central negativity for written SO-sentences as compared to SS-sentences continuing through the processing of the main clause (post-RC). ERPs indicated a difference between the two sentence types as soon as there was a WM load difference between them. Moreover, in accordance with the largest reaction time and reading time effects, these ERPs to visually presented SS- and SO-sentences showed reliable differences after the end of the relative clause (post-RC) at the main clause verb. SO-sentences elicited a larger left-anterior negativity (LAN) which was taken to index some aspect of working memory load at this point (King and Kutas, 1995). Comparable ERP differences for the reading of German SS- and SO-relatives were observed in sentence-length ERPs when the relative clauses had an unambiguous syntactic structure such as in the English materials (Muente et al., 1997).

In order to determine whether these effects were specific to sentence reading or were modality independent, Mueller et al. (1997a) examined sentence-length ERPs of participants listening to the King and Kutas sentences presented as natural speech. ERP effects were comparable to those with the written sentences, though generally more widespread and somewhat more pronounced over right hemispheric leads. Increased right hemispheric involvement during the processing of the more complex SO-sentences was demonstrated via fMRI measurements (Just et al., 1996).

In the current study our aim was to examine differences in EEG coherence between center-embedded SS- and SO-relatives using a specific spectral analysis technique that affords coherence estimates continuously across time, for a variety of frequency bins (Schack et al., 1995a,b). Previously, we examined the EEG coherence in this sentence material with a different approach by the means of Fourier Transform which yielded initial indications (1) that coherence at left frontal sites changes considerably during sentence processing and (2) that specific frequency bands might play different roles in the information transfer during sentence processing (Weiss et al., 2001, 2002; Weiss and Mueller, 2003). However, the temporal resolution of that analysis method was relatively low (1 s) and only activity in lower frequency bands was analyzed (<18 Hz). In the present study, therefore, we chose to use an adaptive fitting procedure for bivariate autoregressive-moving-average (ARMA) models with time-varying parameters, which allows continuous calculation of coherence with a frequency resolution that accurately tracks the dynamic changes of the EEG signal during sentence processing.

Our second aim was to describe the pattern of oscillations within distinct frequency ranges possibly engaged in processing different subcomponents of language processing within the brain. Recent studies in humans strongly suggest that theta varies with episodic or working memory processes (e.g., Klimesch, 1999; Sarnthein et al., 1998; Weiss et al., 2000; Weiss and Rappelsberger, 2000) and theta power tends to change during the course of visual sentence processing (Bastiaansen et al., 2002; Roehm et al., 2001). Thus, we hypothesized that theta band coherence would differ for SO- and SS-relatives as soon as there is a working memory load—i.e., from the beginning of the relative clause and last until the sentence end. There are only a handful of studies that point to the possible roles that activity in other frequency ranges may play in language or language-related processing. Gamma oscillations were affected by episodic verbal memory (e.g., Fell et al., 2003b; Schack and Weiss, 2003, 2005) and correlated with lexical processing (Pulvermueller et al., 1997), semantic integration in sentence processing (Braeutigam et al., 2001), selective attention (Fell et al., 2003a,b) and task complexity (Simos et al., 2002). The role of lower beta frequencies seems even more diverse, having been correlated with semantic word processing (Weiss and Rappelsberger, 1996), syntactic analysis during sentence comprehension (Mueller et al., 1997b), general sentence comprehension (Roehm et al., 2001), and semantic working memory demands (Haarmann et al., 2002). We thus hypothesized that gamma and/or beta frequencies reflect more than working memory load and therefore would show different coherence patterns across different parts of the sentence comparisons and in different brain regions.

Finally, we were interested in the possible differential participation of the left and right hemispheres and the involvement of frontal and parieto-temporal regions as indicated by previous ERP- and fMRI data (Just et al., 1996; King and Kutas, 1995; Mueller et al., 1997a). We thus examined whether signals at left- and right-hemispheric anterior and posterior electrode positions would show increased interaction during sentence processing, in particular the processing of the more complex SO-relatives.

2. Materials and methods

2.1. Participants

Twenty-four university students (12 f, 12 m) participated in the experiment. All of the participants were right-handed according to the Edinburgh Handedness Inventory, monolingual English native speakers between 19 and 35 years (Ø=23.3±3.5). After applying strict criteria for rejecting trials with muscle artifact (as this can adversely affect spectral analysis, especially in the gamma band), 18 participants' data were available for the coherence analysis.

2.2. Stimuli and experimental procedure

Two hundred sixteen syntactically and semantically congruent English sentences were aurally presented to the participants sitting in a sound attenuating chamber. The critical sentences consisted of 36 subject–subject (SS)- and 36 subject–object (SO)-relative sentences pseudo-randomly interspersed among 144 filler sentences. Almost these same sentence materials were previously studied with behavioral measures and ERPs (King and Just, 1991; King and Kutas, 1995). The combinations of agent and patient nouns were carefully chosen so that they would not lead to semantically or pragmatically induced interpretations. A detailed description of the experimental setup is given in Mueller et al. (1997a).

Care was taken to ensure that the 72 critical sentences were equal in spoken duration. As can be seen in Fig. 2 (lower panel), the variances of the durations of the different sentence intervals (pre-RC=interval before the beginning of the relative clause; RC=relative clause; post-RC=interval after the end of the relative clause) are quite small.

While their EEG was being recorded participants were asked to listen to the sentences and to answer comprehension questions, which followed a random 38% of the sentences. A tone signaled an impending probe, which was a TRUE/FALSE question that queried the immediately preceding sentence (for details see King and Kutas, 1995).

2.3. Data acquisition and analysis

2.3.1. EEG recording

EEG was recorded from 17 scalp sites including 11 channels placed according to the 10/20 system and 6 additional electrodes (Bl, Br, Wl, Wr, L41, R41) which were nominally over Broca's area, Wernicke's area and their right hemispheric homologues and bilateral primary auditory cortices. To test our hypotheses concerning the topography of coherence changes outlined in Introduction, signals at anterior and posterior electrode positions were analyzed while those at Cz, L41 and R41 were not (see Fig. 1). In addition, the electrooculogram (EOG) was recorded from 4 channels and signals were also recorded from over the left and right mastoids (M1, M2). Originally, all electrodes were referenced against a balanced non-cephalic pair of electrodes. The EEG was analog-filtered during acquisition between 0.01 and 100 Hz with a 60 Hz notch filter. The data were digitized on-line at a sampling rate of 250 Hz.

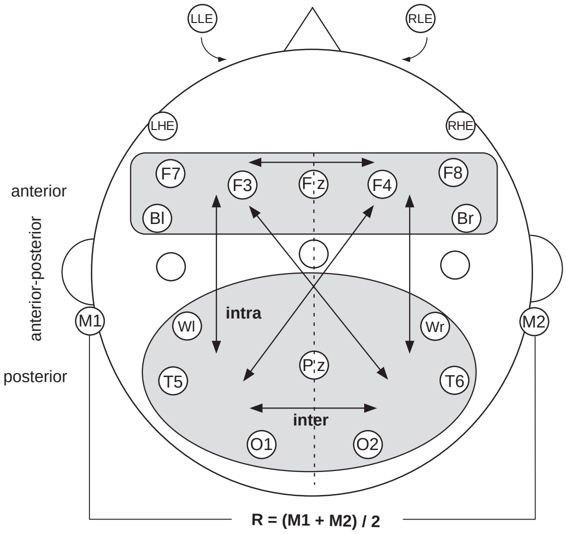

Fig. 1. Electrode positions, reference- (M1, M2) and EOG-electrodes (LLE=left lower eye; RLE=right lower eye; LHE=left horizontal eye; RHE=right horizontal eye) are mapped onto a schematic head scheme. The topography of electrode positions (anterior, posterior, anterior–posterior) used for ANOVAs is illustrated with grey boxes and arrows. INTRA denotes coherence within a hemisphere, INTER denotes coherence between hemispheres. Electrode positions presented as empty circles were omitted for the current analyses.

