Left inferior frontal gyrus mediates morphosyntax

cortex 86 (2017) 156–171

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Left inferior frontal gyrus mediates morphosyntax: ERP evidence from verb processing in left-hemisphere damaged patients

Stefanie Regel [a,*], *Sonja A. Kotz* [a,b], *Ilona Henseler* [a] and *Angela D. Friederici* [a]

[a] *Max-Planck-Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, Leipzig, Germany*
[b] *Faculty of Psychology and Neuroscience, Department of Neuropsychology and Psychopharmacology, Maastricht University, Maastricht, The Netherlands*

ARTICLE INFO

Article history:
Received 28 April 2015
Reviewed 19 July 2015
Revised 4 January 2016
Accepted 8 November 2016
Action editor Cynthia Thompson
Published online 18 November 2016

Keywords:
Event-related potentials (ERPs)
Left inferior frontal gyrus (LIFG)
Broca's area
(Morpho-)syntax
Language processing

ABSTRACT

Neurocognitive models of language comprehension have proposed different mechanisms with different neural substrates mediating human language processing. Whether the left inferior frontal gyrus (LIFG) is engaged in morpho-syntactic information processing is currently still controversially debated. The present study addresses this issue by examining the processing of irregular verb inflection in real words (e.g., *swim* > *swum* > *swam*) and pseudowords (e.g., *frim* > *frum* > *fram*) by using event-related brain potentials (ERPs) in neurological patients with lesions in the LIFG involving Broca's area as well as healthy controls. Different ERP patterns in response to the grammatical violations were observed in both groups. Controls showed a biphasic negativity-P600 pattern in response to incorrect verb inflections whereas patients with LIFG lesions displayed a N400. For incorrect pseudoword inflections, a late positivity was found in controls, while no ERP effects were obtained in patients. These findings of different ERP patterns in the two groups strongly indicate an involvement of LIFG in morphosyntactic processing, thereby suggesting brain regions' specialization for different language functions.

1. Introduction

The neural basis mediating human language comprehension is controversially debated with regard to whether particular brain regions are specialized for specific language functions. Accordingly, the language system is characterized either as a modular system with specified modules for the computation and the retrieval of linguistic information (e.g., dual-system approaches, see Clahsen, 1999; Friederici & Frisch, 2000; Pinker, 1999; Pinker & Prince, 1988; Pinker & Ullman, 2002),

* *Corresponding author*. Max-Planck-Institute for Human Cognitive and Brain Sciences, Department of Neuropsychology, PO Box 500 355, D-04303 Leipzig, Germany.
E-mail address: regel@cbs.mpg.de (S. Regel).
http://dx.doi.org/10.1016/j.cortex.2016.11.007
0010-9452/

or as a unitary system depending on a memory-based mechanism (e.g., connectionist approaches, see Bybee, 1995; Joanisse & Seidenberg, 1999; McClelland & Patterson, 2002; Rumelhart & McClelland, 1986). While both approaches agree that the left hemisphere (LH) critically supports language functions, disagreement exists about the involvement of the relevant brain regions, specifically, the left inferior frontal gyrus (LIFG) including Broca's area [i.e., the pars opercularis and the pars triangularis (Brodmann area – BA 44 and 45)].

Modular-system approaches separate syntactic from lexical-semantic processes and generally accord with the suggestion that the LIFG supports the computation of syntactic information at the phrase and the sentence level (for review see Friederici, 2011; Friederici & Kotz, 2003; Grodzinsky, 2000). The posterior portion of Broca's area is associated with particular language functions involved in syntactic structure building processes. A prominent view within the class of dual system approaches [i.e., the declarative/procedural model (Pinker & Ullman, 2002; Ullman, 2001; Ullman et al., 1997)], holds that primarily the frontal cortex in connection with the basal ganglia (BG), the parietal cortex, and the dentate nucleus of the cerebellum underlie a procedural memory system responsible for the computation of grammatical structures. This proposal makes the prediction that the fronto-BG circuit supports the processing of regularly inflected verbs consisting of a stem and affix (e.g., *walk* + *-ed*). A second system (i.e., the declarative memory system) engaging the medial temporal lobe is involved in the processing of lexical-semantic information, but also comes into play when processing irregularly inflected verbs (e.g., *caught*) that are stored and retrieved as whole word forms from the mental lexicon. Irregular verbs underlying similar inflection patterns (e.g., *sing* > *sang*, *ring* > *rang*) are captured by lexical redundancy rules within the mental lexicon. These lexical rules allow the inflection patterns to generalize over stored verb forms and to extend to novel forms. Another quite similar view, the decompositional approach of Marslen-Wilson and Tyler (1998, 2007) attributes to the LIFG a role in morpho-phonological segmentation of regular words into separate morphemes, whereas temporal lobe structures mediate the meaning access to these morphemes as well as to unseparable irregular words. Considerable evidence for the involvement of the LIFG in morphosyntactic information processing stems from neuropsychological studies showing that patients with lesions in the LIFG had difficulties with regular verbs, while the processing of irregular verbs remained largely unimpaired (Tyler, deMornay-Davies, et al., 2002; Tyler, Randall, & Marslen-Wilson, 2002; Ullman et al., 1997, 2005). Moreover, in neuroimaging studies greater activation of the LIFG was observed for the processing of past tense inflection of regular verbs than irregular ones (de Diego Balaguer et al., 2006; Oh, Tan, Ng, Berne, & Graham, 2011; Sahin, Pinker, & Halgren, 2006; Tyler, Stamatakis, Post, Randall, & Marslen-Wilson, 2005).

In contrast, in view of unitary approaches, a single mechanism engaging a network of neural connections is proposed to be responsible for the processing and representation of both regular and irregular verbs (Joanisse & McClelland, 2015; Joanisse & Seidenberg, 1999, 2005; Rumelhart & McClelland, 1986). Therein, both types of verbs are represented as overlapping whole forms sharing certain phonological and semantic features. The observation of different activation patterns for regular and irregular verbs (e.g., in the left and right inferior frontal gyrus – IFG) has been related to differences in phonological complexity between those verbs engendering enhanced phonological processing (Joanisse & Seidenberg, 1999, 2005). Due to the addition of affixes (e.g., *-ed*) for past tense inflection regular verbs are phonologically more complex than irregular verbs, which, by contrast, consist of stem alternations (e.g., *swim* > *swam*), and overt (e.g., *catch* > *caught*) or zero suffixation (e.g., *put* > *put*). Neuropsychological studies showing that phonological impairment primarily causes difficulties with regular verb inflection rather than deficits in morphological processing has been taken as support for this approach (Bird, Lambon Ralph, Seidenberg, McClelland, & Patterson, 2003; Joanisse & Seidenberg, 2005; Penke & Westermann, 2006). Due to confounds of phonological and morphological aspects in these studies, the functional contribution of the LIFG is still debated. Examining this issue by means of irregular verbs that were shown to engage rule-based processes may provide further insights on the functions of this brain region.

In linguistic theory analysis of different inflection patterns revealed that irregular verbs rely on morphological rules (i.e., subregularities), instead of comprising idiosyncratic and unpredictable tense forms (Wiese, 2008). The occurrence of particular inflection patterns has been accounted for by morphosyntactic properties [i.e., abstract inflectional features, such as (past tense) and (finiteness)][1] and morphological rules of insertion (i.e., principle of specificity).[2] The insertion of past tense forms occurs systematically and is functionally defined in a linguistic theory, called underspecification (Wiese, 2008). Based on those subregularities even irregular verbs involve morphosyntactic computations, which are presumably mediated by the syntactic component of the language system. The presence of subregularities underlying irregular inflection has been recently confirmed for German by measuring event-related brain potentials (ERPs) in healthy adults during language comprehension (Opitz, Regel, Müller, & Friederici, 2013; Regel, Opitz, Mueller, & Friederici, 2015), as well as for language production in healthy and aphasic adults (Penke & Krause, 2002). Investigating the

[1] While the past tense form appears to be most specific (i.e., carrying the features [+past, +finite]), the past participle form is less specific (i.e., carrying only the feature [+past]), and the present tense form is underspecified (i.e., carrying an empty set of features [ ]).

[2] This principle states that more specific forms take precedence over less specific ones. In case of the ABC pattern (e.g., *swim* > *swum* > *swam*), gradually specific stem forms exist, allowing a systematic insertion of the differentially altered past tense stem forms. In an ABB inflection pattern (e.g., *buy* > *bought* > *bought*), however, no most specific past tense form exists, so that the next less specific form (i.e., the past participle form) is inserted as past tense. A pattern of ABA, however, in which a more specific form B would take precedence over a less specific one (i.e., A) is precluded.

processing of such irregular verbs in patients with lesions in the LIFG by means of ERPs should allow a further specification of the neural correlates of morphosyntactic information processing.

