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Research Report

An inverse relation between event-related and time–frequency violation responses in sentence processing

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ABSTRACT

The relationship between semantic and grammatical processing in sentence comprehension was investigated by examining event-related potential (ERP) and event-related power changes in response to semantic and grammatical violations. Sentences with semantic, phrase structure, or number violations and matched controls were presented serially (1.25 words/s) to 20 participants while EEG was recorded. Semantic violations were associated with an N400 effect and a theta band increase in power, while grammatical violations were associated with a P600 effect and an alpha/beta band decrease in power. A quartile analysis showed that for both types of violations, larger average violation effects were associated with lower relative amplitudes of oscillatory activity, implying an inverse relation between ERP amplitude and event-related power magnitude change in sentence processing.

1. Introduction

Electrophysiology has been applied in sentence processing research to understand how words are incrementally interpreted during sentence comprehension. Because words are understood sequentially over time, measures of brain activity for sentence processing must resolve activity associated with each individual word as it appears within a sentence. Event-related potential (ERP) components, obtained by averaging EEG data with respect to the onset of a word embedded within a sentence, are now commonly used for measuring this response. EEG represents a spatial average of the bulk depolarization of groups of neurons that are oriented in such a way that their synchronized post-synaptic activity sums together as it fluctuates over time (Nunez and Srinivasan, 2006). Because of this, ERP responses can be used to investigate those aspects of post-synaptic neural activity which are sufficiently organized in time to be observed with EEG (or MEG) in the course of understanding a sentence. However, ERP responses only represent certain aspects of the information available in EEG recordings (Buzsáki, 2006; Başar, 1980), and there are additional methods available to examine event-related oscillatory activity which is not necessarily revealed with ERP averaging. The present work investigates whether semantic and grammatical processing produces similar event-related changes in power, and how ERP responses are related to this oscillatory activity during sentence processing.

Two of the most robust ERP components related to sentence-level processing are the N400 effect observed in response to semantic violations relative to control sentences (Kutas and Hillyard, 1980; Kutas and Federmeier, 2000), and the P600 effect (or Syntactic Positive Shift) observed in response to grammatical violations relative to control

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sentences (Hagoort et al., 1993; Osterhout and Holcomb, 1992). In either of these two effects, the response to a critical word (CW) embedded within a sentence is measured using either EEG or MEG sensors in an event-related violation design. In the case of semantic violation responses, the violation CW is arranged so that in a given sentence it is difficult to integrate the lexical meaning of the CW with the sentential meaning of the words that have preceded it (e.g., "The pizza was too hot to *cry*", Kutas and Hillyard, 1984). In the case of grammatical violation responses, the violation CW is chosen to be incompatible with a principle of grammar such as number agreement (e.g., "The children *walks* to school", Osterhout and Mobley, 1995) or a phrase structure principle (e.g., "Max's proof the *of* theorem…," Neville et al., 1991). Responses to violation CWs are compared to control CWs otherwise matched for important stimulus characteristics in order to determine when neural activity related to the violation first occurs after CW onset. This is taken as evidence that the linguistic contrast in question has been encoded or decoded in some form by the cortical network responsible for the ERP effect. In EEG recordings with commonly used reference electrode locations, the N400 effect is observed as a greater amplitude negative difference in potentials over posterior electrodes between responses to violation and control CWs at approximately 300 to 500 ms after CW onset. The P600 effect also has a posterior distribution and is observed as a greater average positive difference in potentials in a time window approximately 500 to 800 ms after CW onset. These two responses are seen by many researchers as indexes of neural activity related to either semantic (N400) or grammatical (P600) processing during sentence comprehension, although counterexamples or additional features of the effects are sometimes reported (Osterhout, 1997; Kuperberg et al., 2006).

In addition to the ERP averaging method, there are complementary time–frequency analysis techniques that can be used to investigate how the amplitude of oscillatory activity changes with time, also known as event-related synchronization or desynchronization analysis (Pfurtscheller et al., 1996; Demiralp et al., 1999; see Pfurtscheller and da Silva, 1999, for a review). These techniques have been more recently applied to data from sentence processing experiments using event-related designs (Bastiaansen and Hagoort, 2003, 2006), but the empirical relationship between oscillatory activity and ERP magnitude during sentence processing remains to be investigated. Conventional ERP averaging produces a measure which reflects activity which is (a) both oscillatory and aligned in phase with respect to the CW onset and/or (b) non-oscillatory, but occurring within a regular time window after CW onset. The assumption with ERP averaging is that background noise activity will cancel in the averaging process, leaving the phase-aligned and/or non-oscillatory responses. In contrast, in time–frequency analysis, each trial is analyzed in separate frequency bands or scales using band-pass filters, wavelet methods, or a Hilbert transform to produce a time-resolved measure of spectral power, which is then averaged over trials (for a review, see Bruns, 2004). The resulting average can reveal changes in power (as well as inter-trial coherence) as a function of time and frequency that are not apparent using ERP averages because it is not necessary that the EEG waveform be aligned in phase relative to the CW onset. Rather, changes in power which regularly occur sometime after CW onset will sum together in the average, whether or not the EEG waveform is aligned in phase with CW onset. These power changes are likely to be related to many different cognitive functions, because power changes in cortical activity have been observed in numerous other non-linguistic tasks (for reviews, see Başar et al., 1997; Klimesch, 1999; Klimesch et al., 2005; Makeig et al., 2004; Pfurtscheller et al., 1996; Pulvermueller, 2001; Tallon-Baudry and Bertrand, 1999; and the chapters in Neuper and Klimesch, 2006). Nevertheless, they can be taken as evidence of changes in neural activity in specific frequency bands, related to different experimental contrasts in linguistic tasks. In principle, differences observed using these techniques may be independent of ERP differences.

Previous research using time–frequency analysis has shown changes in power during sentence processing, although the frequencies with reported power changes vary across studies. Upper alpha band (10 to 12 Hz) power is reduced during auditory sentence listening, relative to either a rest control period (Krause et al., 1994) or relative to reversed presentation (Krause et al., 1997). In serial visual sentence presentation, increased power in the theta band has been observed over the course of a sentence (Bastiaansen et al., 2002a; Roehm et al., 2004). Similarly, power analyses applied to responses to individual words within sentences have shown that both theta and alpha band power can change after word presentation, and the response may be different depending on lexico-syntactic class. For example, a widespread reduction in alpha as well as beta band power after word onset has been observed, as well as an increase in theta band power over left hemisphere electrodes for open-class but not closed-class words (Bastiaansen et al., 2005; but see Khader and Rösler, 2004, for a report of a theta band decrease). In addition, measures of coherence (an index of a systematic phase relationship between signals recorded at different sensors at different frequencies or within a single sensor at different times) have shown the involvement of power in the theta, beta, and gamma bands in relative clause and working memory processing (Weiss et al., 2005; Haarmann and Cameron, 2005), the alpha band in spoken story comprehension (Kujala et al., 2006), and the theta band in response to semantic violations (Allefeld et al., 2005). As a whole, these studies indicate that power changes in the theta band (most often an increase) and the alpha band (most often a reduction) are related to word processing in sentence contexts.

Event-related violation designs can be used to examine responses to individual words within sentences. These designs have revealed changes in power in frequency bands like those reported for whole-sentence analyses, but in addition have shown how semantic or grammatical violations affect band power. Semantic violations are associated with an increase in theta band power versus a matched control CW (Bastiaansen et al., 2005; Hald et al., 2006), and similarly, world knowledge violations in a sentence context are also associated with an increase in theta band power, as well as the absence of a gamma band increase seen in response to control CWs (Hagoort et al., 2004). Braeutigam et al. (2001) observed a phase-locked gamma-band response to semantic violations using MEG. While there have been comparatively few tests for grammatical violation effects in event-related power, grammatical gender and number violation effects (in Dutch) have been shown to elicit a widely distributed theta band increase in power (Bastiaansen et al., 2002b). Roehm et al. (2004) also reported an increase in theta band power to case violations. It appears that across the event-related violation studies, an increase in theta band power is most often observed in response to either semantic or grammatical violations.

