Fractionating language comprehension via frequency characteristics of the human EEG

Dietmar Roehm, Matthias Schlesewsky, Ina Bornkessel, Stefan Frisch and Hubert Haider

We present a new analysis technique for EEG research on language comprehension, which dissociates superficially indistinguishable event-related potential (ERP) components. A frequency-based analysis differentiated between two apparently identical but functionally distinct N400 effects in terms of activity in separable frequency bands, and whether the activity stemmed from increased power or phase locking. Whereas linguistic problem detection is associated with theta band activity (~3.5-7.5 Hz), conflict resolution correlates with activity in the delta band (1-3 Hz). The data further differentiate between the neuronal processing mechanisms involved in different types of conflict resolution on the basis of frequency characteristics (power vs phase locking).

Key words: Conflict resolution; Delta band; Evoked power; Language comprehension; N400; Phase-locking index; Theta band; Whole power

INTRODUCTION

During everyday communication, the human language processing system is often confronted with conflict engendering events that must be resolved if comprehension is to proceed smoothly. The enhanced processing costs thus arising have long been used to gain insight into language comprehension mechanisms [1-4]. A promising methodological approach to this area of research became available with the advent of event-related potentials (ERPs), which provide not only precise temporal resolution, but also various dimensions for the classification of processing conflicts (e.g. polarity, topography). A seminal finding in this regard was that lexical-semantic processing difficulties consistently elicit a centro-parietal negativity peaking at 400 ms after critical word onset (N400) [5,6]. However, more recent findings have cast doubt on the association between the N400 and a homogeneous set of neural processes. Studies examining mental arithmetic [7] and face processing [8] have shown that the N400 is not confined to language. Furthermore, it has been elicited by linguistic manipulations independent of the lexical-semantic domain [9-12].

A way of disentangling the relationship between linguistic domains and ERP effects, which is already established in other areas of higher-level cognition [13], lies in the analysis of EEG frequency characteristics. Previous work indicates that activity in different frequency bands may correlate with distinct linguistic subdomains [14-16]. Here, we show that two N400 effects that are of distinct linguistic origin but indistinguishable in terms of latency and topography are dissociable via frequency characteristics. To this end, we reanalyse the data of an ERP study [17] in which two N400s were observed. The first formed part of a biphasic N400-P600 pattern in (ill-formed) German sentences with two subjects, whereas the second obtained in grammatical sentences with an inanimate subject (Table 1, Fig. 1). Only condition A does not lead to difficulties in determining who is doing what to whom. In condition B, the comprehension system is confronted with an inanimate, and thereby atypical subject. The difference between A and B is analogous to that between sentences such as The girl hit the boy and The stone hit the boy. Whereas both are well-formed, the latter violates the expectation that a subject (a causer of an event) is also a willfully controlling agent, thereby eliciting enhanced processing cost [9]. Conditions C and D, by contrast, are ill-formed in a similar way to She hit he, in which the pronoun in object position (he) is a form only applicable to subjects (cf. He hit him). In contrast to English, which unambiguously signals the interpretive relationship between participants (who is doing what to whom) by means of linear order, German also allows objects to precede subjects (as in A). Therefore, morphological case marking (e.g. welchen/der, which/the SUBJECT is welchen/den, which/the OBJECT) is the only reliable means of establishing interpretive relationships and this process fails when both arguments are identically marked. Between 200 and 500 ms after onset of the critical second argument, the ungrammatical conditions (C/D) and the grammatical inanimate condition (B) elicit an N400 in comparison to the control condition (A). Additionally, the ungrammatical conditions (C/D) show a late positivity (P600) between 600 and 1000 ms. The P600 may be seen as a correlate of ungrammaticality detection [18]. With regard to the N400s,
sures reported are relative to the second argument (in italics). Segmentation for stimulus presentation is indicated with vertical bars.

D. UNGRAM-IN

B. GRAM-IN

C. UNGRAM-AN

Negativity is plotted upwards.