In order to investigate human language comprehension, ERPs are most suitable for differentiating distinct processing mechanisms by providing highly time-sensitive measures of the neural activity engaged in the stimulus processing. For the processing of syntactic and morphosyntactic information, a biphasic ERP pattern consisting of LAN (i.e., a left anterior negativity between 300 and 500 msec) and P600 (i.e., late centro-parietal positivity) has often been observed (Coulson, King, & Kutas, 1998; Gunter, Friederici, & Schriefers, 2000; Münte, Heinze, & Mangun, 1993). The LAN typically shows a left anterior topography, albeit a more widespread scalp distribution is sometimes reported (e.g., Friederici & Frisch, 2000; Hasting & Kotz, 2008; Jakuszeit, Kotz, & Hasting, 2013). The more broadly distributed negativity commonly preceding the P600 is found, in particular, for the processing of morphosyntactic violations (e.g., stem formation rules) of verb stems across different languages (including Italian, Catalan, German) and tasks (Gross, Say, Kleingers, Clahsen, & Münte, 1998; Regel et al., 2015; Rodriguez-Fornells, Clahsen, Lleo, Zaake, & Münte, 2001) suggesting a reliable effect. The neural generators of early syntactic ERP components in response to word category violations have been localized primarily in Broca's area and adjacent regions (Friederici, 2011; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003), as well as the anterior superior temporal gyrus (Friederici & Kotz, 2003). The neural generators for the morphosyntax-related LAN or negativity preceding the P600 are less well specified. For the processing of lexical-semantic information, by contrast, most robustly N400 (i.e., a centro-parietal negativity with a peak latency of around 400 msec post-stimulus) is evoked (for review Kutas & Federmeier, 2011). The sources of the N400 have been identified in the left temporal lobe (for review see Lau, Phillips, & Poeppel, 2008).

Rule-based processing underlying regular inflection was confirmed in previous studies for (over)regularization of irregular verbs (e.g., **bringed vs brought*) by the emergence of a LAN-P600 pattern (Gross et al., 1998; Morris & Holcomb, 2005; Penke et al., 1997; Rodriguez-Fornells et al., 2001). In contrast, for (over)irregularizations of regular verbs (e.g., *seeped* > **sept*) such syntax-related ERP pattern was absent (Morris & Holcomb, 2005; Penke et al., 1997). Still, for irregular verbs relying on rule-based stem alternations ERP evidence for subregularities underlying irregular inflection was shown (Regel et al., 2015). In line with underspecification-based approaches (Wiese, 2008), the processing of incorrect irregular real word past tense forms [e.g., **sung* (sung)/**sing* (sing)] lead to a modulation of P600 in the observed negativity-P600 pattern. For comparable subregularities in pseudowords (e.g., **tung*/**ting*), a modulation of N400 was found. This indicates that subregularities are processed through syntactic computations when dealing with real words, and through predictive processing when dealing with pseudowords.

This hypothesis was tested in patients with lesions in the LIFG, but unaffected temporal cortex in an established ERP paradigm in German that allows a fine grained analyses of the rule-based processing of irregular verbs (Regel et al., 2015). In the morphosyntax experiment, behavioral judgments on the grammaticality of past tense forms, as well as the appropriateness of equivalent pseudowords were gathered to assess participants' performance. ERPs were recorded for irregular past tense forms containing different morphosyntactic properties [i.e., most specified (correct), specified (incorrect), and unspecified (incorrect) ones] with the aim to test the involvement of the LIFG for the processing of these forms. For the processing of these forms different approaches make different predictions. Modular-system approaches predict that: If the LIFG is engaged in morphosyntactic processing, ERPs in response to the incorrect irregular verbs are expected to differ between patients and healthy controls. For the control group, a syntax-related ERP pattern consisting of negativity and P600 for systematically varied past tense forms (i.e., for specified and unspecified forms relative to correct most specified ones) is expected thereby replicating the findings of Regel et al. (2015). For the pseudoword items, a gradual modulation of N400 with largest amplitude for unspecified forms, and medium amplitude for specified forms relative to the expectable correct ones is predicted. For the patient group, in the absence of a syntax-related ERP pattern an N400 might be observed under the assumption that lexical-semantic processing mechanisms are compensatory engaged. For the pseudoword items, however, no ERP effects are hypothesized since subregularities may not be recognized and thus neither syntactic, nor lexical-semantic compensatory mechanisms should be active. In the behavioral judgments, the controls are expected to answer adequately and immediately in both tests, whereas patients even when showing recovery of their language function, may still show more difficulties in both judgments. The more general dual-system approach that only distinguishes between regular and irregular inflection (e.g., Pinker & Ullman, 2002) predict for controls and patients similar ERP responses (i.e., N400) for violation of systematic irregular inflection patterns by involving lexical redundancy rules operated in temporal cortex. Connectionist approaches (e.g., Joanisse & McClelland, 2015) which propose a network of neural connections to mediate the processing of irregular verbs and generalization to pseudowords predict similar ERP patterns (i.e., N400) for incorrect inflection patterns for controls and patients as the LIFG should not specifically be engaged.

2. Methods

2.1. *Participants*

In the current study, nine patients with left-hemisphere lesions in the IFG were selected from the patient databank of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. All patients had an intact temporal cortex, and showed either none, or, at most, residual symptoms of aphasia according to their clinical diagnostic profile. Time since lesion was at least 2 years. Individual patients' characteristics including demographic data, etiology, description of lesion, language impairment, and education is displayed in Table 1. A lesion overlay is presented in Fig. 1. Patients [4 female, mean age 62.7 (standard deviation (SD) 9.96)] had normal or corrected-to-normal vision, and were paid for their participation. In addition, nine age- and education-matched right-handed healthy controls [4 female, mean age 63.7 (SD 7.82)] participated. Prior to the experiments, all participants gave signed informed consent in accordance with the declaration of Helsinki. The study was approved by the ethics committee of the medical department at the University of Leipzig.

2.2. Pre-experiment: production test

To control for participants' language competence, and to assess selective impairments in production of regular and irregular verb inflection, a production test was conducted prior to the ERP experiments. In this test, participants were asked to state the past tense forms of eight regular and irregular verbs each presented in sentential contexts. For a full list of verbs see Appendix A. Both the regular and irregular verbs were mainly two-syllabic with an average word length of 6.6 letters per word. All items were read aloud by the experimenter and the participants read along the items on a sheet of paper, on which the critical verbs that required past tense inflection were underlined.

2.3. Visual oddball experiment

Immediately prior to the morphosyntax experiment, a visual oddball experiment was conducted to control for potential attentional deficits in the patients (see e.g., Picton, 1992). In this test, two types of visual stimuli differing in their physical properties [i.e., opened (standards) *vs* closed (deviants) geometric forms] were presented in a pseudo-randomized order with a rate of 3 to 1 (i.e., 225 standards, 75 deviants). Stimuli appeared in a rapid serial visual presentation (1000 msec per item, inter-stimulus-interval – ISI of 200 msec) in the middle of a monitor. During measurement of the electroencephalography (EEG), participants were asked to count the deviants as accurately as possible, and to state the counted total at the end of the experiment. This task was conducted without pauses and lasted approx. 7 min.

Table 1 – Description of the patients' characteristics.

Patient	Sex	Age	Time since lesion	Handedness	Etiology	Lesion site	Lesion location	Lesion volume	Brodmann areas (BA)	Language impairment	Education
01	F	71	8	R	MCA ischemia	L	IFG (op, tri, orb), MFG, PrC, OP, INS, STR	67,7	44, 45, 46, 43, insula	No aphasia	h.e.
02	F	61	5	R	Tumor	L	IFG (op, tri)	1,3	44, 45	No aphasia	s.e.
03	M	62	11	R	MCA ischemia	L	IFG (op, tri), PrC, PoC, INS	74,3	44, 45, 6, 43, insula	Residual aphasia	l.s.e.
04	M	73	6	R	MCA ischemia	L	IFG (op, tri, orb), PrC, OP, INS	61,9	44, 45, 47, 6, 43, insula	Residual aphasia	h.e.
05	M	64	5	L	MCA ischemia	L	IFG (op, tri, orb), MFG, PrC, OP, INS	56,4	44, 45, 46, 6, 43, 9, insula	Amnestic aphasia	s.e.
06	F	76	5	R	MCA ischemia	L	IFG (op, tri), MFG, PrC, INS	19,8	44, 6, 43, insula	No aphasia	l.s.e.
07	F	61	2	R	MCA ischemia	L	IFG (op, tri), MFG, PrC, OP, INS, CE	45,4	44, 45, 46, 6, insula, cerebellum	Residual aphasia	h.e.
08	M	49	2	R	MCA ischemia	L	IFG (op, tri, orb), MFG, PrC, OP, INS, IPL, AG, SMG, STG	90,0	44, 45, 46, 6, 40,7	Residual aphasia	s.e.
09	M	47	3	R	MCA/ACA ischemia	L	IFG (tri, orb), MFG, SFG, SMA, CG, INS	99,7	45, 46, 10	Residual aphasia	s.e.