There is some evidence that ERP responses are related to event-related changes in power. Yordanova et al. (2001) have shown that during a (non-linguistic) oddball detection task, latencies of the peak P300 response were correlated with the magnitude of an alpha power reduction. Some results suggest that the P300 effect is the result of (phase-locked) power differences at sub-alpha frequencies (theta and delta; Başar-Eroglu et al., 1992; Yordanova and Kolev, 1998). To the extent that the P300 effect is similar to the violation responses for semantic and grammatical violation responses, it might be hypothesized that violation effect power differences would be found at these frequencies as well. In addition, previous work in sentence processing has not directly investigated the relationship between ERP violation responses and event-related power violation responses. The aim of the present research is to determine how ERP violation responses are related to power measures in sentence processing. Semantic and grammatical violation responses are compared within the same participants, as well as by relating variation over trials in the ERP response to variation over trials in the event-related power in different frequency bands.

2. Results

2.1. Event-related potentials

Fig. 1 shows the isopotential topography of the contrast between violation and control for the semantic, phrase structure, and number violation conditions, as well as traces of the ERP responses. In all cases, violation effects were observed in the time windows outlined in the Introduction. The semantic contrast was associated with a greater average negative potential over posterior electrodes in a time window of 300 to 500 ms post-onset of the critical word ($M=-1.21$ μV), consistent with an N400 effect, sum-$t=66.62$, $p<0.001$, with 17 electrodes (1, 3:7, 11:17, 26:29) in one cluster, the contrast negative in all participants. The phrase structure contrast was associated with a greater positive potential in a time window of 500 to 900 ms on posterior electrodes ($M=0.93$ μV), consistent with a P600 effect, in one centro-posterior cluster, sum-$t=19.34$, $p=0.006$, on seven electrodes (1, 4:6, 12:14), the contrast positive in 15/20 subjects. The number violation contrast was associated with a greater positive potential ($M=1.09$ μV) in a slightly shorter time window (600 to 800 ms), consistent with a P600 effect, in one marginally significant cluster, sum-$t=12.46$, $p=0.053$, in five posterior electrodes (13:14, 16, 27, 29), the contrast positive in 17/20 subjects. There were no significant Pearson correlations among the amplitudes of the ERP effects (Sem:Ps, $r=-0.174$; Sem:Nmbr, $r=-0.016$; Ps:Nmbr, $r=-0.131$, all n.s.). A comparison of earlier time windows in the phrase structure condition did not reveal any evidence of an anterior negativity, and a comparison of later time windows in the semantic condition did not reveal any evidence of a positive shift following the semantic violation.

The mixed effects analysis showed that for the semantic violation contrast, there was a significant main effect of violation, $F(1,2337)=23.674$, $p<0.001$; as well as a significant interaction between type of sentence and electrode location, $F(61,2337)=6.394$, $p<0.001$. Multiple comparisons revealed significant negative differences at seven central-posterior electrodes (1, 4:6, 13:15), as well as significant positive differences at four frontal electrodes (36, 49, 51, 61). The phrase structure violation resulted in a significant main effect of electrode location, $F(61,2337)=10.873$, $p<0.001$; as well as a significant interaction between type of sentence and electrode location, $F(61,2337)=2.842$, $p<0.001$; with significant positive differences at two central-posterior electrodes (14, 28), and significant negative differences at two frontal electrodes (36, 50). For the number violation, there was again a main effect of electrode location, $F(61,2337)=5.730$, $p<0.001$; as well as a significant interaction between type of sentence and electrode location, $F(61,2337)=1.850$, $p<0.001$; with a significant positive difference at electrode 14, and a significant negative difference at electrode 50.

The combined violation contrast was associated with a greater positive potential ($M=0.7655$ μV) in a 500- to 900-ms time window in one significant cluster, sum-$t=60.5721$, $p<0.001$, on 17 posterior electrodes (4:6, 12:16, 24:30, 41:42), the contrast positive in 18/20 participants. There was also a comparable negative cluster ($M=-0.7945$ μV), sum-$t=-37.6412$, $p=0.0016$, on 11 frontal electrodes (20:22, 34:37, 48:51, 61) in the same time window.

For mixed effects analysis of the combined condition, there was again a main effect of electrode location, $F(61,2337)=11.656$, $p<0.001$; as well as a significant interaction between type of sentence and electrode location, $F(61,2337)=5.6925$, $p<0.001$; with significant positive differences at six central-posterior electrodes (5, 13:15, 26, 28), and significant negative differences at four frontal electrodes (20, 36:37, 50).

2.2. Event-related power

Semantic violations were associated with an increase in theta band power (3 to 7 Hz) at bilateral posterior and left anterior electrode locations, as shown in Fig. 2. In contrast to this, phrase structure violations were associated with significant reduction of alpha band power with a broad scalp distribution, but no significant increase of theta band power. Somewhat similar to the phrase structure violation, the number contrast was associated with alpha band power reduction with a broad topographical distribution, and no theta power increase.

For the semantic contrast, there were two theta band clusters indicating a power increase for the semantic violation effect ($M=0.1131$ dBV at 3 to 7 Hz; 300 to 500 ms); the first sum-$t=44.06$, $p=0.002$, on 14 electrodes (12:14, 22:28, 38, 41:42, 51), and the second sum-$t=13.26$, $p=0.03$, on four electrodes (32, 48:49, 61). Summing over clusters, the contrast was positive in 19/20 participants. There was no significant power