Prior to analysis, data were mathematically re-referenced to the average of the signals at the mastoids (M1+M2)/2 (Fig. 1) which yields a good reference for coherence analysis (Essl and Rappelsberger, 1998), and band-pass filtered between 1 and 50 Hz.

EEG data were screened for artifacts (eye blinks, horizontal and vertical eye movements, muscle activity, electrocardiogram) by visual inspection. This afforded a highly reliable exclusion of EEG artifacts which is especially critical for the analysis of higher frequencies using spectral analysis methods.

2.3.2. Coherence analysis

Spectral coherence of artifact-free EEG signals recorded as participants listened to SS- and SO-sentences was calculated by means of an adaptive fitting procedure for bivariate autoregressive-moving-average (ARMA) models with time-varying parameters. Details of the methods are extensively discussed in Schack et al. (1995a,b, 1999). The basic idea of the method is as follows: Due to the recursive structure of the algorithms used, continuous calculation of cross-spectral density is possible, affording a detailed time-coherence analysis. In principle, this method enables adaptation to structural changes in the signals and allows for continuous investigation of coherence for each sample point with an arbitrarily high frequency resolution. For the current study a frequency resolution of 0.5 Hz was chosen and coherence values were obtained every 4 ms during sentence processing given the sampling rate (250 Hz) at which the EEG data were initially sampled.

Computerized marks were placed at the beginning of each of the critical sentence intervals for each of the 36 SS- and 36 SO-sentences for each of the 18 participants such that the relevant EEG epochs could be submitted to spectral analysis and subsequent statistical analysis (ANOVA). Critical marks were placed at (1) the beginning of each sentence, (2) the beginning of the relative clause and (3) the beginning of the post-relative clause. The resulting critical sentence intervals whose borders approximate the linguistic constituent boundaries of interest comprise the interval before the beginning of the relative clause (pre-RC), the relative clause (RC) and the interval after the relative clause (post-RC) (see Fig. 2, upper panel).

Cross spectra were computed for each sample point and electrode pair for each critical sentence interval. Thereafter coherence was calculated for all possible electrode pairs, thus yielding 91 values per frequency bin according to the 14 electrode positions analyzed.

Pre-RC	RC	Gap	Post-RC
(SS) *The fireman who* (SO) *The fireman who*	*speedily rescued the cop* *the cop speedily rescued*		*sued the city over working ...* *sued the city over working ...*
(SS) 300-490ms (SO) 300-589ms	930 - 1798 ms 985 - 2000 ms		2964 - 3797 ms 3012 - 3776 ms

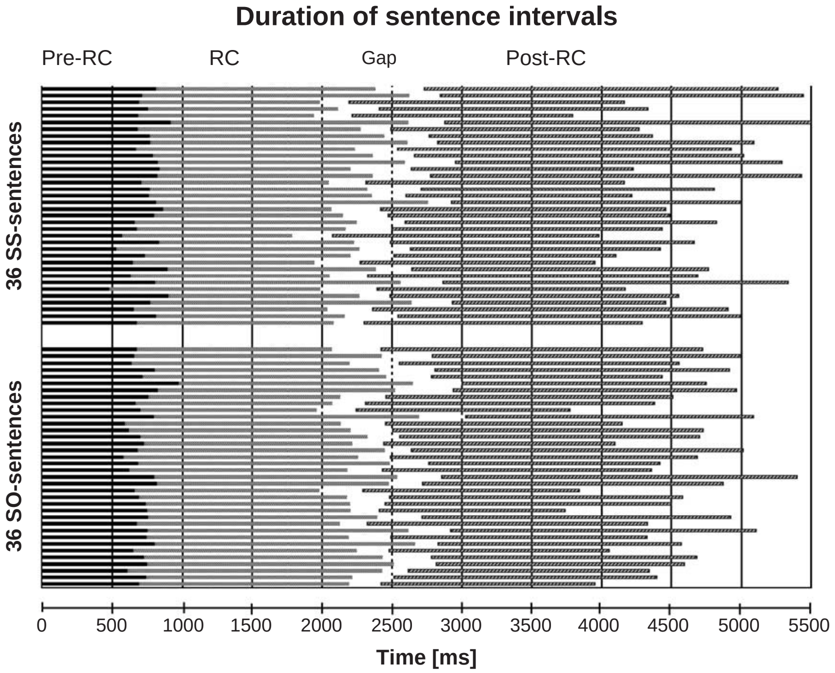

Fig. 2. Upper panel: Relevant sentence intervals and the corresponding time intervals used for the ANOVAs. The reason why the analysis of the pre-RC (pre-relative clause) did not start before 300 ms lies in the properties of the adaptive algorithm used (e.g., Schack et al., 1995a) which needs on average about 70 sample points (dependent on the frequency range investigated) to adapting to the EEG signal analyzed. Lower panel: Absolute duration of each of the 72 SS- and SO-sentences. Different sentence intervals (pre-RC, RC, gap, post-RC) are mapped in different shades of grey showing only a very small temporal variance between the sentences. Gap denotes the articulatory pause between RC and post-RC.

Specific frequency bands presumably important for sentence processing were selected according to previous studies of sentence processing (Bastiaansen et al., 2002; Haarmann et al., 2002; Mueller et al., 1997b; Weiss and Mueller, 2003; Weiss et al., 2001, 2002). These included: theta (4–7 Hz), beta-1 (13–18 Hz), beta-2 (20–28 Hz) and gamma (30–34 Hz). Coherence was averaged across frequency bins for each of these frequency bands (the frequency resolution was 0.5 Hz).

For the purpose of statistical analyses (ANOVA) Fisher-z-transformed coherence was averaged over different topographical regions (anterior, posterior and anterior–posterior) (see Fig. 1) for each participant. Coherence values were then averaged over all relevant sentence intervals of each sentence type and each participant and a grand average of the 18 participants data was computed. This estimate of mean time coherence is useful because of the high variability of the EEG which in turn leads to high variability in the adaptive EEG coherence during cognitive processing.

3. Results

Fisher-z-transformed coherence values were submitted to repeated measures ANOVA. Separate ANOVAs were conducted for three different sentence intervals (pre-RC, RC, post-RC), for each of the four frequency bands and for each of three different brain regions. The different brain regions (anterior, posterior, anterior–posterior) were selected since results of previous ERP studies (King and Kutas, 1995; Mueller et al., 1997a) suggested the participation of frontal and posterior temporal brain regions in processing SS- and SO-sentences. Effects of the within-subjects factors TYPE (SS- vs. SO-sentences), HEMIS (left vs. right) and TOPO (intra vs. interhemispheric values) were tested for mean coherence values. Analyses started at the beginning of each interval and lasted until the end of the shortest sentence so that no irrelevant sentence segment fell into the analysis interval. In Fig. 2 (upper panel) the sentence intervals are indicated. The mean length of the critical sentence intervals submitted to ANOVAs were (1) for the pre-RC interval: SS-sentence = 190 ms, SO-sentence = 289 ms; (2) for the RC: SS-sentence = 868 ms, SO-sentence = 829 ms and finally (3) for the post-RC: SS-sentence = 829 ms and SO-sentence = 764 ms. Results of the ANOVAs concerning the main factor TYPE and its interactions are presented in Table 1.