Abbreviations: M = male; F = female; Age (years); Time since lesion (years); R = right; L = left; MCA = middle cerebral artery; ACA = anterior cerebral artery; Lesion locations: inferior frontal gyrus (IFG), pars opercularis (op), triangularis (tri), and orbitalis (orb), middle frontal gyrus (MFG), superior frontal gyrus (SFG), cingulate gyrus (CG), precentral gyrus (PrC), postcentral gyrus (PoC), fronto-temporal operculum (OP), insula (INS); inferior parietal lobule (IPL), angular gyrus (AG); superior temporal gyrus (STG), supramarginal gyrus (SMG), striatum (STR), cerebellum (CE); h.e. = general certificate of higher education; s.e. = general certificate of secondary education; l.s.e. = general certificate of lower secondary education.

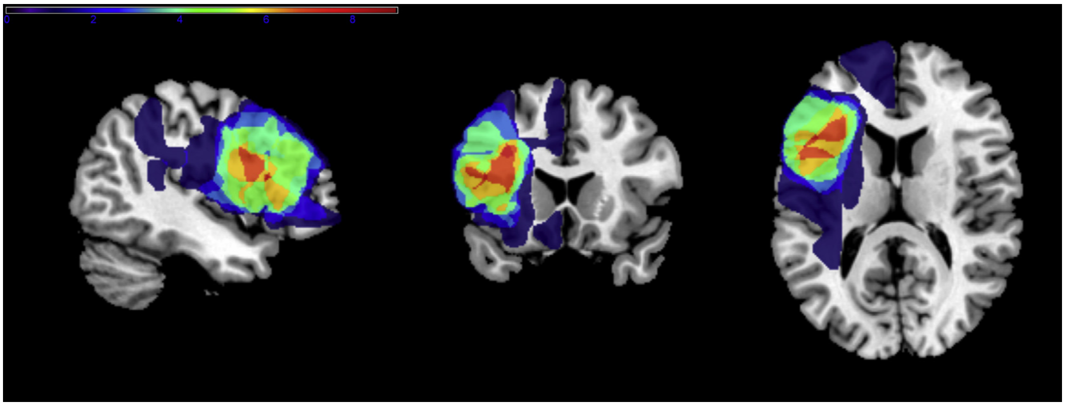

Fig. 1 – Lesion overlay of patients' lesions. Lesions overlap maximally in the LIFG [BA44: MNI (Montreal Neurological Institute and Hospital) coordinates −31, 19, 29, and BA45: MNI coordinates −43, 19, 14], as shown by the red area. Temporal cortex is unaffected.

2.4. *Morphosyntax experiment*

2.4.1. *Stimulus material*

The stimuli contained 42 irregular verbs and 42 equivalent pronounceable pseudowords embedded in minimal syntactic contexts and marked for different tenses (i.e., future,[3] past perfect, and past tense) [e.g., *er trank* (he drank), *er stahl* (he stole)]. All verbs consisted of stem alternations in the present tense, past participle, and the past tense [e.g., *singen* (sing) > *gesungen* (sung) > *sang* (sang)] thereby denoting the inflection pattern of ABC (see Wiese, 2008). The critical past tense form was systematically manipulated, and was either correct, or incorrect by replacement of the past tense stems with past participle stems [e.g., **er trunk* (he drunken), **er stohl* (he stolen)] for the specified condition, and with present tense stems [e.g., **er trink* (he drink), **er stehl* (he steal)] for the unspecified condition. An item contained all three tenses presented in a series, each beginning with future, followed by past perfect and past tense [e.g., *er wird beginnen* (he will begin), *er hat begonnen* (he begun), *er begann* (he began)]. The experimental paradigm for the real word items is displayed in Table 2. In total, 126 inflected verb series with 42 items per condition, and 14 fillers to match the number correct and incorrect items were included. The full list of materials is presented in Appendix B. The past tense forms were primarily monomorphemic [mean number of syllables 1.19 (SD .39)] with a mean word length of 5.30 (SD 1.25) graphemes, and an average frequency class[4] of 12 (SD 3.11) according to the *Leipzig vocabulary project* (www.wortschatz.uni-leipzig.de). To avoid the repetition of an item within an experimental block, all items were divided onto three lists in a pseudorandom order with 56 items each (i.e., 42 experimental items, and 14 filler items). Experimental conditions were counterbalanced across all versions. Participants received only one list. In each group, equal numbers of participants were presented with each list. Except for six additional verbs and pseudowords that were included to enhance the number of items, the stimuli and paradigm were identical to Regel et al. (2015).

The pseudoword block consisted of 42 pronounceable pseudowords (e.g., *bimmen*, *gezinnen*), as well as 14 pseudoword fillers. For the full list of pseudoword materials see Appendix C. Equivalent to the real word items, the pseudowords were presented in tense series consisting of future, past perfect and past tense. In total, 126 pseudoword items, and 14 filler items were included and divided onto three lists (with 56 items each), in a separate pseudorandom order.

For experimental presentation, real word and pseudoword items were presented in separate experimental blocks always beginning with the real word block. In order to increase the number of trials, both blocks were presented a second time in the same order (i.e., repeated presentation).

2.4.2. *Procedure*

During the EEG recording, participants were seated in an electrically shielded and sound-attenuated cabin with a monitor in front of them. A trial sequence started off with the presentation of a fixation cross for 200 msec in the middle of the monitor (see Fig. 2). After an ISI of 300 msec, item series were presented visually with 1500 msec for each item and an ISI of 500 msec pause in between (a rate that was comfortable for participants). All elements of an item (i.e., future, past perfect, and past tense inflection) appeared as whole utterances consisting of subject and verb on the monitor. Past tense utterances subtended 2°–3.5° of horizontal, and .9° of vertical visual angle. After offset of the stimulus presentation and an additional interval of 1500 msec, subjects had to perform the experimental task (response time of maximal 3000 msec). For the real word block, a grammaticality judgment of the past

[3] In German, future is marked by a modal verb in combination the main verb, which includes the present tense stem. Henceforth, present tense stems are referred to.

[4] Frequency classes state the related type frequency of words in numeric classes from 0 to 30. The more frequent the words are, the lower their classification.

Table 2 – Systematic manipulation of irregular past tense forms according to the morphological analysis of Wiese (2008), exemplarily shown for the verb *sprechen* (speak). Present tense and past participle stems are underlined.

Condition	Present	Past participle	Past tense	Morphosyntactic properties
Correct	*er wird sprechen* (he will speak)	*er hat gesprochen* (he has spoken)	*er sprach* (he spoke)	[+past, +finite]
Incorrect: specified	*er wird sprechen* (he will speak)	*er hat gesprochen* (he has spoken)	**er sproch* (he spoken)	[+past]
Incorrect: unspecified	*er wird sprechen* (he will speak)	*er hat gesprochen* (he has spoken)	**er sprech* (he speak)	[ ]

tense forms was required. For the pseudoword block, participants had to judge whether the pseudoword past tense form was appropriate for a particular tense series (appropriateness judgment). Responses (given via button press) were followed by an inter-trial-interval of 1000 msec, before the next trial started. *Yes* and *no* answers were completely balanced across all experimental conditions as well as blocks in avoidance of a decision-related expectancy. The whole experiment lasted about 1 h. Within and after each block, participants were allowed to pause for as long as needed.

The participants' task was to read attentively all tense series and to reply as accurately as possible to the experimental task (see above). Prior to each experimental block, participants received an instruction and a short training phase.

2.5. *Data recording and analysis*

The continuous EEG was recorded from 52 Ag–AgCl electrodes[5] and referred to the right mastoid. After recording, the EEG signals were re-referenced to the average of the left and right mastoids. To control for eye movement artifacts bipolar horizontal and vertical electrooculograms (EOG) was also recorded. Resistance of all electrodes was kept below 5 kΩ. EEG and EOG signals were recorded continuously with a sampling rate of 500 Hz. EEG data were filtered offline using a digital bandpass filter of .5–20 Hz. To remove eye artifact, a correction procedure was employed, in which for each participant eye movement artifacts were classified manually as prototypical blinks or moves (i.e., approx. 20 prototypical blinks and moves each). Based on this prototype classification a propagation factor was calculated, and applied for correction of those trials containing respective eye movement artifacts (i.e., approx. 46% of all trials). In the ERP analysis, only artifact-free and corrected trials were included.

2.5.1. *Analysis of the ERP data*

For evaluation of the ERPs, epochs of −200 to 1000 msec according to the stimulus onset were averaged separately for each participant. In the visual oddball and the morphosyntax experiment, average ERPs were calculated for the critical items (i.e., in the oddball task the standards and deviants, and in the morphosyntax task the past tense items) for each electrode position for each condition. Averages were aligned to a 200 msec pre-stimulus baseline. For the real word items, statistical analysis included only correctly answered trials. For the pseudoword items, each trial entered the analysis. Due to artifacts, approx. 3% of the trials had to be excluded from the averages in the visual oddball experiment, and approx. 2% of the trials in the morphosyntax experiment.

For distributional ERP analyses, two topographical factors *anterior/posterior* (2) and *hemisphere* [left (LH)/right (RH)] were defined and completely crossed, yielding four different ROIs each containing five electrodes: left anterior (Fc3, C5, C3, Cp5, Cp3), left posterior (P5, P3, Po7, Po3, O1), right anterior (FC4, C4, C6, Cp4, Cp6), and right posterior (P4, P6, Po4, Po8, O2).