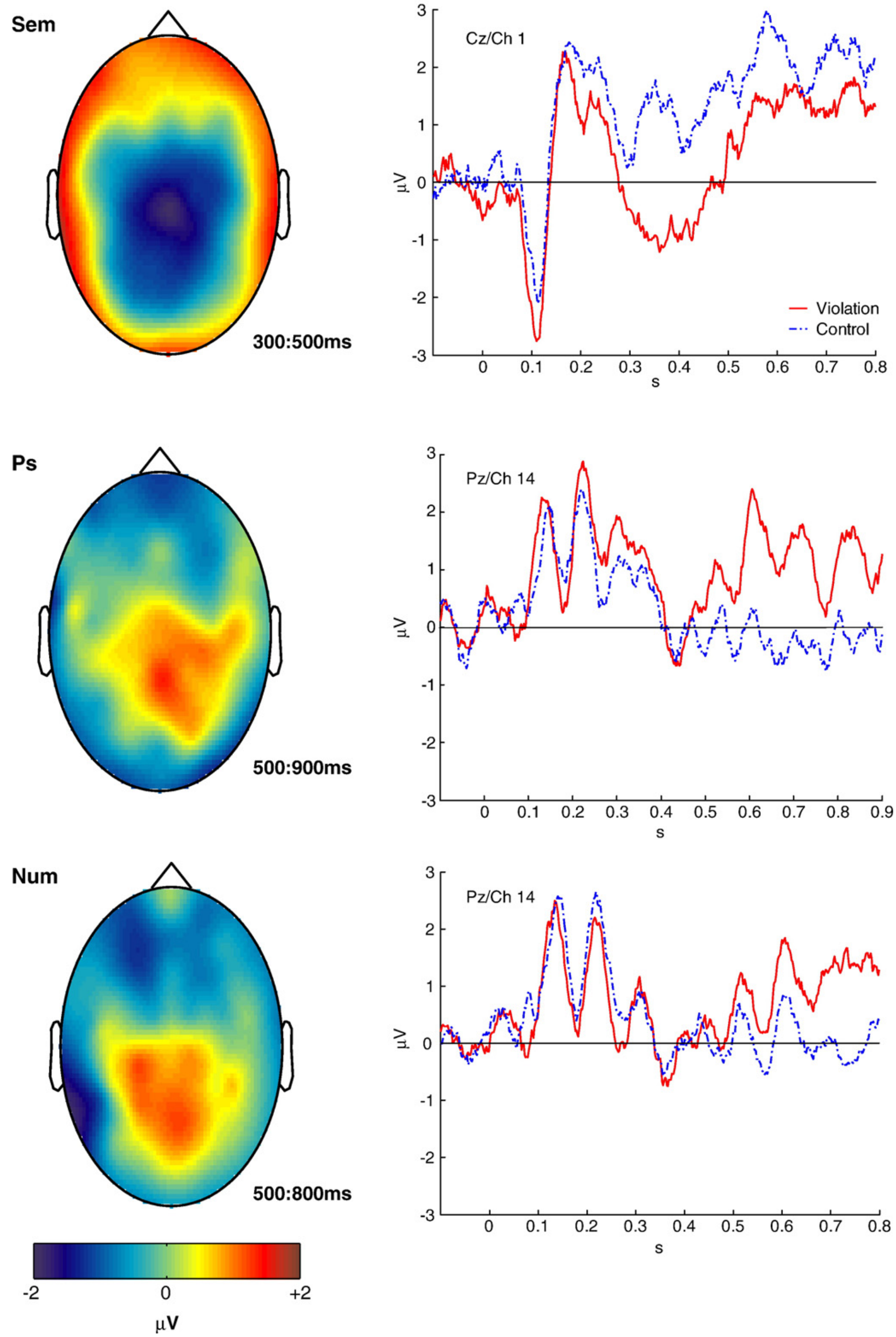

Fig. 1 – Semantic, phrase structure, and number violation ERP effects (violation–control). In the ERP traces, positive voltage is plotted upwards.

reduction for the semantic contrast. The mixed effects analysis showed a significant main effect of type of sentence for the semantic contrast, $F(1,2337)=211.371$, $p<0.001$; as well as a significant effect of electrode location, $F(61,2337)=1.508$, $p=0.007$; but no interaction between type of sentence and electrode location.

For the phrase structure contrast, in a combined alpha and beta band there were two significant clusters indicating a power decrease ($M=-0.1116$ dBV; 8 to 30 Hz; 500 to 900 ms), the first, sum-$t=33.79$, $p=0.005$, on 13 electrodes (6, 15:19, 30:34, 48, 50); the second, sum-$t=17.36$, $p=0.03$, on five electrodes (24:25, 38:40). Summing across the two clusters, the contrast

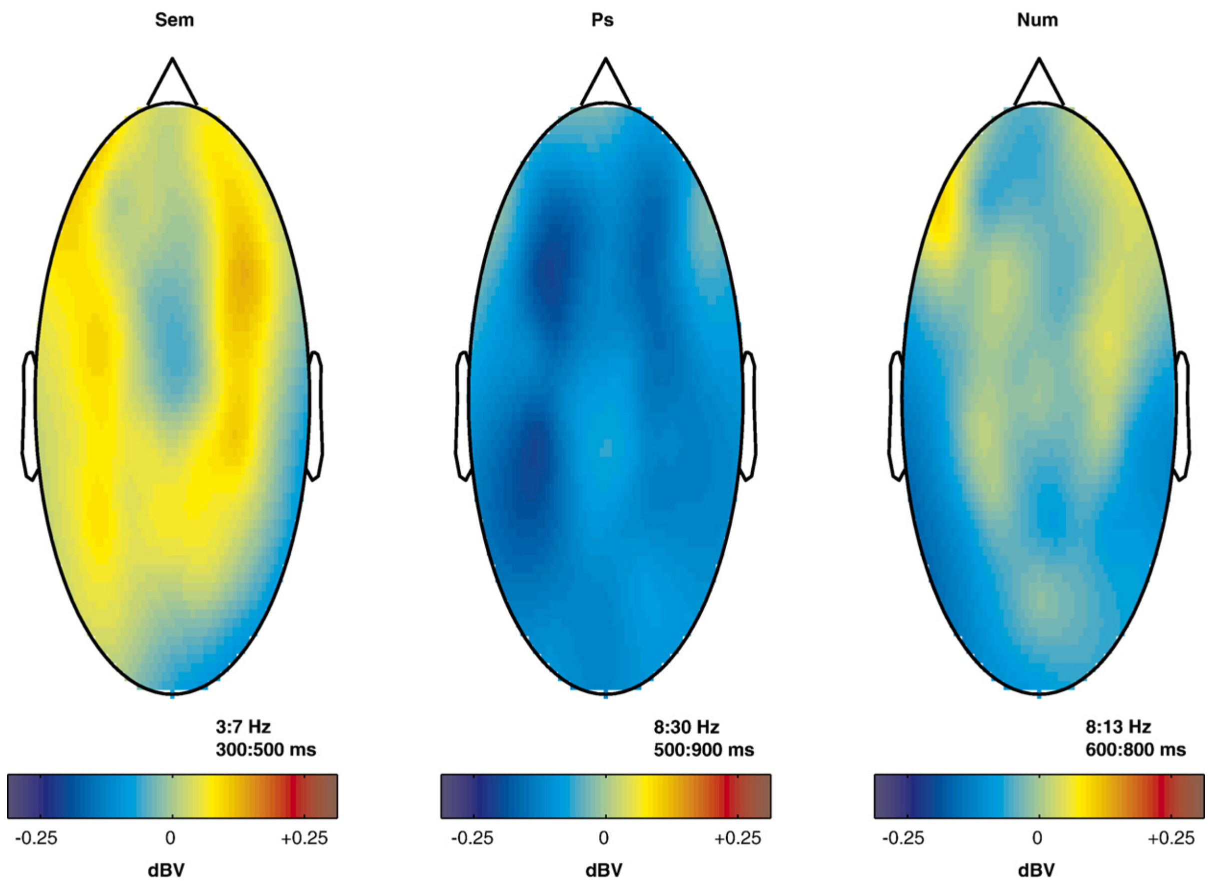

Fig. 2 – Semantic, phrase structure, and number violation relative power change effects (violation–control).

was negative in 18/20 participants. Separate analyses of the beta band (13 to 30 Hz, sum-t=14.22, p=0.04, on four electrodes (24, 38:40)), and the alpha band (8 to 12 Hz, sum-t=87.48, p<0.001, on 27 electrodes (2:3, 6:11, 16:22, 30:34, 44:47, 50, 57:58)) both revealed power reductions, although the alpha band effect was more widespread. There was no change in theta band power for the phrase structure contrast in the same time window. One electrode (6) shared both the P600 phrase structure violation and the alpha/beta reduction effect. The mixed effects analysis showed a significant main effect of the type of sentence, $F(1,2337)=314.457$, $p<0.001$; as well as a marginal effect of the electrode location, $F(61,2337)=1.290$, $p=0.07$, but no interaction between the type of sentence and electrode location.

For the number violation contrast, in the alpha band there was also a decrease in power ($M=-0.1596$ dBV; 8 to 13 Hz; 600 to 800 ms), in one marginally significant cluster, sum-t=10.375, p=0.069, on four electrodes (41, 53:55), the contrast negative in 15/20 participants. There were no event-related power differences in the theta or beta bands for the number contrast. There were no significant correlations among the amplitudes of the TFR effects (Sem:Ps, $r=-0.128$; Sem:Nmbr, $r=-0.312$; Ps:Nmbr, $r=0.198$, all n.s.). The mixed effects analysis showed a significant main effect of the type of sentence, $F(1,2337)=170.978$, $p<0.001$; but no main effect of electrode location or interaction between type of sentence and electrode location.

For the combined phrase structure and number violation contrast, there was a decrease in power in the alpha band ($M=-0.1357$ dBV; 8 to 13 Hz; 500 to 900 ms), in one significant cluster, sum-t=30.90, p=0.019, on 12 electrodes (14, 27:28, 41:45, 55:58), the contrast negative in 15/20 participants. In the beta band there was also a decrease in power ($M=-0.0866$ dBV; 14 to 30 Hz; 500 to 900 ms), in one significant cluster, sum-t=32.12, p=0.008, on 11 electrodes (23:26, 38:41, 53:55), the contrast negative in 17/20 participants. There was no event-related power difference in the theta band for the combined contrast. There were four electrodes (24:26, 41) showing the beta effect that also showed the ERP violation effect. The alpha reduction effect itself was moderately correlated with the beta reduction effect, $r=0.583$, $p=0.007$, but only two electrodes (41, 55) overlapped between the two. The mixed effects analysis showed a significant main effect of type of sentence, $F(1,2337)=243.011$, $p<0.001$; but no main effect of electrode location or interaction between type of sentence and electrode location. Fig. 3 shows time–frequency representations of the semantic and combined syntactic conditions, averaged over the electrodes included in the significant clusters identified in the above analysis.