The EEG was recorded from 15 Ag/AgCl electrodes with a sampling rate of 250 Hz (impedances < 5 kΩ) and referenced to the left mastoid (re-referenced to linked mastoids offline). The horizontal and vertical electrooculograms (EOGs) were monitored. Only artefact-free trials for which the (first) judgement task was performed correctly entered the data analysis. Three measures were applied: evoked power (EPow), whole power (WPow), and phase locking index (PLI). All measures were determined by Gabor wavelet analyses in frequency bins of 0.33 Hz. EPow measures the proportion of evoked EEG activity in a specific frequency band relative to critical stimulus onset and was calculated on the basis of ERPs per participant, condition and electrode and then averaged over all participants [19]. WPow measures the total power in a frequency band on the basis of single trial analyses and was calculated on the basis of individual trials for each condition and participant with subsequent averaging [13]. The PLI (also known as phase-locking value, PLV, phase-averaging) measures the degree of inter-trial variation in phase between the responses to critical stimuli and thereby quantifies phase-locking of oscillatory activity irrespective of its amplitude [19–21]. The PLI ranges between 0 and 1, i.e. it is close to 1 when there is little variance in phase across trials and close to 0 otherwise. The PLI was determined per condition, time-point, frequency and electrode site for each participant and then averaged over participants. The analyses presented here are restricted to electrode PZ for the sake of brevity. Note that the wavelet transformation leads to a smearing of effects in both the time and frequency domains [22]. Thus, the edges of the effects shown in the figures should be interpreted with caution. For the statistical analysis, multifactorial ANOVAs were computed per value of interest for each participant, condition, time window and averaged frequency bin using the factors grammaticality (grammatical vs ungrammatical) and animacy (animate vs inanimate). For EPow, analyses were computed using the Gabor coefficients of the averaged conditions. In the case of WPow, Gabor coefficients were determined per trial for each participant, condition, time window and frequency bin and then averaged before entering the statistical analysis. The PLI was determined by comparing single trials per condition, participant, time window and frequency bin, with the average values for each participant entering the statistical analysis. On the basis of this analysis, only relative effects between the conditions can be interpreted, with the animate grammatical condition (A in Table 1) serving as the control condition.

RESULTS

We present analyses restricted to the delta and theta frequency bands (1–7.5 Hz). Visual inspection of the time-frequency plots showed no systematic variations across conditions in higher frequency bands with regard to the measures applied here.

Table 1. Example stimuli in each of the four experimental conditions (from [17]).

<table>
<thead>
<tr>
<th>Condition</th>
<th>Example</th>
</tr>
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<tbody>
<tr>
<td>A. GRAM-AN</td>
<td>Peter fragt sich, welchen Arzt der J/C204ger gelobt hat.</td>
</tr>
<tr>
<td>B. GRAM-IN</td>
<td>Peter fragt sich, welchen Arzt der Zweig gestreift hat.</td>
</tr>
<tr>
<td>C. UNGRAM-AN</td>
<td>Peter fragt sich, welcher Arzt der J/C204ger gelobt hat.</td>
</tr>
<tr>
<td>D. UNGRAM-IN</td>
<td>Peter fragt sich, welcher Arzt der Zweig gestreift hat.</td>
</tr>
</tbody>
</table>

Abbreviations: GRAM (‘grammatical’), UNGRAM (‘ungrammatical’), AN (‘second argument is animate’), and IN (‘second argument is inanimate’). All measures reported are relative to the second argument (in italics). Segmentation for stimulus presentation is indicated with vertical bars.

MATERIALS AND METHODS

Frequency-band analysis was applied to the original data from [17]. In this study, 16 participants read 40 sentences in each of the critical conditions (Table 1) randomly interpersed with 160 similar filler sentences. Grammaticality was counterbalanced, i.e. 50% of all sentences were ungrammatical in order to avoid strategies. Sentences were presented visually in the centre of a computer screen (segmentation as in Table 1), with presentation times of 450 ms (plus 100 ms interstimulus interval, ISI) for the first argument in the subordinate clause, 400 ms (100 ms ISI) for the second argument and 300 ms (200 ms ISI) for all other segments. After 800 ms pause at the end of a sentence, participants were asked to judge its well-formedness within 2500 ms by means of a button press. In 25% of all trials (randomly distributed), participants performed a second task, in which they judged whether a probe word had occurred in the preceding sentence.

The EEG was recorded from 15 Ag/AgCl electrodes with a sampling rate of 250 Hz (impedances < 5 kΩ) and referenced to the left mastoid (re-referenced to linked mastoids offline). The horizontal and vertical electrooculograms (EOGs) were monitored. Only artefact-free trials for which the (first) judgement task was performed correctly entered the data.
As is evident from Fig. 2, in the upper theta band (6–7.5 Hz), the two inanimate conditions (B/D) show higher EPow than their animate counterparts (A/C) independently of grammaticality. This observation is confirmed by the statistical analysis, which revealed a main effect of animacy ($F(1,15) = 5.29, p < 0.04$) between 200 and 400 ms (averaged frequency bins 6.33–7.33 Hz). Thus, the inanimate conditions lead to a higher degree of stimulus-evoked activity in the upper theta band. In the lower theta band (3.5–5 Hz), by contrast, the two ungrammatical conditions (C/D) show significantly higher EPow than the grammatical conditions (A/B) in the same time window ($F(1,15) = 5.06, p < 0.04$; averaged frequency bins 3.66–4.66 Hz). In this frequency band, it is therefore the grammatical violation that leads to a higher degree of stimulus-evoked activity. These findings show that the N400 elicited by ungrammaticality and that elicited by inanimate subjects, which were indistinguishable on the surface, correspond to evoked activity in two clearly separable frequency ranges.