For statistical analysis of the P300 response, the time window of *300–600 msec* was chosen based on visual inspection (see Fig. 3). A repeated measure analysis of variance (ANOVA) was performed on the mean amplitude values of all dependent variables. Factors included the between subject factor *group* (patients/controls) and the within subject factors *condition* (standard/deviant) and the topographical factors *anterior/posterior* (2) and *hemisphere* (LH/RH).

For statistical analysis of the ERP data obtained in the morphosyntax experiment, three latency windows were employed: *300–500 msec* (negativity), *400–700 msec* (N400), and *600–800 msec* (P600) for real word items, *150–300 msec* (early positivity) and *800–950 msec* (late positivity) for pseudoword items. These latency windows were determined to match potential ERP effects that were visually salient in the grand average ERPs (see Figs. 4 and 5), as well as to allow for comparison with previous findings (Regel et al., 2015). A repeated-measures ANOVA was conducted separately for real word and pseudoword items on all dependent variables. The between-subject factor *group* (patients/controls), and the within-subject factors *condition* (correct/incorrect: specified/incorrect: unspecified), *block* (first/second), *anterior/posterior* (2) and *hemisphere* (LH/RH) were included. Whenever the main analysis showed interactions between two or more factors, additional analyses were carried out. Midline electrode positions (Cz, Cpz, Pz, Poz, Oz) were analyzed separately. To avoid problems concerning sphericity the Huynh–Feldt correction was applied to all ANOVA calculations including the within-subject factors. To elucidate main effects of condition, post-hoc t-tests for pairwise comparison were applied. Main effects and interactions were evaluated as significant with an alpha level of <.05, and as marginally significant with an alpha level of <.10.

[5] Fp1, Fpz, Fp2, Af7, Af3, AfZ, Af4, Af8, F7, F5, F3, Fz, F4, F6, F8, Ft7, Fc5, Fc3, Fcz, Fc4, Fc6, Ft8, T7, C5, C3, Cz, C4, C6, T8, Tp7, Cp5, Cp3, Cpz, Cp4, Cp6, Tp8, P7, P5, P3, Pz, P4, P6, P8, Po7, Po3, Poz, Po4, Po8, O1, Oz, O1, and right mastoid.

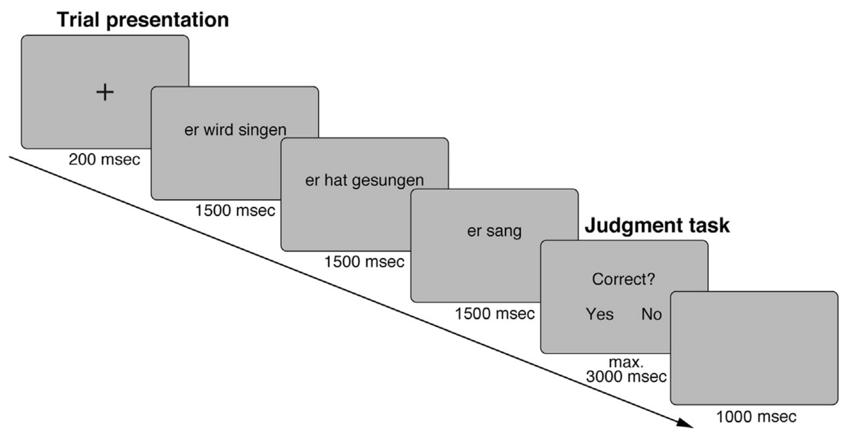

Fig. 2 – Schematic illustration of trial structure. The chronological sequence is illustrated by the arrow at the left. The time intervals show the duration of each phase. The textual sequence is depicted in the screenshots.

2.5.2. *Analysis of the behavioral data*

Behavioral data of the morphosyntax experiment were analyzed separately for the real word and pseudoword items in a repeated-measures ANOVA with the factors *group* (patients/controls) and *item list* (3) as between subject factors, and *condition* (correct/incorrect: specified/incorrect: unspecified) and *block* (first/second) as within subject factor. All within-subject factors calculations were corrected by the Huynh–Feldt procedure.

For analysis of the behavioral data obtained in the production task prior to the ERP experiments, a repeated-measures ANOVA with the between subject factor *group* (patients/controls), and the within subject factor *condition* (regular/irregular verbs) was conducted on the absolute values of the accurate namings.

3. Results

3.1. *Production task*

In stating the correct past tense inflection of regular and irregular verbs both patients and controls performed excellently [for regular verbs mean accuracy rate of 100% (SD .0) in controls and 86.1% (SD 17.05) in patients; for irregular verbs mean accuracy of 98.6% (SD 2.08) in controls and 97.2% (SD 5.5) in patients]. Still, patients had slightly more difficulty in performing this task [mean accuracy rate of 92% (SD 1.6)] than healthy controls [mean accuracy rate of 99% (SD .34)] as shown by a significant between-subjects effect [$F(1,16) = 7.14$, $p < .05$].

3.2. *Visual oddball experiment*

Counting the deviants was comparable in both patients and controls. On average, controls deviated from the true counts by .11 (SD .33), and patients by 3.77 (SD 7.32). An unpaired two-sided *t*-test was carried out on the absolute values of deviants from the true counts and revealed no significant differences between these two groups [$t(16) = 1.50$, n.s.].

Inspection of the ERPs showed the emergence of P300 for the deviants compared to the standards in both patients and controls (see Fig. 3). Statistical analysis of the 300–600 msec latency window revealed an effect of group [$F(1,16) = 13.43$, $p < .01$], and an interaction between group and condition [$F(1,16) = 15.15$, $p < .001$]. The resolution of this interaction by group, showed a significant effect of condition in both patients [$F(1,8) = 15.78$, $p < .01$] and controls [$F(1,8) = 116.39$, $p < .0001$]. Statistical analysis of the midline electrodes also showed an effect of group [$F(1,16) = 13.28$, $p < .01$], and an interaction of group and condition [$F(1,16) = 14.45$, $p < .01$]. In further analysis for each group separately, effects of condition were significant in both patients [$F(1,8) = 17.67$, $p < .01$] and controls [$F(1,8) = 166.57$, $p < .0001$]. The findings indicate that in both groups an oddball P300 was elicited by the deviants. This P300 effect, however, was more pronounced in controls in comparison to patients.

3.3. *Morphosyntax experiment*

3.3.1. *Behavioral data*

The participants' performance in the grammaticality judgment of the past tense forms was very good. Statistical analysis still showed an effect of group [$F(1,16) = 8.97$, $p < .01$] implying that patients had more difficulty [mean accuracy rate of 84.3% (SD 11.54)] than controls [mean accuracy rate of 96.2% (SD 3.02)] in performing this task. Neither main effects of item list [$F(2,14) = .16$, n.s.] nor interactions of item list with block and/or condition [$F(4,28) < .68$, n.s.] were observed implying that presentation lists had no impact on the stimulus processing.

Judging the appropriateness of pseudoword past tense forms was apparently more difficult for patients [mean accuracy rate of 63.4% (SD 5.01) of the expected appropriateness ratings] than for controls [mean accuracy rate of 81.5% (SD 10.26)], which was confirmed by a significant effect of group [$F(1,16) = 24.72$, $p < .0001$]. As seen for the real word items, neither an effect of item list [$F(2,14) = .35$, n.s.] nor interactions of item list with block and/or condition [$F(4,28) < .75$, n.s.] were obtained.

3.3.2. *ERP data for the real word items*

ERPs analyzed at the critical items seen in patients and controls are shown in Fig. 4. Visual inspection of the ERPs suggests differences in the processing of irregular inflection between both groups of participants. In patients, a centro-parietal negativity emerging around 400 msec post-stimulus was evoked for both incorrect (i.e., the specified and unspecified items) past tense forms in comparison to the correct equivalents. By contrast, in controls a late positivity emerging around 600 msec after stimulus onset was elicited by the incorrect past tense forms relative to the correct one. This positivity was broadly distributed and showed a centro-parietal maximum. Moreover, an earlier negativity seemed to antecede this positivity between 300 and 500 msec.

Main analysis of the *400–700 msec* latency window confirmed processing differences between patients and controls by the presence of an effect of group [$F(1,16) = 5.90$, $p < .05$]. Further, marginally significant interactions of group by condition [$F(2,32) = 2.45$, $p < .10$], as well as between group, condition and hemisphere [$F(2,32) = 2.89$, $p < .10$] were observed. Resolving these interactions by group showed a main effect of condition [$F(2,16) = 3.59$, $p < .05$] in patients, but not so in controls [$F(2,16) = .19$, n.s.]. In patients, post-hoc testing of the condition effect revealed significant differences between the correct and both the specified [$t(8) = 5.12$, $p < .05$] and the unspecified condition [$t(8) = 6.02$, $p < .05$] indicating the emergence of a negativity for incorrect irregular verbs.