Before the beginning of the relative clause (pre-RC) there was no significant main effect of TYPE nor any interaction for any frequency band in any topographical area. These results were expected since sentences did not differ linguistically in this interval. However, in the RC, a significant main effect of TYPE was found in the gamma frequency range for anterior, posterior and anterior–posterior coherence (Table 1). And, in the post-RC there was a significant effect of TYPE in the theta frequency range for anterior, posterior and anterior–posterior coherence. A similar main effect was also found for posterior and anterior–posterior coherence in the beta-1 band and for posterior coherence in the gamma band. Inspection of the respective means revealed an overall higher mean coherence for SO- than for SS-sentences both in the RC and post-RC.

In the RC significant TYPE × HEMIS and TYPE × HEHEMIS × TOPO interactions were found in the gamma frequency range for posterior and anterior–posterior coherence indicating higher mean coherence for SO- than for SS-relative clauses specifically within the right hemisphere (Table 1).

A significant TYPE × TOPO interaction in the RC was found for anterior–posterior theta coherence indicating higher intrahemispheric coherence in SO-relative clauses and higher interhemispheric coherence in SS-relative clauses.

In all sentence intervals there was a main effect of the HEMIS factor. In the pre-RC mean coherence in the left hemisphere was higher than in the right hemisphere ($F(1,17)=5.2$; $p<0.03$). This was demonstrated for anterior–posterior coherence in the theta band. However, the opposite pattern was found for anterior–posterior coherence in the beta-2 band showing higher right-hemispheric coherence ($F(1,17)=4,6$; $p<0.04$). A comparable effect was found in the RC ($F(1,17)=6.1$; $p<0.02$) and in the post-RC ($F(1,17)=4.8$; $p<0.04$). In general, mean absolute right-hemisphere coherence is higher than left-hemisphere coherence during rest, when there is no specific cognitive task (Schack et al., 2003); this may be explained by hemispheric differences in anatomy. The right hemisphere has proportionally more fibers than neurons than the left hemisphere (Gur et al., 1980), such that information transfer is primarily via long-range connections whereas the left hemisphere is characterized by a higher neuronal differentiation (Thatcher et al., 1986). The higher anterior–posterior theta coherence over the left hemisphere in the pre-relative clause may be related to the initiation of linguistic analysis since coherence during linguistic analysis is higher in the left hemisphere (Weiss and Rappelsberger, 1998). However, the higher right-hemispheric anterior–posterior coherence in the beta-2 band during the entirety of the sentence processing is difficult to explain. It seems as if long-range cooperation between anterior and posterior electrodes in the beta-2 band is preferentially performed in the right hemisphere independent of sentence type. Since there are no data to support these assumptions and we did not find other reliable results within this frequency range this part of our interpretations has to remain speculative and will not be discussed further.

The significant main effect of the factor TOPO in all frequency bands and for all topographic areas reflects a pattern in which coherence values within each hemisphere (intrahemispheric) were generally higher than coherence values between hemispheres (interhemispheric) and is consistent with scalp coherence generally decreasing with increasing electrode distance. This effect was also found in all other sentence intervals.

The results of the ANOVAs show that coherence during processing of SS- and SO-sentences differs in both the RC and the post-RC interval. Fig. 3 illustrates these findings for anterior, posterior and anterior–posterior coherence.

The gamma band activity (30–34 Hz) predominantly differs between these sentence types in the RC interval whereas theta band activity (4–7 Hz) differences appear after the relative clauses (post-RC). In the post-RC, the gamma band shows a significant difference between SS- and SO-sentences only in posterior coherence.

To determine which single coherence pairs tend to show a difference between SS- and SO-sentences paired Wilcoxon-tests were applied to all possible electrode pairs for

Table 1
Significant results of repeated measures ANOVAs for effects of sentence type

		Pre-RC	RC	Post-RC
TYPE	Anterior	–	Gamma: $F(1,17)=8,6$ ($p<0.009$)	Theta: $F(1,17)=4,3$ ($p<0.05$)
TYPE	Posterior	–	Gamma: $F(1,17)=12,4$ ($p<0.002$)	Theta: $F(1,17)=16,5$ ($p<0.000$) Beta-1: $F(1,17)=5,7$ ($p<0.02$) Gamma: $F(1,17)=4,5$ ($p<0.04$)
TYPE × HEMIS		–	Gamma: $F(1,17)=6,5$ ($p<0.02$)	–
TYPE × HEMIS × TOPO		–	Gamma: $F(1,17)=6,5$ ($p<0.02$)	–
TYPE	Anterior–posterior	–	Gamma: $F(1,17)=7,6$ ($p<0.01$)	Theta: $F(1,17)=14,2$ ($p<0.001$) Beta-1: $F(1,17)=5,1$ ($p<0.03$)
TYPE× HEMIS		–	Gamma: $F(1,17)=6,5$ ($p<0.02$)	–
TYPE × TOPO		–	Theta: $F(1,17)=7,3$ ($p<0.01$) Gamma: $F(1,17)=6,5$ ($p<0.02$)	–

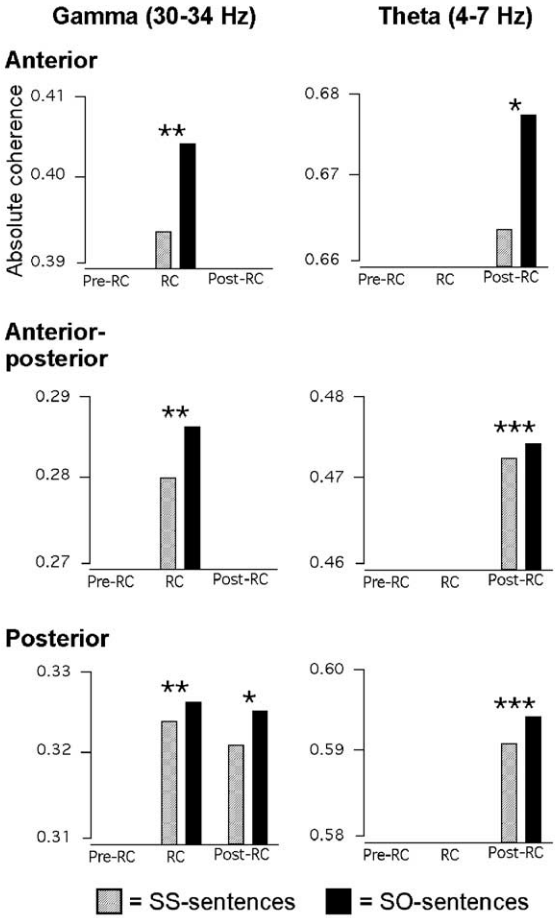

Fig. 3. Absolute mean coherence at anterior and posterior electrodes and between anterior and posterior electrodes for SS- and SO-sentences. Only statistically significant differences related to main TYPE effects obtained by ANOVAs are shown in this figure. In the relative clause (RC) different values for SS- and SO-sentences are mainly reflected in the gamma band whereas in the post-relative clause (post-RC) differences are mainly reflected in the theta band.

the whole post-RC interval in the theta band. Test results were converted to error probabilities and presented as lines between the electrodes in a schematic drawing of the brain (Fig. 4). Normally, with multiple comparisons significance levels should be adjusted to avoid inflated error probability; however, given the large number of variables (electrodes, coherence values) such adjustments would yield extremely low probabilities for rejecting false null hypotheses. Thus, even real EEG effects might be cancelled out. The statistical procedure thus has to be considered as a statistical filter and the obtained error probabilities as purely descriptive, rather than used to confirm or reject the null hypotheses. They are merely intended to provide hints at possible relative coherence differences during the comprehension of SS- and SO-sentences.