The trial-based quartile analysis (see Experimental procedure) showed an inverse relationship between relative band power and violation effect magnitudes for theta and alpha but not beta band power. Fig. 4 shows that for the semantic trials, a greater relative increase in theta power was associated with

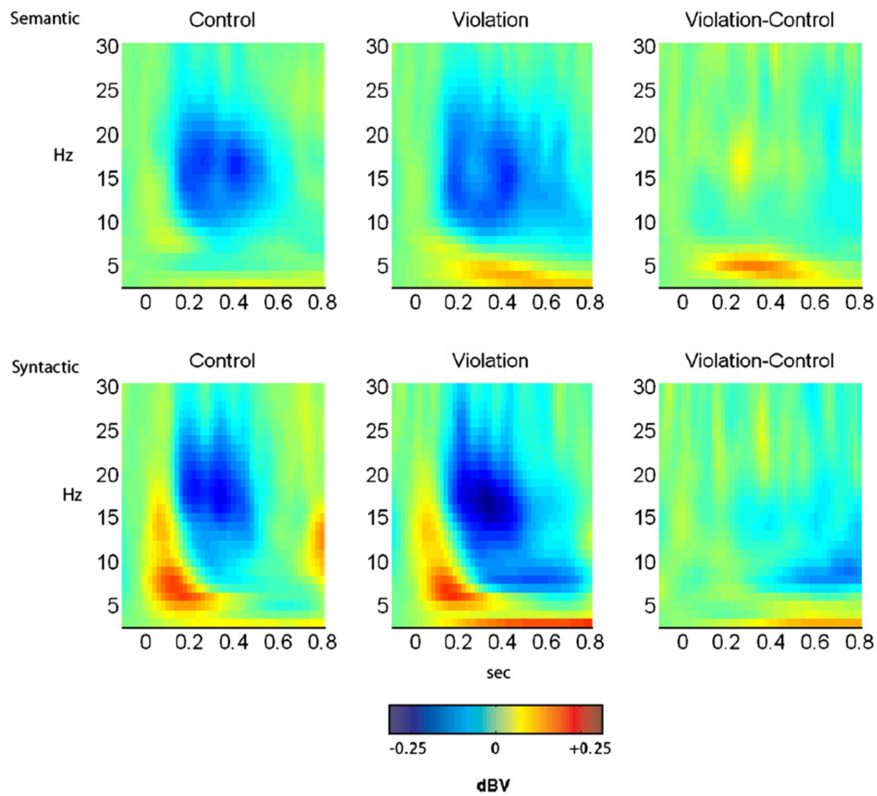

Fig. 3 – Time–frequency representation of relative power changes averaged over significant electrodes for semantic and (combined) syntactic conditions.

a smaller N400 violation effect, $t(57)=-3.499$, $p=0.001$. For the combined grammatical contrast, a greater relative reduction in alpha band power was associated with a larger P600 violation effect, $t(57)=3.018$, $p=0.004$, but a greater reduction in beta band power was not associated with a larger P600 effect, $t(57)=0.430$, $p=$n.s.

Thus, in both the semantic and syntactic contrasts, trials with the lowest magnitude relative power in the theta and alpha bands had the largest ERP violation effects. In the case of the semantic contrast, this occurred when the relative increase in theta power was the lowest, while in the case of the grammatical contrast, this occurred when the relative reduction in alpha power was the greatest.

3. Discussion

In the present experiment, semantic violation effects were associated with an N400 ERP effect, while the phrase structure and number violation effects were associated with a P600 ERP effect. In addition, semantic violations were associated with a theta band increase in power and the grammatical violations were associated with alpha and beta band reductions in power. For both the semantic and grammatical contrasts, a quartile analysis showed an inverse relationship between the size of the ERP violation effects and the relative amplitude of oscillatory power for the same trials. In the case of the semantic contrast, quartiles with a smaller relative increase in theta band power were associated with a larger magnitude N400 violation effect, while in the case of the grammatical contrast, quartiles with a greater relative decrease in alpha band power were associated with a larger magnitude P600 violation effect. Thus, in both types of violation responses, greater relative band power was associated with a smaller magnitude violation effect.

The semantic violation theta band increase is consistent with previous demonstrations of power changes for this type of violation (Bastiaansen et al., 2005; Hald et al., 2006). The reduction in alpha and beta band power to the phrase structure and number violations have not been previously reported. Reduced alpha or beta band power was observed previously in whole-sentence presentation (Krause et al., 1994), and as a response to a visual word presented in a sentence (Bastiaansen et al., 2005), but not in a previous work using event-related violation designs for grammatical violations (Bastiaansen et al., 2002b).

Bastiaansen et al. (2002b) observed a theta band increase in power for number violations, rather than the alpha and beta band reductions observed here. It is not clear why this difference was obtained, but it may reflect variability in the frequency response across participant samples, differences in the way that the power changes are quantified (e.g., induced band power (IBP) versus unadjusted wavelet estimates), or a difference due to stimulus presentation rate of the stimuli. Previous work on a short-term memory task (Krause et al., 2001) has shown that the test–retest correlation of power over two sessions with the same participants decreases with increasing frequency (highest reliability in the theta band,

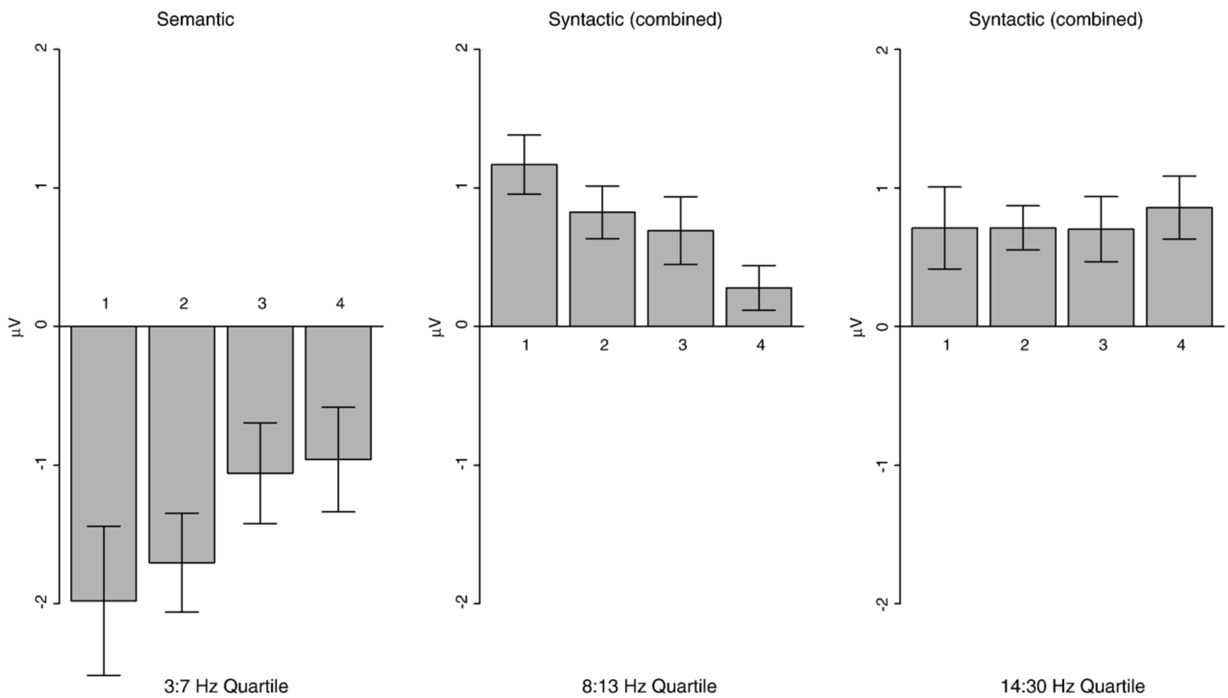

Fig. 4 – ERP violation effect amplitude as a function of quartile of relative band power for the semantic contrast (theta) and the combined syntactic contrast (alpha and beta). The error bars are standard errors of the mean.