The statistical analysis of the midline electrodes revealed an interaction between group and condition [$F(2,32) = 3.40$, $p < .05$]. Additional analyses for each group separately showed a main effect of condition [$F(2,16) = 4.86$, $p < .05$] in patients only. The results of the post-hoc testing confirm the presence of a negativity for both incorrect past tense forms in relation to the correct ones [for the specified condition: ($t(8) = 6.22$, $p < .05$), for the unspecified condition: ($t(8) = 7.79$, $p < .05$)] over the midline electrode sites.

In the statistical analysis of the *600–800 msec* latency window an effect of group [$F(1,16) = 9.11$, $p < .01$] was found. Moreover, the main analysis showed a significant two-way interaction between group and condition [$F(2,32) = 6.49$, $p < .01$], as well as a marginally significant four-way interaction between group, condition, anterior/posterior and hemisphere [$F(2,32) = 2.47$, $p < .10$]. In controls, the resolution of the two-way interaction by group showed a significant effect of condition [$F(2,16) = 5.81$, $p < .05$], whereas no such effect [$F(2,16) = 1.42$, n.s.] was seen in patients. The occurrence of a late positivity for both incorrect past tense forms in comparison to the correct equivalents was attested in controls. In the post-hoc testing, marginal significant differences were observed between the correct specified and the specified condition [$t(8) = 4.18$, $p < .10$], and significant differences between the correct and the unspecified condition [$t(8) = 10.90$, $p < .01$].

The analysis of the midline electrodes in the *600–800 msec* latency window showed a significant interaction between group and condition [$F(2,32) = 9.01$, $p < .001$]. In separate analyses of the ERPs in patients and controls, a significant effect of condition [$F(2,16) = 6.90$, $p < .05$] was only seen in controls. Post-hoc testing confirms the presence of a positivity in response to the incorrect compared to the correct past tense forms [for the specified condition: ($t(8) = 5.70$, $p < .05$), for the unspecified condition: ($t(8) = 11.79$, $p < .01$)] seen in the control group.

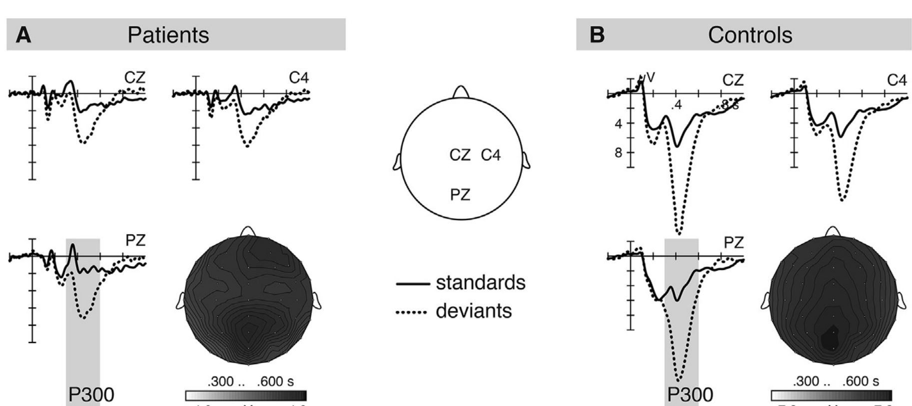

Fig. 3 – Grand average ERPs seen for the oddball experiment in patients (column A) and controls (column B). For the deviants (dotted line) relative to the standards (solid line) a P300 was evoked in both groups of participants. The topographic maps display the scalp distribution of the P300 effects.

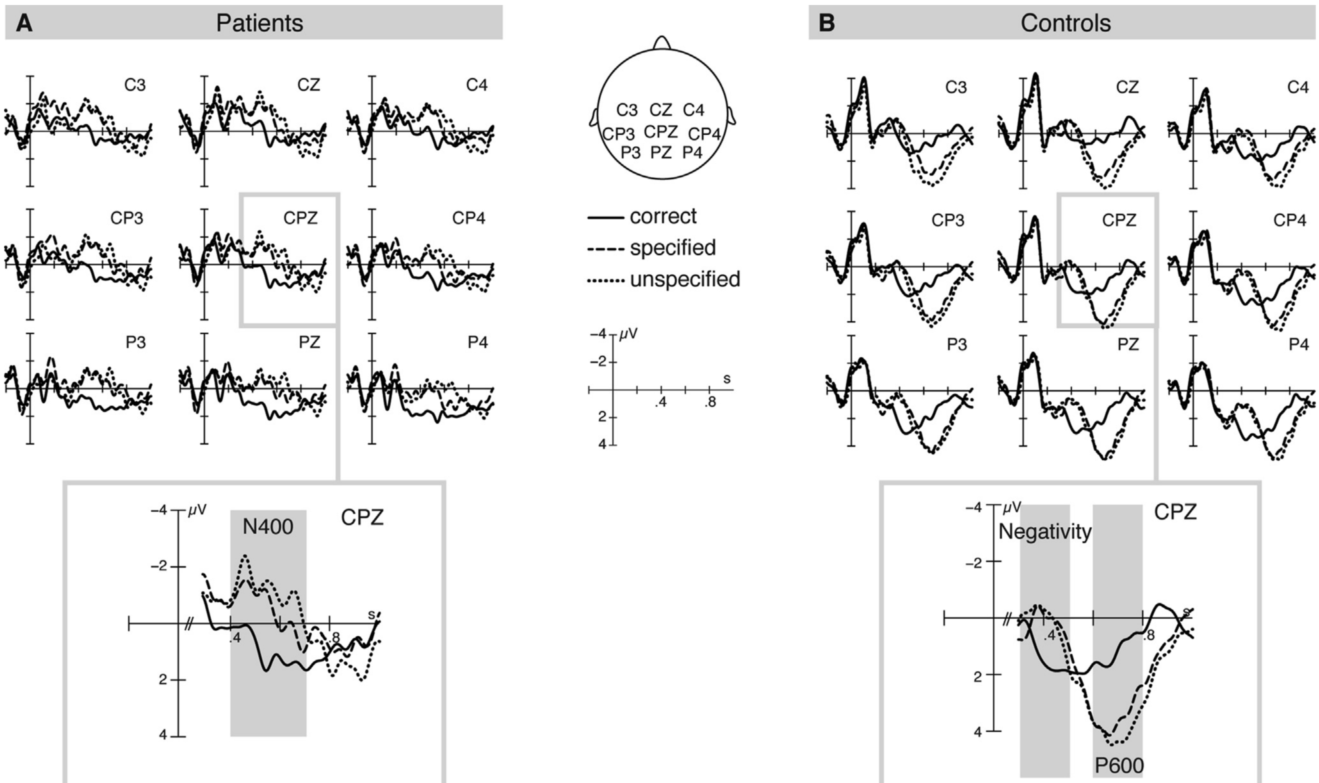

Fig. 4 – Grand average ERPs elicited by the real words in patients (column A) and controls (column B). In patients, for incorrect verbs [i.e., specified (dashed line) and unspecified (dotted line)] an N400 is seen in comparison to correct verbs (solid line). In controls, by contrast, for equivalent incorrect verbs a negativity followed by P600 was found relative to correct verbs. The zoom of the CPZ electrode below of each column illustrates the observed ERP effects.

In order to examine the emergence of an earlier negativity response as seen by Regel et al. (2015), an additional latency window of *300–500 msec* was analyzed. In controls, this analysis revealed a significant interaction of condition with anterior/posterior [$F(2,16) = 4.91$, $p < .05$]. In separate analyses for anterior and posterior electrode sites a main effect of condition was seen for posterior electrode sites [$F(2,16) = 5.52$, $p < .05$]. Post-hoc testing confirms a negativity for both incorrect past tense forms relative to the correct equivalent [for the specified condition: ($t(8) = 7.61$, $p < .05$), for the unspecified condition: ($t(8) = 6.99$, $p < .01$)]. The analysis of the midline electrodes showed no effect of condition [$F(2,16) = 2.18$, n.s.]. In patients, neither a main effect of condition [$F(2,16) = 1.39$, n.s.] nor interactions with condition [$F(2,16) < .32$, n.s.] were seen in the overall analysis. Similarly, in the analysis of the midline electrodes an effect of condition was absent [$F(2,16) = 1.06$, n.s.].

Statistical analysis of all latency windows reported above showed neither an effect of block [$F(1,16) < .27$, n.s.] nor significant interactions of block with group and condition [$F(2,32) < 2.06$, n.s.] suggesting that repetition of items had no impact on the processing of irregular verbs.

3.3.3. *ERP data for the pseudoword items*

A comparison of patients' and controls' ERPs observed for the pseudoword items is displayed in Fig. 5. Visual inspection of the ERPs suggests that the brain potentials for pseudoword past tense forms did not differ in patients. In controls, however, an early positivity emerging around 150 msec followed by a later positivity with a latency onset of around 800 msec seems to be present for incorrect in relation to correct past tense forms. Although showing a delayed latency onset, the latter positivity seems to be comparable in its sensitivity and topography to the late positivity seen for the real word items.

Main analysis of the *150–300 msec* latency window revealed an interaction between group, inflection, and hemisphere [$F(2,32) = 3.55$, $p < .05$]. The resolution of this interaction by group showed a main effect of inflection [$F(2,16) = 4.69$, $p < .05$] in controls only. An early positivity was elicited by the unspecified relative to the correct condition as obtained in the post-hoc testing [$t(8) = 14.30$, $p < .01$].