In the post-RC region, subject–object sentence analysis is accompanied by a prominent coherence increase between anterior leads, between left anterior and posterior sites and also between the electrodes Br and Wl. SS-sentences show a comparable pattern of coherence increase at anterior electrodes, between left frontal and posterior electrodes and between right frontal and left posterior electrodes. However, processing of SS-sentences is associated with fewer and weaker coherence changes in the post-RC region. The left frontal electrodes F7 and Bl seem to be specifically important in sentence processing since they participate in most of the coherence changes observed. The coherence between hemispheres, especially between frontal electrodes is more prominent during SO-sentence processing.

However, in this paper our main focus was not on the examination of single coherence changes but rather in the illustration of global coherence differences between SS- and SO-sentences processing. Therefore we calculated the mean band coherence for the gamma and theta frequency bands which yielded time curves as in Fig. 5. Mean band coherence was estimated from 300 ms after the beginning of each sentence onwards for each sample point. Afterwards coherence values were averaged over trials, participants and topographic areas. Fig. 5 illustrates the temporal course of mean anterior–posterior coherence in the gamma and the theta band as participants listened to SS- and SO-sentences.

In contrast to later detailed time-coherence analysis (Fig. 6) the time curves of mean band coherence only allowed the illustration of sentence intervals that were smeared and did not have clear boundaries as for instance those shown in Fig. 6 or as sentence intervals used for ANOVAs. Nevertheless, prominent coherence differences between SS- and SO-sentences were found, indicating a continuous higher coherence for SO- than for SS-sentences. Anterior–posterior gamma coherence predominantly differs at the beginning of the relative clause and decreases in the course of sentence processing. In contrast, theta band coherence becomes higher for SO-sentences later in time, showing the most striking effects at the beginning of the post-RC.

To avoid smearing across sentence intervals, detailed time-frequency matrices for coherence were calculated for each single trial. The full time-frequency information of coherence allows determination of frequency bands in which coherence changes correlate with the time course of the cognitive process. Coherence was calculated time-locked to the beginning of each relevant sentence interval and averaged across trials and participants. Fig. 6 illustrates the anterior–posterior coherence difference for SS- and SO-sentences for the electrode pair Bl–Wl.

Frequency bands that showed differences between SS- and SO-sentences within different sentence intervals in the previous ANOVAs and mean band coherence computations also exhibited characteristic differences for SO- and SS-sentences in this detailed time-frequency analysis. Whereas before the beginning of the RC (pre-RC) there are no obvious coherence differences between sentence types, both the RC and the post-RC intervals exhibit prominent coherence differences for the SS- and SO-sentences. Coherence is higher for SO-sentences at the beginning of and during the relative clause mainly within higher frequency ranges (30 to 50 Hz) and later in the course

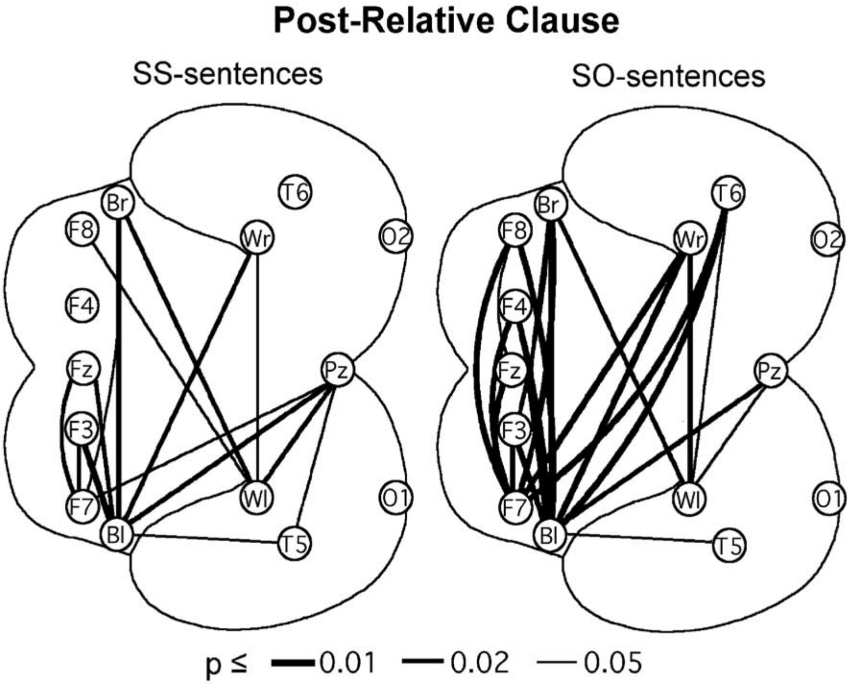

Fig. 4. Coherence changes in the post-RC for subject–subject (SS)- and subject–object (SO)-sentences compared to the mean coherence before sentence onset (1500 ms pre-sentence baseline) for the theta band. The significance of coherence changes corresponds to the thickness of the lines between two electrodes. The thickest line relates to an error probability of $p \leq 0.01$, the other lines to error probabilities of $p \leq 0.02$ and $p \leq 0.05$, respectively.

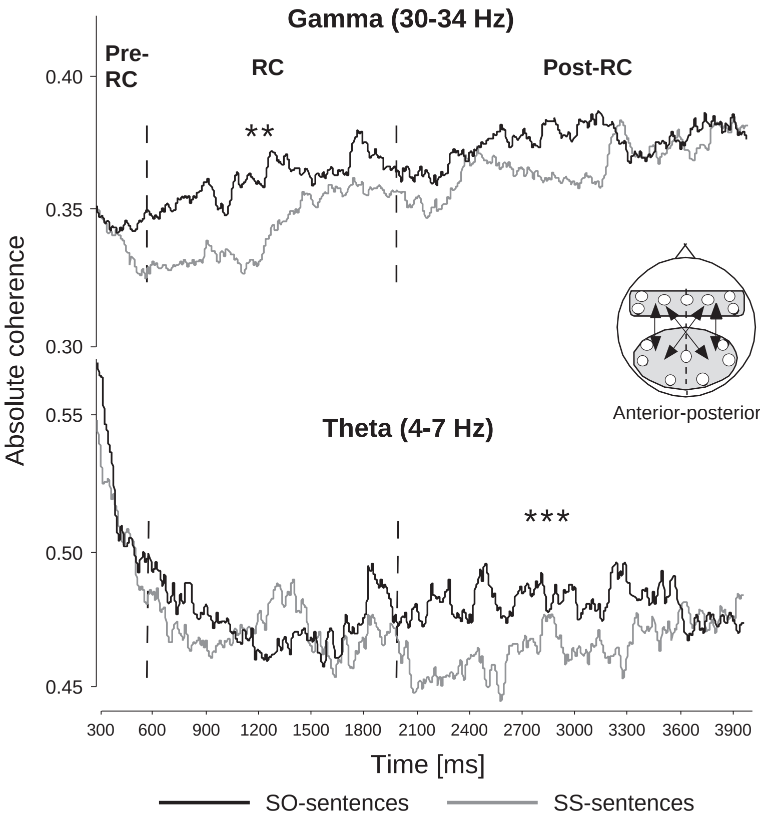

Fig. 5. Absolute coherence in the course of sentence comprehension. Coherence is mostly higher whilst participants are processing SO-sentences. However, theta and gamma frequency ranges exhibit this ubiquitous effect differently dependent on the sentence interval analyzed. Significant differences in the sentence intervals obtained with ANOVAs are marked with stars.