lowest at upper alpha), suggesting that it is possible that alpha band power dynamics are more variable than theta band dynamics. As previous reports have also shown individual differences in the ERP response to grammatical violations (Osterhout, 1997), it cannot be excluded that there are differences in the power response across studies as well. This factor is related to the second difference between the studies, which is the way that band power changes were quantified. Bastiaansen et al. (2002b) calculated IBP changes based on individual alpha peak frequency, based on the recommendations by Klimesch (1999), while in the present work time–frequency estimates were averaged over participants without the individual adjustment, which is also a common data analysis strategy for time–frequency analysis (e.g., Bastiaansen et al., 2005; Tallon-Baudry et al., 1998). Note that in the present experiment, we observed a grammatical alpha band effect *without* the adjustment, suggesting that it is possible to observe alpha band effects in the absence of the adjustment suggested by Klimesch (1999). Future work to extend random effects analysis to model individual differences in time–frequency representations would be helpful to address this point in more detail. A third possible difference between Bastiaansen et al. (2002b) and the present study is the presentation rate of the words within the sentences. Bastiaansen et al. (2002b) presented words at a rate of 2 words/s, while the present experiment used a rate of 1.25 words/s. It is possible that different stimulus presentation rates entrain participants to different oscillatory rhythms, and that this difference modulates the frequencies at which violation effects are observed. Alternatively, the longer inter-word interval of the present experiment might have allowed for the temporal development of the alpha reduction to a greater extent than in Bastiaansen et al. (2002b). With the longer intervals between words, the alpha reduction might have been more easily observed in the present study. The precise parameters that determine the time–frequency response to words remain an important avenue for future research on time-varying stimuli like speech or serially presented text.

Given these considerations, the alpha and beta band reduction observed in the present experiment is consistent with the basic observation that word presentations lead to a theta band increase in concert with an alpha and beta band decrease in power (Bastiaansen et al., 2005). In general, the alpha and beta band power reductions likely reflect an increase in the cortical area that is recruited for grammatical processing shortly after the violation is encountered, as previous work has suggested that cortical areas become disengaged with increasing involvement of an oscillating alpha network (Klimesch, 1999; Pfurtscheller and da Silva, 1999). The alpha and beta band violation-related reduction observed here may therefore reflect an additional change in band power activity superimposed on a more basic response which is observed to visual words in a sentence context (see also the comments in Bastiaansen and Hagoort, 2006).

Concerning the relationship between the ERP violation effect amplitudes and the power changes observed here, the trial-based analysis showed that ERP violation effect amplitude is inversely related to the violation power change amplitude. Previous work has suggested that the relationship between oscillatory activity and ERP patterns can be modeled with either shared generator or dual generator models (Mazaheri and Jensen, 2006), implying that the ERP and the oscillation response differences are produced in the same neuron population or at least partially distinct neural populations. While we cannot exclude either of these models on the basis of the present EEG data, the relative lack of electrode overlap of the ERP and power effects for either the semantic or grammatical violation contrasts (in the clustering analysis) would suggest that at least some of the activity giving rise to these effects originates from distinct cortical populations, which is in accord with the dual generator model. While this conclusion is supported by the clustering analysis, it should be noted that there were no condition by channel interactions with the parametric analyses of the event-related power, despite the main effects of condition. Future work with source modeling may be helpful in resolving this discrepancy.

The ERP–power relations that were observed in the present experiment suggest several functional relationships between activity related to the violation ERP response and oscillatory power. For the alpha/beta–P600 relation, one potential functional relation is that the state of the network of language areas when the violation CW is encountered is responsible for the relative magnitude of the alpha/beta and P600 effects. One plausible assumption is that the state of this network is determined primarily by how participants deploy attention over time as a sentence is being presented. Some support for the assumption that alpha power depends on attention can be found from work showing that during spatial cuing tasks, alpha amplitude is modulated consistent with the direction of spatial attention (Worden et al., 2000; Thut et al., 2006). In the present experiment, on the trials in which participants are actively attending the words as they appear over the course of the sentence, alpha and beta power would be relatively low. When the violation word appears, a relatively large violation ERP response would be expected because participants are engaged in the task and attending the words. On the same trials, the change in the alpha and beta power in response to the violation would be relatively less, because it is already relatively low because of the high attentional state. In contrast, when participants are not actively engaged in the task, alpha and beta power would be relatively high. When the violation word appears, a relatively smaller violation ERP would be expected (as participants are not actively engaged), and on the same trials, the change in the alpha and beta power would be relatively greater, because it is initially relatively high. Therefore, on this account, the state of the language network at the point in which the violation word appears determines the relationship between ERP violation effect and violation power change effect.

The same mechanism would not explain the theta–N400 relationship, however, because the band power response to the semantic violation was an increase in power. Given that there is a strong relation between theta band power increases and working memory encoding and retrieval (Bastiaansen et al., 2005; Klimesch, 1999), it appears more likely that the inverse ERP–power relation may reflect how semantic violation detection triggers lexical–semantic memory retrieval. It may be the case that the N400 effect amplitude and the theta band power increase reflect different aspects of lexical–semantic memory retrieval, such as detection of the violation versus the integration into the sentential context. During trials in which the violation CW is successfully detected as an anomalous completion (triggering an N400 ERP effect), participants may have made no further attempts to integrate the meaning of the violation CW into the sentential context. In contrast, during trials in which there was uncertainty regarding whether the violation CW was a violation, there may have been an attempt to integrate the meaning of the violation CW into the sentential context, leading to a relative theta band power increase. This distinction between anomaly detection versus integration would account for the inverse relationship between the N400 effect amplitude and the relative theta band power. Note that another difference between the semantic violation trials and the grammatical violation trials was that the semantic violation CWs occurred at the end of the sentence in the present experiment, whereas the grammatical violation CWs occurred at earlier points within the sentence. The relative position of the CW within the sentence may in part determine the response dynamics of the electrophysiological response, as well as the specific relationship between the ERP effect amplitude and the relative oscillatory response amplitude.

A benefit of identifying differences in event-related power in sentence processing research is that these differences may provide a link between measures of physiological activity with high spatial resolution (fMRI) with measures with high temporal resolution (EEG or MEG). Multimodal imaging has revealed that changes in local field power are correlated with changes in the blood–oxygen level-dependent (BOLD) signal recorded with fMRI, more so than with multi-unit spike activity (Logothetis, 2002). A number of non-sentence processing EEG/fMRI studies concerning alpha band power, usually employing a baseline versus active period comparison of activity with participants' eyes closed versus eyes open, have shown a negative correlation between the BOLD signal and the amplitude of alpha band power (Feige et al., 2005; Moosmann et al., 2003; Laufs et al., 2003; Gonçalves et al., 2006). This has been most often observed in occipital areas but has included parietal and frontal areas as well (e.g., Laufs et al., 2003). This evidence suggests that a decrease in alpha band power is associated with an increase in cortical activity (as measured by the BOLD signal). Although few studies have employed tasks with linguistic or sentential materials, Singh et al. (2002) reported that during a word generation task, cortical desynchronization (as revealed by an MEG source model over a wide band of frequencies) was associated with frontal and parietal areas that were similarly active during an fMRI version of the task. Band power differences, such as the differences observed in the present study, appear to be a candidate electrophysiological measure for the link between BOLD effects and electrophysiology in sentence processing research (see also Kuperberg et al., 2003; Hagoort et al., 2004).