Statistical analysis of the midline electrodes showed neither an effect of group [$F(1,16) = 1.09$, n.s.], nor an interaction between group and condition [$F(2,32) = 1.96$, n.s.].

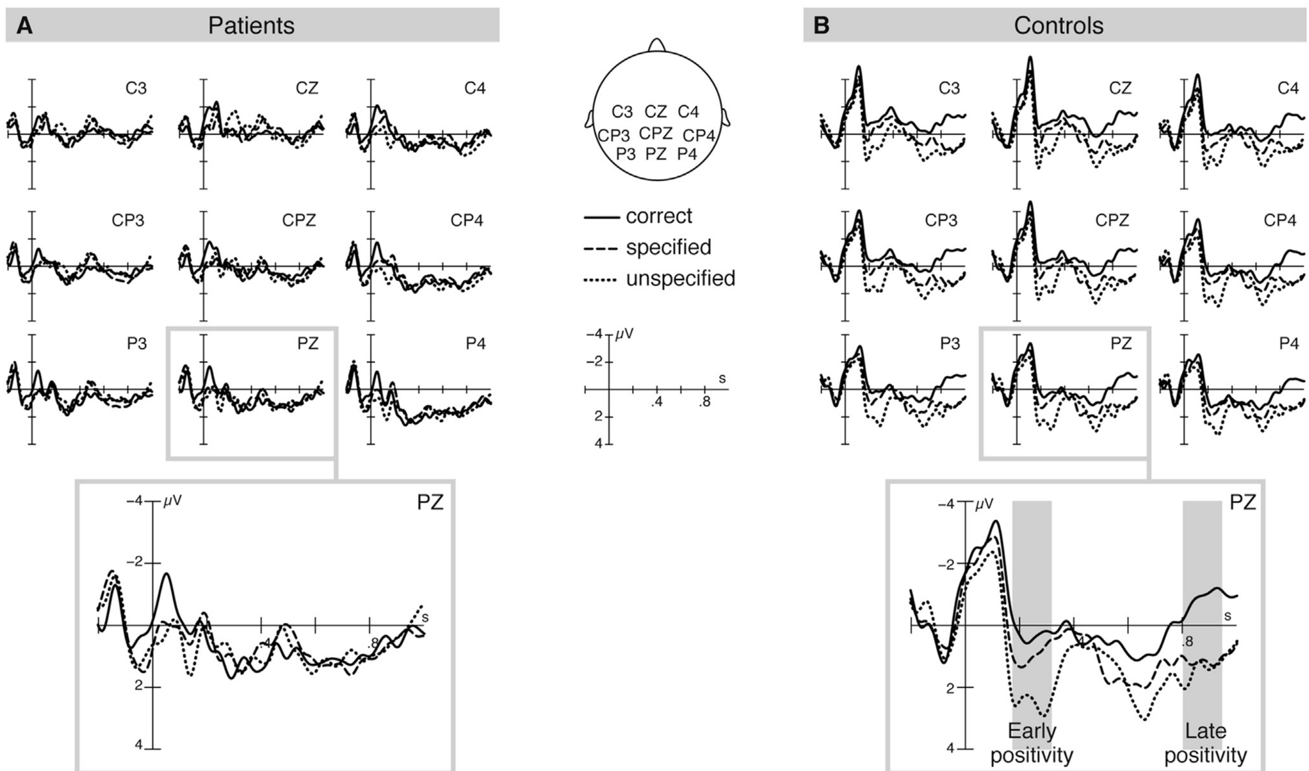

Fig. 5 – Grand average ERPs evoked by the pseudowords in patients (column A) and controls (column B). While for controls a late positivity emerged for incorrect items [i.e., specified (dashed line) and unspecified (dotted line)] in relation to correct ones (solid line), for patients no differences in the ERPs were seen. The zoom of the CPZ electrode below of each column demonstrates these findings.

In the statistical analysis of the 800–950 *msec* latency window, a marginally significant two-way interaction between group and inflection [$F(2,32) = 2.83$, $p < .10$] was found. Resolving this effect by group, revealed in controls a main effect of condition [$F(2,16) = 7.88$, $p < .01$]. The emergence of a late positivity for both incorrect past tense forms in relation to the correct one was confirmed in the post-hoc testing [for the specified condition: ($t(8) = 8.69$, $p < .05$), for the unspecified condition: ($t(8) = 25.75$, $p < .001$)].

Analyzing the midline electrode positions in the 800–950 *msec* latency window showed a marginal interaction between group and condition [$F(2,32) = 3.06$, $p < .10$]. Separate analyses in the patient and control group revealed a significant effect of condition [$F(2,16) = 9.41$, $p < .01$] in controls only. Post-hoc testing confirms the occurrence of a late positivity for both incorrect past tense forms in comparison to their correct equivalents [for the specified condition: ($t(8) = 10.52$, $p < .01$), for the unspecified condition: ($t(8) = 22.92$, $p < .001$)].

As seen for the real word items, effects of block [$F(1,16) < 1.02$, n.s.] as well as significant interactions of block, group, and condition [$F(2,32) < 2.70$, n.s.] were not found in both the overall and midline analysis ruling out an effect of repetition of items on the processing of pseudowords.

4. Discussion

The present study investigated the contribution of the LIFG to morphosyntactic processing as a test of current neurocognitive models of language (Friederici, 2012; Joanisse & McClelland, 2015; Pinker & Ullman, 2002; Ullman, 2001). ERPs to irregular verb inflection (i.e., most specified, specified, and unspecified stem forms) of real word and pseudowords were compared between patients with left inferior frontal lesions, but intact temporal cortex and age-matched healthy controls. The present findings provide evidence for the involvement of distinct processing mechanisms in the processing of those verbs in patients and controls. LIFG patients showed a centro-parietal negativity, resembling an N400 component, elicited by incorrect past tense forms, whereas in controls a late positivity (i.e., a P600 component) was observed, respectively. In controls the P600 component was preceded by an earlier negativity emerging around 300 msec post-stimulus replicating previous findings of a negativity-P600 pattern observed for irregular verb inflection in young adults (Regel et al., 2015). Despite revealing a comparable latency onset, the present negativity was less broadly distributed, which may be best explained by inter-individual or age-related differences as similar paradigms and stimuli were employed in both studies.[6] For the pseudowords, in controls a late positivity emerged for both incorrect items as well as an early positivity for the unspecified relative to the correct items, whereas in patients no differences in the ERPs were seen. Behaviorally, patients had more difficulties in the grammaticality judgment of the real words, as well as in the appropriateness judgment of the pseudowords. The patients' linguistic knowledge on past tense inflection was confirmed in the productive elicitation task prior to the ERP experiments. As both patients and controls revealed a P300 response in the visual oddball experiment, the observed differences in the ERPs of the morphosyntax experiment are unlikely related to attentional deficits. The present findings are discussed with respect to the functional contribution of the LIFG.

4.1. *Unimpaired morphosyntactic processing*

The observation of a negativity and P600 for morphosyntactically violated verbs in controls suggests the presence of a syntax-related ERP pattern. This negativity resembled negativity effects seen for violations of stem formation rules (Gross et al., 1998; Regel et al., 2015; Rodriguez-Fornells et al., 2001). Processing morphosyntactic information enclosed in verb stems seems to recruit an extended neural network involving partially different mechanisms than indexed by LAN. As the present violation included existing stem forms that were initially encountered in the preceding tenses, the observed negativity seems less likely to equate N400 associated with lexical-semantic processing seen for irregularizations (cf. Penke et al., 1997; Weyerts, Penke, Dohrn, Clahsen, & Munte, 1997). In case those verbs could not be lexically accessed (i.e., semantic and syntactic information cannot be activated), merely an N400 would have been emerged, instead of a subsequent P600 indicating further stimulus processing. While this negativity may rather be sensitive to word-form bound morphosyntactic analysis of the incorrectly inflected verbs, the subsequent P600 most likely reflects syntactic reanalysis processes (e.g., Friederici, 2002; Gouvea, Phillips, Kazanina, & Poeppel, 2010). In previous studies, similar P600 responses, in absence of N400, were seen for irregular verbs comprising existing stem forms suggesting that whenever verb stems are morphological identifiable syntactic processes are engaged (Allen, Badecker, & Osterhout, 2003; Newman, Ullman, Pancheva, Waligura, & Neville, 2007). Most importantly, the present morphosyntactic violation did not affect the verbs' morphological and phonological complexity, so that the obtained ERP effects are unlikely associated with such differences (cf. Joanisse & Seidenberg, 1999, 2005).

When dealing with pseudowords, the presence of an early positivity for unspecified compared to correct items suggests enhanced phonological and orthographic processes (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Simon, Bernard, Largy, Lalonde, & Rebai, 2004) for the violation of morphological principles. While specified items refer to an existing irregular inflectional pattern (i.e., ABB), unspecified items are not licensed (i.e., an ABA pattern is nonexistent). Moreover, the finding of a late positivity for incorrect items, rather than N400 (see Regel et al., 2015), is surprising. Instead of predictive processing of the morphophonological properties of potential past tense forms, this positive effect suggests the occurrence of rule association processes triggered in relation to morphosyntactic properties of real irregular verbs.