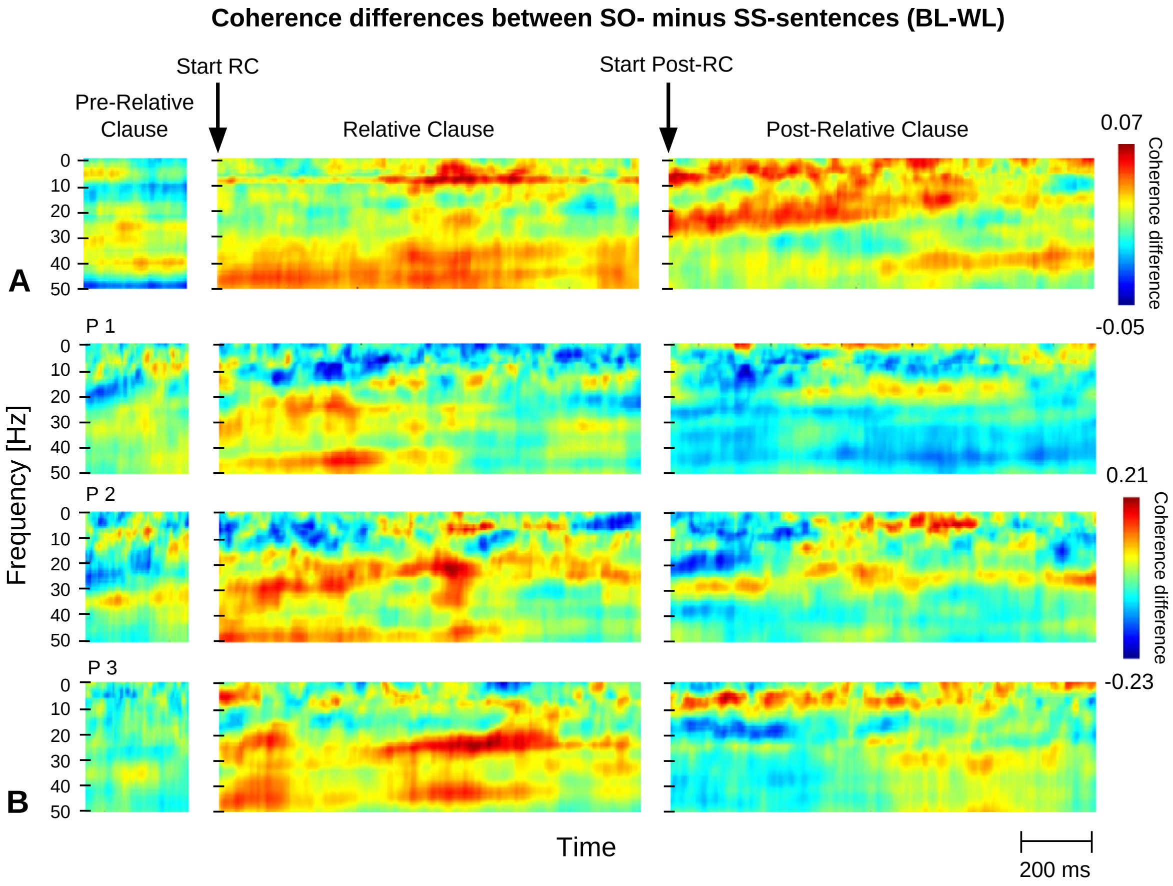

Fig. 6. Time-frequency matrices of coherence demonstrating the differences between SO- and SS-sentences for the electrode pair bl–wl. (A) Grand average (18 participants). (B) Results of three different single participants (P1, P2, P3). The frequency range goes from 0 to 50 Hz, with a resolution 0.5 Hz. Red color means higher coherence for SO-sentences. The most sensitive frequencies reflecting higher coherence for SO-sentences in the relative clause lie in the gamma range (30 to 50 Hz) and later in time also in the theta and alpha ranges (2–10 Hz). Exactly at the beginning of the post-relative clause they switch to theta, alpha and beta ranges (2 to approximately 30 Hz).

of the relative clause also in lower frequency bands (2 to 10 Hz). In contrast, the most prominent coherence differences in the post-RC are in lower frequency bands (2–8 Hz and 20 to 30 Hz) throughout (Fig. 6A). Fig. 6B demonstrates the individual time-frequency patterns for three single participants.

4. Discussion

The main finding in the present study was that EEG coherence did reliably differ during the processing of SS-relatives and SO-relatives both across the relative clause (RC) and in the post-relative clause region (post-RC). Moreover, the particular frequency bands (theta, beta-1, gamma) within which these coherence differences were observed were a function of the sentence interval examined.

4.1. Theta oscillations across the relative clause

Though gamma seemed to be the most prevalent frequency band affected in the RC, the theta band also showed a significant anterior–posterior coherence difference between the two sentence types—a difference that increased during the course of the RC interval. Specifically, anterior–posterior theta coherence was greater for SO-relative clauses within each hemisphere but greater for SS-relative clauses between hemispheres. The greater anterior–posterior theta coherence accompanying the processing of SO-relative clauses may reflect the greater demands these clauses impose on verbal working memory and fits well with the hypothesized involvement of a bilateral fronto-parietal network in verbal working memory processes (Mottaghy et al., 2002; Sarnthein et al., 1998; Weiss et al., 2000; Weiss and Rappelsberger, 2000). In ERP studies, SO-relative clause processing elicits a greater relative negativity at frontal and central sites in both the visual and auditory modalities hypothesized to reflect an increased load on verbal working memory (King and Kutas, 1995; Mueller et al., 1997a). A greater WM load could be expected during the RC for SO-relative clause sentences either because the main clause noun lacks a thematic role for a greater duration, or because a provisional role (of agent) must be revised during RC processing. In the SS-relative clause sentence, the actor represented by the main clause noun has a known role earlier in processing, and if a provisional canonical role (agent) were assigned, it would not require revision during the RC. It is this added verbal WM load for SO-relative clauses that is presumably reflected in the increasing anterior–posterior coherence observed. This accords with prior reports that theta activity during language processing is associated with the activation of the verbal working memory and episodic memory (Bastiaansen and Hagoort, 2003; Klimesch, 1999; Roehm et al., 2001; Weiss et al., 2000). Specifically, episodic memory encoding was associated with an increase in spectral coherence between frontal and temporo-parietal sites (Weiss and Rappelsberger, 2000; Weiss et al., 2000) and higher theta phase synchronization (Schack and Weiss, 2003, 2005). Theta power also was observed to gradually increase in the course of sentence processing at temporal electrodes of both hemispheres as well as over anterior–central electrodes (Bastiaansen et al., 2002). This was tentatively taken to mean that theta power reflects the gradual building up of a memory trace related to the encoding of the linguistic episode. Bastiaansen and Hagoort (2003) hypothesized that two different theta processes–theta phase resetting and power increase–underlie general WM operations and storage or retrieval processes. This distinction seemed to be confirmed in a recent study (Schack and Weiss, 2003, 2005) demonstrating that at least two mechanisms were associated with increased theta power during memory encoding: namely, theta power increases in the 5.5–7.5 Hz range indicating engagement of more neural resources during successful memory encoding and theta power increase in the 4.0–5.0 Hz range, caused by more precise time-locking, indicating that these slow theta waves occurred with the same latency after stimulus onset. Since spectral coherence would not separate out these processes we can assume that both the activation of more neuronal resources and a more precise time-locking may have contributed to the present findings in the theta frequency range.