In summary, the present experiment has shown distinct event-related power changes for semantic and grammatical violations, two types of responses which have proven useful in past research on sentence processing. In addition, ERP violation responses were found to be of a greater magnitude when changes in the magnitude of oscillatory responses were smaller, suggesting that during sentence processing, the ERP violation response and the spectral dynamics of the violation response are co-determined by the state of the language network when the violation is encountered.

4. Experimental procedures

4.1. Participants

Twenty-one native Dutch speakers (average age 22.8 years; 19 females; all right-handed) from Radboud University Nijmegen were recorded, with one participant excluded because of recording problems. Participants were paid for their participation, and all were screened for neurological health and vision problems. The experiment itself was approved by the local ethics board at Radboud University Nijmegen. All participants completed a second session with English materials as well, the results of which will be given in a separate report.

4.2. Design and procedure

The experiment was a two-factor within participants design (violation type, violation status). Example sentences for the sentences were as follows (CW underlined, first the control CW, then the violation CW): subject–verb number agreement (Num), “Het kleine verwende kind *gooit/gooien* het speelgoed op de grond” (“The spoiled little kid *throws/throw* the toy on the ground”); phrase structure (Ps), “De directeur [*van* de]/[*de* van] bank geeft het geld” (“The director [*of* the]/[*the* of] bank gives the money”). Examples for the semantic (Sem) sentences include: “Het meisje spreekt drie *bomen*” (semantic violation, “The girl speaks three *trees*”); “De wind speelt met de *bomen*” (semantic control, “The wind swept through the *trees*”).

Participants read the sentences presented one word at a time on the center of a computer monitor with a fixed duration of 400 ms per word and an ISI of 800 ms between the onset of each word. At the start of each trial, a fixation cross was presented at the center of the monitor for 3000 ms, and immediately following a blank screen for 1000 ms, and then successive words of the sentence. Participants were asked not to blink or move during the presentation of the sentences, but to do so during the presentation of the fixation cross in between trials if necessary. Participants were monitored with a video camera during recording and were given several breaks during the recording session, or whenever they requested one.

4.3. Materials and apparatus

For each of the three sentence types, 90 items (45 acceptable, 45 unacceptable) were created, for a total of 270 sentences presented during the experiment. The critical words for the grammatical conditions were presented sentence internally while the CW for the semantic condition was presented at the end of the sentence. The average length (range) of the sentences was the same for the control and violation sentences (Sem: 5.4 (3:9), Num: 5.6 (4:8), Ps: 8.1 (7:9)). The average (range) CW position for the phase structure Ps sentences was 4.5 (3:8) from the start of the sentence, for the Num sentences 3.0 (3:4), and for the Sem condition the CW occurred at the end, average position 5.4 (3:9). The semantic violation sentences were created by exchanging the words of normally completing sentences (not high closure probability sentences) to form anomalous sentences, while the phrase structure and number sentences were created by changing the word order or verb morphological marking respectively. The words were presented in white Arial size 21 font on a black background. For each participant, a pseudo-random order was created so that no more than three unacceptable sentences and no more than three sentences from the same condition were presented successively.

After data recording, participants performed a paper and pencil sentence rating test (on a 5-point scale on which 5 = unacceptable) using a sample of 10 sentences from each condition in the experiment. Compared to the control sentences ($M = 1.9$), the violation sentences were rated worse: Sem ($M = 3.3$, $t(45) = 4.39$, $p < 0.001$), Ps ($M = 3.0$, $t(45) = 3.52$, $p < 0.001$), and Num ($M = 3.9$, $t(45) = 6.45$, $p < 0.001$). The same pattern of effects held with an analysis of the median ratings.

4.4. Data recording and analysis

Continuous EEG from 64 electrodes was recorded using an elastic cap (EasyCap, Inc.) with approximately equidistant spacing of electrodes. Fig. 5 shows the array of electrodes for the caps. The reference during acquisition was the left mastoid, and both vertical and horizontal eye movements were recorded. After recording, the data were re-referenced using an average reference of all the recorded electrodes. Recordings were made with BrainAmp amplifiers (Brain Products GmbH), sampled at 250 Hz. A band-pass filter of 0.02 to 100 Hz was applied during acquisition, and electrode impedances were kept below 50 kΩ throughout the experiment, with the input impedances at the amplifiers at 10 MΩ (see Ferree et al., 2001).

After recording, each single trial was screened by eye for amplifier drift or blocking, as well as movement artifacts, eye movements, or eye blinks. Screening was conducted for a time region around the critical word, including the baseline and the

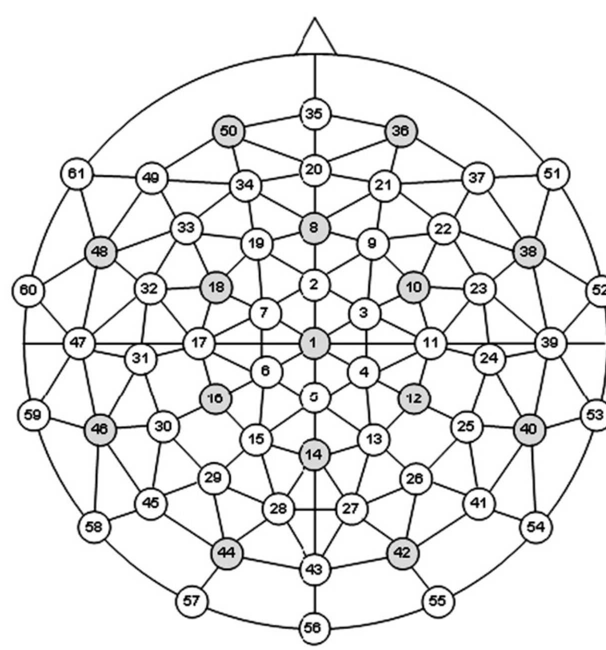

Fig. 5 – Electrode array layout. Electrode numbers corresponding to approximate 10–20 locations are shown in grey.

period after the CW onset. Trials with absolute amplitude greater than 150 μV were excluded. A denoising source separation procedure (Särelä and Valpola, 2005) was applied to correct for eye movements, and all other artifact trials were excluded from further analysis. The median proportions of trials entering the final analysis were the following: Sem violation (0.74) and control (0.71), Ps violation (0.82) and control (0.81), and number Num violation (0.82) and control (0.78).

The data were analyzed using the Fieldtrip open source toolbox (Oostenveld et al., 2007, documentation and algorithms available at http://www.ru.nl/fcdonders/fieldtrip). The recorded EEG was averaged following a baseline normalization using the average of the EEG in the interval −100 to 0 ms before critical word onset. The time–frequency analysis consisted of evoked power computed using a Morlet wavelet (width of 5 cycles, 3 SD Gaussian time window function) by convolution in the frequency domain on single trials over an interval between −2.0 and 2.0 s centered at the critical word onset, performed with the wltconvol function in the Fieldtrip toolbox. The same wavelet analysis was applied to the ERP calculated over the same time interval. The power of the ERP was then subtracted from the average power based on the single trials in order to estimate the power not accounted for by the ERP. The relative change in power was then computed as 2*log10 of the ratio of the power in the active period to the average power in the baseline period (−100 to 0 ms; the same as in the ERP analysis). The result represents the relative change of the power in the active period following CW onset, expressed in dBV.

The statistical significance of observed differences was assessed using a clustering and randomization test, implemented in Fieldtrip. The randomization approach is a modified version of the procedure described in Maris (2004) and is described more fully in Takashima et al. (2005) and Tuladhar et al. (2006), as well as in the Fieldtrip documentation. Similar nonparametric approaches to statistical inference for topographies are described by Achim (2001), Galán et al. (1997) and Karnisky et al. (1994). In this procedure, a randomization distribution of cluster statistics is constructed and used to evaluate statistically significant differences between conditions. Specifically, *t*-statistics are computed for each electrode, and a clustering algorithm forms groups of electrodes based on significant *t*-tests between conditions in a contrast. The sum of the *t*-statistics in this group is then used as a cluster-level statistic (termed here sum-*t*), which is then tested for significance using a randomization test (4000 random draws in all the analyses reported below). The advantage of the cluster-level statistic is that it controls the type I error rate for the complete set of electrodes in the contrast. For clusters of activity, the average ERP effect or change in power is reported for groups of electrodes in the cluster, the frequency range, and the time window for the effect.