The present findings imply the engagement of rule-based mechanisms underlying irregular verb processing (i.e., morphosyntactic analysis followed by reanalysis), and support underspecification-based accounts proposing that irregular inflection is based on subregularities (Wiese, 2008). With respect to dual-system approaches (Pinker & Ullman, 2002; Ullman, 2001), the observation of negativity-P600 asks for an extension of the proposed procedural memory system. Procedural mechanisms may not only apply to regular verbs, but at least to those irregular verbs belonging to the inflection pattern tested here. In absence of a mono-phasic N400 in response to irregular inflection patterns, the processing of such patterns may have not been operated by lexical redundancy rules within the mental lexicon. A generalization of those patterns to novel forms based on lexical rules cannot be supported as an N400-like effect in response to pseudowords was not seen. The assumption that all irregular verbs require lexical access as whole forms, thus, is not confirmed. Moreover, with regard to connectionist approaches, no evidence was found that inflected verbs are represented as overlapping whole forms, and involve memory-based processing mechanisms (Joanisse & McClelland, 2015; Rumelhart & McClelland, 1986). If such mechanisms were engaged, an N400 component, instead of a negativity-P600 pattern, should have been elicited by the incorrect verbs.

4.2. *The role of the LIFG in mediating morphosyntactic processing*

Patients with lesions in the LIFG showed a different pattern of results for both the processing of real words and pseudowords than controls. The emergence of an N400 response to the morphosyntactic violation, in absence of a syntax-related ERP pattern, suggests an involvement of memory-based processing mechanisms. Since the incorrect verbs had no lexical entry as potential past tense forms in the mental lexicon, this may have resulted in increased lexical access during the retrieval of adequate meanings. Such an interpretation is in accordance with previous findings showing that the amplitude of N400 is reliably associated with meaning access (for review see e.g., Kutas & Federmeier, 2011). This memory-based mechanism is presumably supported by patients' unaffected temporal cortex (see Marslen-Wilson & Tyler, 2007; Ullman, 2001; Ullman et al., 1997). The

[6] In contrast to the study by Regel et al. (2015), a bandpass filter was applied to the data to improve the signal-to-noise ratio. Potential filter-based distortions by producing artifactual components, such as P600 being preceded by a negativity, and N400 being preceded by P200 (Tanner, Morgan-Short, & Luck, 2015) are rather unlikely to have occurred. The negativity-P600 pattern in controls was previously seen for unfiltered data (Regel et al., 2015), and earlier effects preceding the N400 in patients were absent.

present data suggest an essential role of the LIFG in mediating morphosyntax, and confirm its engagement in rule-based processing mechanisms (Friederici & Kotz, 2003; Friederici, von Cramon, & Kotz, 1999; Marslen-Wilson & Tyler, 2007; Tyler, Cheung, Devereux, & Clarke, 2013; Ullman, 2001).

Further evidence for this functional contribution of the LIFG stems from the ERPs in response to pseudowords. When encountering the pseudowords, in patients no differences in the ERPs were seen, whereas controls revealed a late positivity for incorrect items. While healthy controls may have applied rule-association processes for the pseudowords, comparable processing mechanisms seemed to be intermitted after damage to the LIFG. Since the meaning of the pseudowords could not be accessed from the mental lexicon, compensatory lexical-semantic processing mechanisms as seen for the real words could not be engaged.

The findings accord with dual-system approaches that the frontal cortex, including Broca's area, crucially supports rule-based (procedural) processes (Friederici, 2012; Marslen-Wilson & Tyler, 2007; Pinker & Ullman, 2002; Ullman, 2001), therein being not restricted to default inflection patterns. As the morphological and phonological complexity of inflected verbs remained constant, the data allow a clear implication on the involvement of the LIFG. While the patients suffered only from left-hemispheric frontal damage, the present data also indicate that this function of the LIFG could not be undertaken by the remaining intact brain regions including the right hemisphere. If so, patients would have shown similar ERP patterns as controls for both the real words and the pseudowords. This observation accords with previous studies showing that the left and the right IFG are functionally distinct and not convertible (e.g., Papoutsi, Stamatakis, Griffiths, Marslen-Wilson, & Tyler, 2011; Ullman, 2001).

4.3. *Implications for the neural bases of human language*

With respect to the neural bases of human language the present findings substantiate a modular system with distinct brain regions specified for particular language functions (Friederici, 2011; Pinker & Ullman, 2002; Ullman, 2001). Rule-based mechanisms enabling morphosyntactic processing appear to be mediated by the intact LIFG, in particular by Broca's area. After damage to these brain regions, respective mechanisms were permanently intermitted. While patients were still able to produce and judge inflected verbs, compensatory memory-based mechanisms may have been accessed presumably supported by patients' intact temporal cortex. The obtained findings are in favor of neurocognitive models of language comprehension (Friederici, 2002, 2011, 2012), in which syntactic and semantic processes recruit different brain regions (i.e., Broca's area supporting syntactic structure building processes, and medial temporal lobe mediating lexical-semantic processes). As distinct processing mechanisms were seen in patients and controls, the findings cannot support a unitary language system with brain regions non-selectively involved in diverse language tasks (Joanisse & McClelland, 2015; Rumelhart & McClelland, 1986).

To conclude, the present data on verb processing in patients with lesions in the left inferior frontal cortex, and age-matched healthy controls confirm a relevant contribution of the LIFG, in particular Broca's area, in mediating morphosyntactic processing. Despite patients' recovered language ability, rule-based processing mechanisms underlying irregular verbs were absent after damage to these regions.

Acknowledgments

We thank Anne-Kathrin Franz for her assistance with the recruitment of the participants, and Ina Koch for her support with the acquisition of the EEG data. We also thank Anika Stockert for her help with compiling lesion information of the patients. Furthermore, we are grateful to all the participants for their willingness and commitment to our research. This research was supported by the German Science Foundation Grant (FR 519/19-1) to Angela D. Friederici and Gereon Müller.

Appendix A. List of regular and irregular German verbs in present and past tense inflection with approximate English translation applied in the pre-experiment production task.

Present	Past tense
Regular verbs	
fegen (to sweep)	fegte
üben (to practice)	übte
baden (to bath)	badete
musizieren (to make music)	musizierte
kochen (to cook)	kochte
rauchen (to smoke)	rauchte
beantworten (to respond)	beantwortete
taufen (to baptize)	taufte
Irregular verbs	
fahren (to drive)	fuhr
bestehen (to exist)	bestand
singen (to sing)	sang
fallen (to fall)	fiel
schlafen (to sleep)	schlief
kommen (to come)	kam
waschen (to wash)	wusch
rufen (to call)	rief

Appendix B. List of real irregular German verbs and filler verbs used in each condition with approximate English translation. Incorrect past tense forms are indicated by an asterisk.

Present tense	Past participle	Past tense		
		Correct	Incorrect: specified	Incorrect: unspecified
binden (to bind)	gebunden	band	*bund	*bind
dringen (to urge)	gedrungen	drang	*drung	*dring
finden (to find)	gefunden	fand	*fund	*find
gelingen (to succeed)	gelungen	gelang	*gelung	*geling
klingen (to sound)	geklungen	klang	*klung	*kling
mißlingen (to fail)	mißlungen	mißlang	*mißlung	*mißling
ringen (to struggle)	gerungen	rang	*rung	*ring
schlingen (to bolt)	geschlungen	schlang	*schlung	*schling
schwinden (to fade)	geschwunden	schwand	*schwund	*schwind
schwingen (to swing)	geschwungen	schwang	*schwung	*schwing
singen (to sing)	gesungen	sang	*sung	*sing
sinken (to sink)	gesunken	sank	*sunk	*sink
springen (to jump)	gesprungen	sprang	*sprung	*spring
stinken (to stink)	gestunken	stank	*stunk	*stink
trinken (to drink)	getrunken	trank	*trunk	*trink
winden (to wind)	gewunden	wand	*wund	*wind
wringen (to wring)	gewrungen	wrang	*wrung	*wring
zwingen (to force)	gezwungen	zwang	*zwung	*zwing
bergen (to recover)	geborgen	barg	*borg	*berg
bersten (to burst)	geborsten	barst	*borst	*berst
brechen (to break)	gebrochen	brach	*broch	*brech
gelten (to pertain)	gegolten	galt	*golt	*gelt
helfen (to help)	geholfen	half	*holf	*helf
schelten (to chide)	gescholten	schalt	*scholt	*schelt
erschrecken (to startle)	erschrocken	erschrak	*erschrock	*erschreck
sprechen (to speak)	gesprochen	sprach	*sproch	*sprech
stechen (to sting)	gestochen	stach	*stoch	*stech
sterben (to die)	gestorben	starb	*storb	*sterb
treffen (to hit)	getroffen	traf	*trof	*treff
verderben (to spoil)	verdorben	verdarb	*verdorb	*verderb
werben (to advertise)	geworben	warb	*worb	*werb
werfen (to throw)	geworfen	warf	*worf	*werf
stehlen (to steal)	gestohlen	stahl	*stohl	*stehl
befehlen (to order)	befohlen	befahl	*befohl	*befehl
empfehlen (to recommend)	empfohlen	empfahl	*empfohl	*empfehl
nehmen (to take)	genommen	nahm	*nohm	*nehm
beginnen (to begin)	begonnen	begann	*begonn	*beginn
gewinnen (to win)	gewonnen	gewann	*gewonn	*gewinn
rinnen (to flow)	geronnen	rann	*ronn	*rinn
schwimmen (to swim)	geschwommen	schwamm	*schwomm	*schwimm
sinnen (to think)	gesonnen	sann	*sonn	*sinn
Filler verbs				
beißen (to bite)	gebissen	biß	–	–
gleiten (to slide)	geglitten	glitt	–	–
kneifen (to pinch)	gekniffen	kniff	–	–
leiden (to suffer)	gelitten	litt	–	–
pfeifen (to whistle)	gepfiffen	pfiff	–	–
reißen (to tear)	gerissen	riss	–	–
reiten (to ride)	geritten	ritt	–	–
schleichen (to creep)	geschlichen	schlich	–	–
schleifen (to whet)	geschliffen	schliff	–	–
schneiden (to cut)	geschnitten	schnitt	–	–
streichen (to paint)	gestrichen	strich	–	–
streiten (to argue)	gestritten	stritt	–	–
steigen (to rise)	gestiegen	stieg	–	–
weisen (to show)	gewiesen	wies	–	–