As mentioned above, SS-relatives also showed increased anterior–posterior coherence in the theta band during the relative clause but only across the hemispheres. Perhaps, this effect is related to the presence of a phasic negativity in the ERP at the end of the relative clause in SS-relatives compared to the more prolonged negativity characterizing the relative clause in SO-relatives. Following this negativity, ERPs to SS-relative clauses show a large frontal positivity which might index successful integration in the SS-sentences whereas the ERP for the SO-sentences stays negative (Mueller et al., 1997a). Meaning construction is a highly dynamic process which temporally differs for these two sentence types. Whereas the semantic–pragmatic analysis in the SS-relative clause may begin early in the relative clause and may be finished around the time of the clause end, it presumably begins substantially later in the SO-sentences and is more prominent in the post-RC interval. The earlier onset of analysis in the SS-relative clauses is likely to impose earlier demands on the episodic memory system which might be expressed in increased interaction between hemispheres in the theta band during the course of the relative clause. In SO-sentences the higher demands on episodic memory start later and continue beyond the relative clause consistent with our finding that interhemispheric anterior–posterior theta coherence for SO-sentences was higher in the post-relative clause region. Based on the literature, we expected semantic–pragmatic analyses to be associated with higher coherence for SS-sentences in the beta bands, since beta activities have been correlated with sentence comprehension and semantic memory processes (Haarmann et al., 2002; Mueller et al., 1997a; Roehm et al., 2001; Weiss and Rappelsberger, 1996). Though mean beta coherence was higher for SS than SO sentences in the RC-interval this effect was not significant.

4.2. Gamma oscillations across the relative clause

We also obtained prominent coherence differences in the gamma band. At the beginning of the relative clause, as soon as there was a working memory difference for SS- vs. SO-relatives, the processing of SO-sentences was associated with higher gamma coherence. This effect was widespread, being evident in anterior, posterior and anterior–posterior coherence. This coherence difference in the gamma band continued until the end of the RC, though unlike the concomitant coherence in the theta band, it tended to decrease across the course of the relative clause. Posterior and anterior–posterior gamma coherence was especially high for SO-sentences over right hemispheric electrodes.

Although these gamma coherence differences occurred at the beginning of the relative clause and gamma oscillations have been related to memory processes, a mere association with working memory load does not seem very plausible. Frequencies in the gamma range have been found to be very sensitive to task-related cerebral activation in humans and to be affected by episodic verbal memory. Increased gamma synchronization at fronto-central and parietal scalp electrode sites in healthy humans (Schack and Weiss, 2003, 2005) and between rhinal cortex and hippocampus regions in individuals with epilepsy (Fell et al., 2001) was found to be correlated with successful verbal memory encoding. Gamma activity with a frontal and occipito-temporal focus also has been associated with the maintenance of information in visual short-term memory (e.g., Bertrand and Tallon-Baudry, 2000). If the gamma band activity in our study were related to working memory or episodic memory processes, then we would have expected the coherence differences to have continued beyond the relative clause into the post-relative clause region. However, this was only true for posterior gamma coherence which is not a very likely index of working memory processes, because this difference between SO- and SS-relatives decreased in the post-RC.

Considering that our results showed widespread gamma coherence for SO-relative clauses, it is intriguing to suggest that other cognitive activities–such as selective attention (Fell et al., 2003a,b)–also may contribute to the observed gamma synchronization. It is not unreasonable to assume that SO-relatives require greater attentional effort to process as listeners realize not only that they are faced with a relative clause construction (as heralded by the "who") but that it is the less frequently occurring, more difficult SO-relative rather than an SS-relative clause. If this is basis for the increased gamma coherence, it is related to the general finding that gamma synchronization is influenced by task complexity (Simos et al., 2002). Gamma involvement during semantic integration in sentence processing was also demonstrated by Braeutigam et al. (2001). At present, these interpretations are speculative. To assess the extent to which different gamma activities are involved at this aspect of relative clause processing requires further investigations on sentence processing using specific linguistic manipulations.

So far we have discussed coherence changes in the theta and gamma bands independently. According to Basar et al. (2001), however, it is impossible to assign a single function to a given type of oscillatory activity. It is thus unlikely that theta has a single role in language processing. In fact, theta's role and its varying patterns of coherence as a function of task demands may be better seen in its relationship to beta and gamma. Accordingly, it may be important to consider the simultaneous changes in the coherence patterns in the different frequency ranges. In fact, over the past few years, an increasing number of reports have noted various relationships between memory processes and both theta and gamma oscillations in humans (e.g., Kahana et al., 2001 for review). Fell et al. (2003a,b), in particular, proposed that theta-mediated rhinal–hippocampal synchronization may accompany the fast coupling and decoupling processes in the gamma range, which are probably more closely related to declarative memory formation. In their opinion, this finding may partly confirm the "theta–gamma" hypothesis (e.g., Jensen and Lisman, 1998) postulating that theta and gamma interact in the process of storing representations in declarative memory. Consistent with this view, a strong non-linear phase-coupling has been demonstrated via cross-bicoherence between theta and gamma activities at frontal electrode sites during short-term memory processes (Schack et al., 2002). It was hypothesized that different memory items become serially active in sequential gamma subcycles of theta cycles and that gamma frequencies are probably amplitude modulated by theta oscillations (Schack et al., 2002). Moreover, episodic memory encoding was associated with theta–gamma phase synchronization between signals at different cortical sites (Schack and Weiss, 2003, 2005).

4.3. Theta oscillations across the post-relative clause

If theta oscillations do indeed reflect working memory load and updating of episodic memory information during processing of these sentences, we would expect to see continued modulations in this frequency band in the post-relative clause region. In the post-relative clause, different cognitive operations such as semantic–pragmatic analysis and complex thematic role assignment would be expected to have an even greater impact on these memory systems. And, in fact, SO-sentences were associated with greater theta coherence within anterior and posterior and between anterior and posterior sites than SS-sentences in the post RC region. This widespread coherence increase may be related to the ERP data showing a relatively greater prolonged negativity in the post-relative clause of SO-sentences, that was pronounced at posterior temporal sites and tentatively linked to an increased demand on working memory (e.g., King and Kutas, 1995; Mueller et al., 1997a).

Theta coherence was significantly increased for SO-sentences compared to SS-sentences at both anterior and posterior sites. Thus, not only the interaction between anterior and posterior regions but also the interactions within them differed in the post-RC interval. Processing SO-post-relative clauses was associated with increased theta coherence between right and left hemisphere frontal sites. Perhaps the integration of right-hemispheric resources reflects updating and retrieval processes in episodic memory, known to activate right frontal cortex (Tulving et al., 1994).

4.4. Beta oscillations across the post-relative clause

A significant difference between SS- and SO-post-relative clauses was also found in the beta-1 band; this difference was restricted to the post-relative clause interval. SO-relatives were associated with higher posterior and anterior–posterior coherence in the beta-1 frequency band.