For a comparison of the clustering and randomization analysis, we also report a linear mixed effects analysis of the data using the R library nlme (R development team, 2005; Pinheiro et al., 2006; Pinheiro and Bates, 2000). In this analysis, the three-dimensional spatial configuration of electrodes (measured individually for each participant with a Polyhemous device) was factored into the analysis using a spherical spatial correlation function, implemented with the function corSpher in the nlme library. This procedure addresses the problems of correlated error associated with high-density electrode arrays without requiring a correction for non-sphericity (Greenhouse and Geisser, 1958) that is necessary for repeated measures ANOVA (Jennings, 1987; see Bagiella et al., 2000 for a discussion of the mixed effects approach). As an alternative to the clustering and randomization approach, contrasts between the violation and control conditions were conducted for each electrode using a multiple-comparison procedure (Hothorn et al., 2007; Bretz et al., 2001) which tested the violation–control contrast for each electrode against the average violation–control contrast of the remaining electrodes controlling the family-wise error rate at $\alpha<0.05$.

To study the relationship between the amplitude of oscillatory activity and the magnitude of the ERP responses in more detail, the trials from each participant, electrode, and condition were stratified into four quartiles based on the power relative to the baseline on each trial calculated with the wavelet procedure outlined above. This procedure created an index ranking the trials according to the highest to the lowest magnitude band power response within a frequency window and time window of interest. An ERP was calculated for the data in each quartile based on this index, and the difference between violation and control ERP for each quartile was assessed (averaging over all of the electrodes showing a significant ERP violation effect in the main analysis). The aim of this analysis was to determine whether the magnitude of the violation ERP response was related to the magnitude of the relative power change calculated from the same trials. Note that the quartiles were calculated separately for violation and control trials for each participant and electrode individually and independent of the other participants and electrodes.

For the semantic trials separate quartiles were calculated trials for relative theta band power (3 to 7 Hz) in a window from 300 to 500 ms after critical word onset. For the combined phrase structure and number analysis (see Results), the quartiles were based on the relative alpha (8 to 13 Hz) or beta (14 to 30 Hz) band power in a window from 500 to 900 ms after critical word onset. Power was calculated relative to the same baselines as in the previous (non-quartile) analysis. Note that in the semantic analysis, the last quartile contains the greatest theta power increase (see Results), while in the syntactic analysis, the first quartile contains the greatest alpha or beta power decrease (see Results). An ERP was calculated for the violation trials and the control trials in each quartile, and the violation effect calculated from the difference between violation and control. This difference was regressed on quartile as an ordered factor with a mixed effects regression (Pinheiro and Bates, 2000) to test for a statistically significant relation between quartile and violation effect magnitude.

REFERENCES

Achim, A., 2001. Statistical detection of between-group differences in event-related potentials. Clin. Neurophysiol. 112, 1023–1034.

Allefeld, C., Frisch, S., Schlesewsky, M., 2005. Detection of early cognitive processing by event-related phase synchronization analysis. NeuroReport 16, 13–16.

Bagiella, E., Sloan, R.P., Heitjan, D.F., 2000. Mixed-effects models in psychophysiology. Psychophysiology 37, 13–20.
Başar, E., 1980. EEG and Brain Dynamics: Relation Between EEG and Brain Evoked Potentials. Elsevier, Amsterdam.
Başar, E., Hari, R., Lopes da Silva, F.H., Schürmann, M. (Eds.), 1997. Brain Alpha Activity—New Aspects and Functional Correlates. International Journal of Psychophysiology, vol. 26 (special issue).
Başar-Eroglu, C., Başar, E., Demiralp, T., Schürmann, M., 1992. P300-response: possible psychophysiological correlates in delta and theta frequency channels. A review. Int. J. Psychophysiol. 13, 161–179.
Bastiaansen, M.C.M., Hagoort, P., 2003. Event-induced theta responses as a window on the dynamics of memory. Cortex 39, 967–992.
Bastiaansen, M.C.M., Hagoort, P., 2006. Oscillatory neuronal dynamics during language comprehension. In: Neuper, C., Klimesch, W. (Eds.), Progress in Brain Research, vol. 159, pp. 179–196.
Bastiaansen, M.C.M., van Berkum, J.J.A., Hagoort, P., 2002a. Event-related theta power increases in the human EEG during online sentence processing. Neurosci. Lett. 323, 13–16.
Bastiaansen, M.C.M., van Berkum, J.J.A., Hagoort, P., 2002b. Syntactic processing modulates the theta rhythm of the human EEG. NeuroImage 17, 1479–1492.
Bastiaansen, M.C.M., van der Linden, M., ter Keurs, M., Dijkstra, T., Hagoort, P., 2005. Theta responses are involved in lexical–semantic retrieval during language processing. J. Cogn. Neurosci. 17, 530–541.
Braeutigam, S., Bailey, A.J., Swithenby, S.J., 2001. Phase-locked gamma band responses to semantic violation stimuli. Cogn. Brain Res. 10, 365–377.
Bretz, F., Genz, A., Hothorn, L.A., 2001. On the numerical availability of multiple comparison procedures. Biom. J. 43, 645–656.
Bruns, A., 2004. Fourier-, Hilbert- and wavelet-based signal analysis: Are they really different approaches? J. Neurosci. Methods 137, 321–332.
Buzsáki, G., 2006. Rhythms of the Brain. Oxford Univ. Press, New York.
Demiralp, T., Yordanova, J., Kolev, V., Ademoglu, A., Devrim, M., Samar, V.J., 1999. Time–frequency analysis of single-sweep event-related potentials by means of fast wavelet transform. Brain Lang. 66, 129–145.
Feige, B, Scheffler, K., Esposito, F., Di Salle, F., Hennig, J., Seifritz, E., 2005. Cortical and subcortical correlates of electroencephalographic alpha rhythm modulation. J. Neurophysiol. 93, 2864–2872.
Ferree, T.C., Luu, P., Russell, G.S., Tucker, D.M., 2001. Scalp electrode impedance, infection risk, and EEG data quality. Clin. Neurophysiol. 112, 536–544.
Galán, L., Biscay, R., Rodríguez, J.L., Pérez-Abalo, M.C., Rodríguez, R., 1997. Testing topographic differences between event-related brain potentials by using nonparametric combinations of permutation tests. Electroencephalogr. Clin. Neurophysiol. 102, 240–247.
Greenhouse, S.W., Geisser, S., 1958. On methods in the analysis of profiled data. Psychometrika 24, 95–112.
Gonçalves, S.I., de Munck, J.C., Pouwels, P.J.W., Schoonhoven, R., Kuijer, J.P.A., Maurits, N.M., Hoogduin, J.M., Van Someren, E.J.W., Heethaar, R.M., Lopes da Silva, F.H., 2006. Correlating the alpha rhythm to BOLD using simultaneous EEG/fMRI: Inter-subject variability. Neuroimage 30, 203–213.
Haarmann, H.J., Cameron, K.A., 2005. Active maintenance of sentence meaning in working memory: Evidence from EEG coherences. Int. J. Psychophysiol. 57, 115–128.
Hagoort, P., Brown, C., Groothusen, J., 1993. The syntactic positive shift (SPS) as an ERP-measure of syntactic processing. Lang. Cogn. Processes 8, 439–483.
Hagoort, P., Hald, L., Bastiaansen, M., Petersson, K.M., 2004. Integration of word meaning and world knowledge in language comprehension. Science 304, 438–441.
Hald, L.A., Bastiaansen, M.C.M., Hagoort, P., 2006. EEG theta and gamma responses to semantic violations in online sentence processing. Brain Lang. 96, 90–105.
Hothorn, T., Bretz, F., Westfall, P., with contributions by Heiberger, R.M., 2007. Multcomp: Simultaneous inference for general linear hypotheses. R package version 0.991-8.
Jennings, J.R., 1987. Editorial policy on analysis of variance with repeated measures. Psychophysiology 24, 474–478.
Karnisky, W., Blair, R.C., Snider, A.D., 1994. An exact statistical method for comparing topographic maps with any number of subjects and electrodes. Brain Topogr. 6, 203–210.
Khader, P., Rösler, F., 2004. EEG power and coherence analysis of visually presented nouns and verbs reveals left frontal processing differences. Neurosci. Lett. 354, 111–114.
Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. Brain Res. Rev. 29, 169–195.
Klimesch, W., Schack, B., Sauseng, P., 2005. The functional significance of theta and upper alpha oscillations. Exp. Psychol. 52, 99–108.
Krause, C.M., Lang, H.A., Laine, M., Helle, S.I., Kuusisto, M.J., Pörn, B., 1994. Event-related desynchronization evoked by auditory stimuli. Brain Topogr. 7, 107–112.
Krause, C.M., Pörn, B., Lang, A.H., Laine, M., 1997. Relative alpha desynchronization and synchronization during speech perception. Cogn. Brain Res. 5, 295–299.
Krause, C.M., Sillanmaki, L., Haqqqvist, A., Heino, R., 2001. Test-retest consistency of the event-related desynchronization/event-related synchronization of the 4–6, 6–8, 8–10 and 10–12 Hz frequency bands during a memory task. Clin. Neurophysiol. 112, 750–757.
Kujala, A., Pammer, K., Cornelissen, P., Roebroeck, A., Formisano, E., Salmelin, R., 2006. Phase coupling in a cerebro-cerebellar network at 8–13 Hz during reading. Cereb. Cortex (electronic publication doi:10.1093/cercor/bhl059).
Kuperberg, G.R., Holcomb, P.J., Sitnikova, T., Greve, D., Dale, A.M., Caplan, D., 2003. Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. J. Cogn. Neurosci. 15, 272–293.
Kuperberg, G.R., Caplan, D., Sitnikova, T., Eddy, M., Holcomb, P.J., 2006. Neural correlates of processing syntactic, semantic, and thematic relationships in sentences. Lang. Cogn. Processes 21, 489–530.
Kutas, M., Federmeier, K.D., 2000. Electrophysiology reveals semantic memory use in language comprehension. Trends Cogn. Sci. 4, 463–470.
Kutas, M., Hillyard, S.A., 1980. Event-related brain potentials to semantically inappropriate and surprisingly large words. Biol. Psychol. 11, 99–116.
Kutas, M., Hillyard, S.A., 1984. Brain potentials during reading reflect word expectancy and semantic association. Nature 307, 161–163.
Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., Krakow, K., 2003. EEG-correlated fMRI of human alpha activity. Neuroimage 19, 1463–1476.
Logothetis, N.K., 2002. The neural basis of the blood–oxygen-level-dependent functional magnetic resonance imaging signal. Philos. Trans. R. Soc. Lond., Ser B 357, 1003–1037.
Makeig, S., Debener, S., Onton, J., Delorme, A., 2004. Mining event-related brain dynamics. Trends Cogn. Sci. 8, 204–210.
Maris, E., 2004. Randomization tests for ERP-topographies and whole spatiotemporal data matrices. Psychophysiology 41, 142–151.
Mazaheri, A., Jensen, O, 2006. Posterior alpha activity is not