The two distinct frequency-based correlates for the violation N400 and the animacy N400 receive converging support from the delta band analysis (averaged frequency bins 1–2.33 Hz). Here, the two ungrammatical conditions (C/D) show higher EPow between 600 and 1000 ms, whereas the grammatical condition (B) does not ($F(1,15) = 46.74, p < 0.001$). Thus, the two ungrammatical conditions do not differ with regard to EPow in this frequency band. However, an analysis of WPow and PLI measures revealed converse behaviour for the two conditions: whereas the animate ungrammatical condition (C) is associated with a higher PLI ($F(1,15) = 5.59, p < 0.04$), the inanimate ungrammatical condition (D) elicits higher WPow ($F(1,15) = 4.76, p < 0.05$). The generally higher degree of evoked activity for the ungrammatical conditions can therefore be attributed to underlyingly different processes, namely to a larger extent of phase-locking (i.e. more consistent timing across trials) in the animate and a greater synchronisation (i.e. higher activity of the underlying neuronal population) in the inanimate condition.

![Fig. 2](image1.png)

**Fig. 2.** Gabor wavelet-based time/frequency plots showing EPow differences between the ungrammatical animate (C; a), ungrammatical inanimate (D; b), and grammatical inanimate conditions (B; c) in comparison to the control condition (A) at electrode PZ ($n = 16$). The colour scale depicts the magnitude of the wavelet coefficients.

![Fig. 3](image2.png)

**Fig. 3.** Grand average ERPs and Gabor wavelet-based time/frequency plots in the delta band (1–3 Hz) for the ungrammatical animate (C; a), ungrammatical inanimate (D; b), and grammatical inanimate conditions (B; c) in comparison to the control condition (A) at electrode PZ ($n = 16$). ERPs are shown in the far left panel, whereas the remaining three panels depict wavelet coefficient differences in evoked power (EPow; second panel from left) and whole power (WPow; second panel from right) and phase-locking index differences (PLI; far right panel). The colour scale depicts the magnitude of the wavelet coefficient differences for EPow and WPow and the PLI value difference for PLI.
DISCUSSION
We have proposed a new and potentially promising approach to address the vagueness of interpretation associated with traditional language-related ERP components. This radically new perspective, which supplements ERP measures with corresponding frequency-based analyses, not only distinguishes between apparently identical components on the basis of activity in distinct frequency bands, but also provides further insights with regard to the functional organisation of the language comprehension system and its inherent complexity.

Our analyses showed that the two instances of the ERP component generally referred to as the N400 examined here are associated with activity in distinct frequency ranges. The ability to dissociate an upper theta N400 from a lower theta N400 thus constitutes a promising first step in approaching the uncertainty of interpretation regarding language-related ERP components. With regard to the delta band, the PLI increase for the animate ungrammatical condition (C) in comparison to its inanimate counterpart (D) indicates more consistent timing across events [13,23] for the former, which might be taken to suggest a more effective and efficient interaction of various subprocesses. Second, the increase in WPOw for the inanimate ungrammatical (D) in comparison to the animate ungrammatical condition (C) is indicative of higher neuronal synchronisation and thereby a higher degree of neuronal activity either within or across neuronal populations [24]. These differences suggest that the conflict resolution strategies applied differ between the two ungrammatical conditions. In both cases, a processing conflict arises because the presence of two subjects renders the sentence uninterpretable. However, the animate ungrammatical conflict (D) provides a possible solution to the question of who is doing what to whom, because an inanimate argument is less likely to realise the subject function [9]. No such solution is available in the animate ungrammatical case (C). Thus, in the animate ungrammatical condition (C), the irresolvable conflict leads to an abortion of processing and, thereby, to an immediate reorganisation of the language processing system (possibly in the sense of phase resetting) [23]. This results in the more consistent timing across trials reflected in the higher PLI. In the animate ungrammatical condition (D), the repair mechanism prompted by the animacy cue elicits a higher degree of processing effort in working towards an interpretation. These higher reanalysis costs require an increased effort of the neuronal system and thereby result in the higher WP.

More generally, our findings suggest a tentative association between the two theta bands and problem detection on the one hand, and the delta band and general integration of different information types and conflict resolution on the other. Similar interpretations of the theta and delta bands have been proposed on the basis of findings from non-linguistic cognitive processes [13,25]. In this way, the present approach provides a new means of differentiating the neuronal mechanisms underlying cognitive processes with regard to their functional source. Beyond its applicability to the examination of language comprehension, which was illustrated in the present paper, this perspective thereby offers a new way of describing and classifying the neuronal bases of higher-level cognition.

REFERENCES