As previously mentioned, semantic–pragmatic analysis in the sense of building up action-related scenarios, has to be performed during sentence processing. This process presumably peaks in the post-relative clause region where the thematic roles of the SO-sentence must finally be resolved ("who did what to whom"). An association of beta-1 activities with the semantic–pragmatic analysis during this sentence interval is reasonable. Beta oscillations are presumably involved in the building of scenarios and possibly in the integration of semantic word-knowledge from semantic memory in support of meaning construction. This is in line with a recent study reporting increases in beta coherence between frontal and parietal leads in association with the activation of semantic working memory (Haarmann et al., 2002). Beta also has been found to participate in the assignment of syntactic structure in determining sentence meaning (Mueller et al., 1997b; Weiss et al., 2001, 2002), sentence comprehension (Roehm et al., 2001) and word processing at a semantic level (Weiss and Rappelsberger, 1996). Accordingly we suggest that the semantic–pragmatic analysis leading to meaning construction imposes enormous demands on both the episodic and the semantic working memory systems which are expressed in the massive synchronization of theta oscillations in the post-relative clause regions of these sentences. Possible distinct links between the verbal working memory system and theta activity and using syntactic structure to determine sentence meaning and beta activity might follow from patient data showing reduced verbal working memory capacity in the face of reasonable sentence comprehension (Caplan and Waters, 1999).

In conclusion, EEG coherence analyses yielded new results on the temporal dynamics and parallel activation of networks oscillating at different frequencies, thereby providing evidence on the possible roles of different brain oscillations and their involvement in spoken sentence processing. In particular, the use of a temporally more sensitive algorithm for the calculation of EEG coherence allows for monitoring transient functional coherence changes associated with different operations across sentence comprehension. Future studies might be informative by time-locking coherence to specific words within the RC and post-RC epochs such as the main clause verb, for instance. This would allow to make predictions about differences in verb processing between these sentences and to better understand the dynamics of processes that underlie general findings in this paper.

In correspondence with previous ERP data demonstrating an increased widespread negativity during the processing of SO-sentences, we find a concomitant increase in EEG coherences. SS- and SO-relatives showed different large-scale networks of cooperativity in the theta, beta and gamma frequency bands occurring across different regions of sentences with embedded relative clauses causing increased interaction between left- and right-hemispheric and anterior and posterior neuronal resources. We suggested theta changes were associated with memory processes, gamma with attentional effort, and beta-1 with semantic–pragmatic integration. The simultaneous presence of systematic differences in the theta, beta and gamma frequency bands during the processing of SS- and SO-sentences argues for the existence of parallel processes during the comprehension of these sentences. This conclusion accords well with interactive models that suggest that phonologic, morpho-syntactic, semantic and pragmatic levels interact continuously so that the comprehender can arrive at the most plausible meaning of a sentence (e.g., Marslen-Wilson and Tyler, 1980).

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References

Basar, E., Basar-Eroglu, C., Karakas, S., Schürmann, M., 2001. Gamma, alpha, delta, and theta oscillations govern cognitive processes. Int. J. Psychophysiol. 39, 241–248.

Bastiaansen, M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. Cortex 39, 967–992.

Bastiaansen, M.C.M., Berkum, J.J.A., Hagoort, P., 2002. Syntactic processing modulates the θ rhythm of the human EEG. Neuroimage 17, 1479–1492.

Bertrand, O., Tallon-Baudry, C., 2000. Oscillatory gamma activity in humans: a possible role for object representations. Int. J. Psychophysiol. 38, 211–223.

Braeutigam, S., Bailey, A.J., Swithenby, St.J., 2001. Phase-locked gamma band responses to semantic violation stimuli. Cogn. Brain Res. 10, 365–377.

Bressler, S.L., Kelso, J.A.S., 2001. Cortical coordination dynamics and cognition. Trends Cogn. Sci. 5, 26–36.

Brown, C.M., Hagoort, P., 1999. The Neurocognition of Language. Oxford University Press, New York.

Caplan, D., Waters, G.S., 1999. Verbal working memory and sentence comprehension. BBS 22, 7–126.

Cooke, A., DeVita, C., Gee, J., Alsop, D., Detre, J., Chen, W., Grossman, M., 2003. Neural basis for sentence comprehension deficits in frontotemporal dementia. Brain Lang. 85, 211–221.

Essl, M., Rappelsberger, P., 1998. EEG coherence and reference signals: experimental results and mathematical explanations. Med. Biol. Eng. Comput. 36, 399–406.

Fell, J., Klaver, P., Lehnertz, K., Grunwald, T., Schaller, C., Elger, C.E., Fernandez, G., 2001. Human memory formation is accompanied by rhinal-hippocampal coupling and decoupling. Nat. Neurosci. 4, 1259–1264.

Fell, J., Fernandez, G., Klaver, P., Elger, C.E., Fries, P., 2003a. Is synchronized neuronal gamma activity relevant for selective attention? Brain Res. Rev. 42, 265–272.

Fell, J., Klaver, P., Elfadil, H., Schaller, C., Elger, C.E., Fernández, G., 2003b. Rhinal–hippocampal theta coherence during declarative memory formation: interaction with gamma synchronization? Eur. J. Neurosci. 17, 1082–1088.

Grossman, M., Koenig, P., Glosser, G., DeVita, C., Moore, P., Rhee, J., Detre, J., Alsop, D., Gee, J., 2003. Neural basis for semantic memory difficulty in Alzheimer's disease: an fMRI study. Brain 126, 292–311.

Gur, R.C., Packer, I.K., Hungerbuhler, J.P., Reivich, M., Obrist, W.D., Amarnek, W.S., Sackeim, H.A., 1980. Differences in the distribution of gray and white matter in human cerebral hemispheres. Science 207, 1226–1228.

Haarmann, H.J., Cameron, K.A., Ruchkin, D.S., 2002. Neural synchronization mediates on-line sentence processing: EEG coherence evidence from filler-gap constructions. Psychophysiology 39, 820–825.

Holmes, V.M., O'Regan, J.K., 1981. Eye fixation patterns during the reading of relative clause sentences. J. Verbal Learn. Verbal Behav. 20, 417–430.

Homae, F., Yahata, N., Sakai, K.L., 2003. Selective enhancement of functional connectivity in the left prefrontal cortex during sentence processing. Neuroimage 20, 578–586.

Hsiao, F., Gibson, E., 2003. Processing relative clauses in Chinese. Cognition 90, 3–27.

Kahana, M.J., Seelig, D., Madsen, J.R., 2001. Theta returns. Curr. Opin. Neurobiol. 11, 739–744.

King, J., Just, M.A., 1991. Individual differences in syntactic processing. The role of working memory. J. Mem. Lang. 30, 580–602.

King, J.W., Kutas, M., 1995. Who did what and when? Using word- and clause-level ERPs to monitor working memory usage in reading. J. Cogn. Neurosci. 7, 376–395.

Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res. Rev. 29, 169–195.

Kutas, M., 1997. Views on how the electrical activity that the brain generates reflects the functions of different language structures. Psychophysiology 34, 383–398.

Jensen, O., Lisman, J.E., 1998. An oscillatory short-term memory buffer model can account for data on the Sternberg task. J. Neurosci. 18, 10688–10699.

Just, M.A., Carpenter, P.A., Keller, T.A., Eddy, W.F., Thulborn, K.R., 1996. Brain activation modulated by sentence comprehension. Science 274, 114–116.

Mak, W.M., Vonk, W., Schriefers, H., 2002. The influence of animacy on relative clause processing. J. Mem. Lang. 47, 50–68.