phase-reset by visual stimuli. Proc. Natl. Acad. Sci. U. S. A. 103, 2948–2952.
Moosmann, M., Ritter, P., Krastel, I., Brink, A., Thees, S., Blankenburg, F., Taskin, B., Obrig, H., Villringer, A., 2003. Correlates of alpha rhythm in functional magnetic resonance imaging and near infrared spectroscopy. Neuroimage 20, 145–158.
Neuper, Klimesch, W., 2006. Progress in Brain Research, vol. 159. Elsevier, Amsterdam.
Neville, H., Nicol, J.L., Barss, A., Forster, K.I., Garrett, M.F., 1991. Syntactically based sentence processing classes—Evidence from event-related brain potentials. J. Cogn. Neurosci. 3, 151–165.
Nunez, P.L., Srinivasan, R., 2006. Electric Fields of the Brain: The Neurophysics of EEG, 2nd Edition. Oxford Univ. Press, New York.
Oostenveld, R., Fries, P., Jensen, O., 2007. Fieldtrip toolbox. http://www.ru.nl/fcdonders/fieldtrip.
Osterhout, L., 1997. On the brain response to syntactic anomalies: manipulations of word position and word class reveal individual differences. Brain Lang. 59, 494–522.
Osterhout, L., Holcomb, P.J., 1992. Event-related brain potentials elicited by syntactic anomaly. J. Mem. Lang. 31, 785–806.
Osterhout, L., Mobley, L.A., 1995. Event-related brain potentials elicited by failure to agree. J. Mem. Lang. 34, 739–773.
Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and S-PLUS. Springer, New York.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2006. nlme: Linear and nonlinear mixed effects models. R package version 3.1–79.
Pfurtscheller, G., da Silva, F.H.L., 1999. Event-related EEG/MEG synchronization and desynchronization: Basic principles. Clin. Neurophysiol. 110, 1842–1857.
Pfurtscheller, G., Stancak, A., Neuper, C., 1996. Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. Int. J. Psychophysiol. 24, 39–46.
Pulvermueller, F., 2001. Brain reflections of words and their meaning. Trends Cogn. Sci. 5, 517–524.
R development core team, 2005. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, http://www.r-project.org.
Roehm, D., Schlesewsky, M., Bornkessel, I., Frisch, S., Haider, H., 2004. Fractionating language comprehension via frequency characteristics of the human EEG. NeuroReport 15, 409–412.
Särelä, J., Valpola, H., 2005. Denoising source separation. J. Mach. Learn. Res. 6, 233–272.
Singh, K.D., Barnes, G.R., Hillebrand, A., Forde, E.M.E., Williams, A.L., 2002. Task-related changes in cortical synchronization are spatially coincident with the hemodynamic response. NeuroImage 16, 103–114.
Takashima, A., Jensen, O., Oostenveld, R., Maris, E., van de Coevering, M., Fernandez, G., 2005. Successful declarative memory formation is associated with ongoing activity during encoding in a distributed neocortical network related to working memory: A magneto-encephalography study. Neuroscience 139, 291–297.
Tallon-Baudry, C., Bertrand, O., 1999. Oscillatory gamma activity in humans and its role in object representation. Trends Cogn. Sci. 3, 151–162.
Tallon-Baudry, C., Bertrand, O., Peronnet, F., Pernier, J., 1998. Induced gamma band activity during the delay of a visual short-term memory task in humans. J. Neurosci. 18, 4244–4254.
Thut, G., Nietzel, A., Brandt, S.A., Pascual-Leone, A., 2006. Alpha-band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. J. Neurosci. 26, 9494–9502.
Tuladhar, A.M., ter Huurne, N., Schoffelen, J., Maris, E., Oostenveld, R., Jensen, O., 2006. Parietal–occipital sources account for the increase in alpha activity with working memory load. Hum. Brain Mapp. 27, doi:10.1002/hbm.20306 (Epub ahead of print).
Weiss, S., Mueller, H.M., Schack, B., King, J.W., Kutas, M., Rappelsberger, P., 2005. Increased neuronal communication accompanying sentence comprehension. Int. J. Psychophysiol. 57, 129–141.
Worden, M.S., Foxe, J.J., Wang, N., Simpson, G.V., 2000. Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. J. Neurosci. 20, RC63.
Yordanova, J., Kolev, V., 1998. Event-related alpha oscillations are functionally associated with P300 during information processing. Neuroreport 9, 3159–3164.
Yordanova, J., Kolev, V., Polich, J., 2001. P300 and alpha event-related desynchronization ERD. Psychophysiology 38, 143–152.