Marslen-Wilson, W., Tyler, L.K., 1980. The temporal structure of spoken language understanding. Cognition 8, 1–71.

Miyamoto, E.T., Nakamura, M., 2003. Subject/object asymmetries in the processing of relative clauses in Japanese. In: Garding, G., Tsujimura, M. (Eds.), Proceedings of the 22nd WCCFL, Somerville. MA Cascadilla Press, pp. 342–355.

Mottaghy, F.M., Doering, T., Mueller-Gaertner, H.-W., Toepper, R., Krause, B.J., 2002. Bilateral parieto-frontal network for verbal working memory: an interference approach using repetitive transcranial magnetic stimulation (rTMS). Eur. J. Neurosci. 16, 1627–1632.

Mueller, H.M., King, J.W., Kutas, M., 1997a. Event-related potentials elicited by spoken relative clauses. Cogn. Brain Res. 5, 193–203.

Mueller, H.M., Weiss, S., Rappelsberger, P., 1997b. EEG coherence analysis of auditory sentence processing. In: Witte, H., Zwiener, U., Schack, B., Doering, A. (Eds.), Quantitative and Topological EEG and MEG Analysis. Universitätsverlag, Jena, pp. 429–431.

Muente, T.F., Schwirtz, O., Wieringa, B.M., Matzke, M., Johannes, S., 1997. Elektrophysiologie komplexer Sätze: ereigniskorrelierte potentiale auf der wort- und satzebene. Z. EEG-EMG 28, 11–17.

Nikolaev, A.R., Ivanitsky, G.A., Ivanitsky, A.M., Posner, M.I., Abdullaev, Y.G., 2001. Correlation of brain rhythms between frontal and left temporal (Wernickes's) cortical areas during verbal thinking. Neurosci. Lett. 298, 107–110.

Nunez, P.L., Srinivasan, R., Westdorp, A.F., Wijesinghe, R.S., Tucker, D.M., Silberstein, R.B., Cadush, P.J., 1997. EEG coherency I: statistics, reference electrode, volume conduction, Laplacians, cortical imaging, and interpretation at multiple scales. Electr. Clin. Neurophysiol. 103, 499–515.

Petsche, H., Etlinger, S. (Eds.), 1998. EEG and Thinking. Austrian Academy of Sciences, Vienna.

Pulvermueller, F., Birbaumer, N., Lutzenberger, W., Mohr, B., 1997. High frequency brain activity: its possible role in attention, perception and language processing. Prog. Neurobiol. 52, 427–445.

Rappelsberger, P., 1998. Probability mapping of power and coherence: technical aspects. In: Petsche, H., Etlinger, S. (Eds.), EEG and Thinking. Austrian Academy of Sciences, Vienna, pp. 63–78.

Roehm, D., Klimesch, W., Haider, H., Doppelmayr, M., 2001. The role of theta and alpha oscillations for language comprehension in the human electroencephalogram. Neurosci. Lett. 310, 137–140.

Sakai, K.L., Hashimoto, R., Homae, F., 2001. Sentence processing in the cerebral cortex. Neurosci. Res. 39, 1–10.

Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G.L., von Stein, A., 1998. Synchronization between prefrontal and posterior association cortex during human working memory. Proc. Natl. Acad. Sci. U. S. A. 95, 7092–7096.

Schack, B., Weiss, S., 2003. Phase synchronization—a mechanism for neural integration for event-related potentials. Biomed. Tech. 48, 150–153.

Schack, B., Weiss, S., 2005. Quantification of phase synchronization phenomena and their importance for verbal memory process. Biol. Cyber. 92, 275–287.

Schack, B., Bareshova, E., Grieszbach, G., Witte, H., 1995a. Methods of dynamic spectral analysis by self-exciting autoregressive moving average models and their application to analysing biosignals. Med. Biol. Eng. Comput. 33, 492–498.

Schack, B., Grieszbach, G., Arnold, M., Bolten, J., 1995b. Dynamic cross-spectral analysis of biological signals by means of bivariate ARMA processes with time-dependent coefficients. Med. Biol. Eng. Comput. 33, 605–610.

Schack, B., Grieszbach, G., Nowak, H., Krause, W., 1999. The sensitivity of instantaneous coherence for considering elementary comparison processing: Part I. The relationship between mental activities and instantaneous EEG coherences. Int. J. Psychophysiol. 31, 219–240.

Schack, B., Vath, N., Petsche, H., Geissler, H.G., Möller, E., 2002. Phase-coupling of theta–gamma EEG rhythms during short-term memory processing. Int. J. Psychophysiol. 44, 143–163.

Schack, B., Weiss, S., Rappelsberger, P., 2003. Cerebral information transfer during word processing: where and when does it occur and how fast is it? Hum. Brain Mapp. 19, 18–36.

Schriefers, H., Friederici, A.D., Kuehn, K., 1995. The processing of locally ambiguous relative clauses in German. J. Mem. Lang. 34, 499–520.

Simos, P.G., Papanikolaou, E., Sakkalis, E., Micheloyannis, S., 2002. Modulation of gamma band spectral power by cognitive task complexity. Brain Topogr. 14, 191–196.

Singer, W., 1999. Striving for coherence. Nature 397, 391–393.

Singer, W., 2002. Cognition, gamma oscillations and neuronal synchrony. In: Reisin, R.C., Nuwer, M.R., Hallett, M., Medina, C. (Eds.), Advances in Clinical Neurophysiology. Elsevier, pp. 3–22.

Tavakolian, S., 1981. The conjoined clause analysis of relative clauses. In: Tavakolian, S. (Ed.), Language Acquisition and Linguistic Theory. MIT Press, Cambridge, MA.

Thatcher, R.W., Krause, P.J., Hrybyk, M., 1986. Cortico-cortical associations and EEG coherence: a two-compartmental model. Electr. Clin. Neurophysiol. 64, 123–143.

Tulving, E., Kapur, S., Craik, F.I.M., Moscovitch, M., Houle, S., 1994. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. Proc. Natl. Acad. Sci. U. S. A. 91, 2016–2020.

Varela, F., Lachaux, J.-P., Rodriguez, E., Martinierie, J., 2001. The brainweb: phase synchronization and large-scale integration. Nat. Rev., Neurosci. 2, 229–239.

Weiss, S., Mueller, H.M., 2003. The contribution of EEG coherence to the investigation of language. Brain Lang. 85, 325–343.

Weiss, S., Rappelsberger, P., 1996. EEG coherence within the 13–18 Hz band as a correlate of a distinct lexical organisation of concrete and abstract nouns in humans. Neurosci. Lett. 209, 17–20.

Weiss, S., Rappelsberger, P., 1998. Left frontal EEG coherence reflects modality independent language processes. Brain Topogr. 11, 33–42.

Weiss, S., Rappelsberger, P., 2000. Long-range EEG synchronization during word encoding correlates with successful memory performance. Cogn. Brain Res. 9, 299–312.

Weiss, S., Mueller, H.M., Rappelsberger, P., 2000. Theta synchronisation predicts efficient memory encoding of concrete and abstract nouns. NeuroReport 11, 2357–2361.

Weiss, S., Mueller, H.M., King, J.W., Kutas, M., Rappelsberger, P., 2001. EEG-coherence analysis of naturally spoken English relative clauses. Brain Topogr. 13, 317.

Weiss, S., Mueller, H.M., King, J.W., Kutas, M., Schack, B., Rappelsberger, P., 2002. Theta and beta synchronization reflect different processes during language comprehension. Int. J. Psychophysiol. 45, 45.