Appendix C. List of pseudoword verbs and pseudoword filler verbs used in each condition. Incorrect past tense forms are indicated by an asterisk.

Present tense	Past participle	Past tense		
		Correct	Incorrect: specified	Incorrect: unspecified
ginden	gegunden	gand	*gund	*gind
mingen	gemungen	mang	*mung	*ming
kringen	gekrungen	krang	*krung	*kring
pinden	gepunden	pand	*pund	*pind
gewingen	gewungen	gewang	*gewung	*gewing
blingen	geblungen	blang	*blung	*bling
dißtingen	dißtungen	dißtang	*dißtung	*dißting
zingen	gezungen	zang	*zung	*zing
schmingen	geschmungen	schmang	*schmung	*schming
schringen	geschrungen	schrang	*schrung	*schring
tingen	getungen	tang	*tung	*ting
rinken	gerunken	rank	*runk	*rink
splingen	gesplungen	splang	*splung	*spling
stinzen	gestunzen	stanz	*stunz	*stinz
prinken	geprunken	prank	*prunk	*prink
schninden	geschnunden	schnand	*schnund	*schnind
wrinden	gewrunden	wrand	*wrund	*wrind
zwinden	gezwunden	zwand	*zwund	*zwind
zergen	gezorgen	zarg	*zorg	*zerg
wersten	geworsten	warst	*worst	*werst
klechen	geklochen	klach	*kloch	*klech
delten	gedolten	dalt	*dolt	*delt
stelfen	gestolfen	stalf	*stolf	*stelf
relten	gerolten	ralt	*rolt	*relt
erschletten	erschlotten	erschlatt	*erschlott	*erschlett
gechen	gegochen	gach	*goch	*gech
pfechen	gepfochen	pfach	*pfoch	*pfech
zermen	gezormen	zarm	*zorm	*zerm
beffen	geboffen	baf	*bof	*beff
vermerlen	vermorlen	vermarl	*vermorl	*vermerl
werzen	geworzen	warz	*worz	*werz
sterfen	gestorfen	starf	*storf	*sterf
schwehen	geschwohen	schwah	*schwoh	*schweh
berehlen	berohlen	berahl	*berohl	*berehl
entwehmen	entwommen	entwahm	*entwomm	*entwehm
tehnen	getonnen	tahn	*tonn	*tehn
belinnen	belonnen	belann	*belonn	*belinn
gezinnen	gezonnen	gezann	*gezonn	*gezinn
pfinnen	gepfonnen	pfann	*pfonn	*pfinn
bimmen	gebommen	bamm	*bomm	*bimm
stinnen	gestonnen	stann	*stonn	*stinn
splinnen	gesplonnen	splann	*splonn	*splinn
Pseudoword filler verbs				
feißen	gefissen	fiss	–	–
gleifen	gegliffen	gliff	–	–
kneiten	geknitten	knitt	–	–
pleifen	gepliffen	pliff	–	–
kleißen	geklissen	kliss	–	–
geiten	gegitten	gitt	–	–
schmeichen	geschmichen	schmich	–	–
schleiten	geschlitten	schlitt	–	–
wreischen	gewrischen	wrisch	–	–
schneißen	geschnissen	schniss	–	–
spleiten	gesplitten	splitt	–	–
preiten	gepritten	pritt	–	–
steipen	gestiepen	stiep	–	–
weifen	gewiefen	wief	–	–

REFERENCES

Allen, M., Badecker, W., & Osterhout, L. (2003). Morphological analysis in sentence processing: An ERP study. *Language and Cognitive Processes, 18*(4), 405–430.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience, 11*(3), 235–260.

Bird, H., Lambon Ralph, M. A., Seidenberg, M. S., McClelland, J. L., & Patterson, K. (2003). Deficits in phonology and past-tense morphology: what's the connection? *Journal of Memory and Language, 48*, 502–526.

Bybee, J. (1995). Regular morphology and the lexicon. *Language and Cognitive Processes, 10*, 425–455.

Clahsen, H. (1999). Lexical entries and rules of language: A multidisciplinary study of German inflection. *Behavioral and Brain Sciences, 22*, 991–1060.

Coulson, S., King, J. W., & Kutas, M. (1998). Expect the unexpected: Event-related brain response to morphosyntactic violations. *Language and Cognitive Processes, 13*, 21.

de Diego Balaguer, R., Rodriguez-Fornells, A., Rotte, M., Bahlmann, J., Heinze, H.-J., & Münte, T. F. (2006). Neural circuits subserving the retrieval of stems and grammatical features in regular and irregular verbs. *Human Brain Mapping, 27*, 874–888.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences, 6*, 78–84.

Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews, 91*, 1357–1392.

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262–268.

Friederici, A. D., & Frisch, S. (2000). Verb argument structure processing: The role of verb-specific and argument-specific information. *Journal of Memory and Language, 43*, 476–507.

Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: Functional imaging and lesion studies. *NeuroImage, 20*, 8–17.

Friederici, A. D., von Cramon, D. Y., & Kotz, S. A. (1999). Language related brain potentials in patients with cortical and subcortical left hemisphere lesions. *Brain, 1999*(122), 1033–1047.

Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex, 13*(2), 170–177.

Gouvea, A. C., Phillips, C., Kazanina, N., & Poeppel, D. (2010). The linguistic processes underlying the P600. *Language and Cognitive Processes, 25*, 149–188.

Grodzinsky, Y. (2000). The neurology of syntax: Language use without Broca's area. *Behavioral and Brain Sciences, 23*, 1–71.

Gross, M., Say, T., Kleingers, M., Clahsen, H., & Münte, T. F. (1998). Human brain potentials to violations in morphologically complex Italian words. *Neuroscience Letters, 241*(2–3), 83–86.

Gunter, T. C., Friederici, A. D., & Schriefers, H. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *Journal of Cognitive Neuroscience, 12*, 556–568.

Hasting, A. S., & Kotz, S. A. (2008). Speeding up syntax: On the relative timing and automaticity of local phrase structure and morphosyntactic processing as reflected in event-related brain potentials. *Journal of Cognitive Neuroscience, 20*(7), 1207–1219.

Jakuszeit, M., Kotz, S. A., & Hasting, A. S. (2013). Generating predictions: Lesion evidence on the role of left inferior frontal cortex in rapid syntactic analysis. *Cortex, 49*(10), 2861–2874.

Joanisse, M. F., & McClelland, J. L. (2015). Connectionst perspectives on language learning, representation and processing. *Cognitive Science, 6*(3), 235–247.

Joanisse, M. F., & Seidenberg, M. S. (1999). Impairments in verb morphology after brain injury: A connectionist model. *Proceedings of the National Academy of Sciences of the United States of America, 96*, 7592–7597.

Joanisse, M. F., & Seidenberg, M. S. (2005). Imaging the past: Neural activation in frontal and temporal regions during regular and irregular past-tense processing. *Cognitive, Affective, & Behavioral Neuroscience, 5*(3), 282–296.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychophysiology, 62*, 621–647.

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience, 9*(12), 920–933.

Marslen-Wilson, W. D., & Tyler, L. K. (1998). Rules, representations, and the English past tense. *Trends in Cognitive Sciences, 2*(11), 428–435.

Marslen-Wilson, W. D., & Tyler, L. K. (2007). Morphology, language and the brain: The decompositional substrate for language comprehension. *Philosophical Transactions of the Royal Society: Biological Sciences, 362*(1481), 823–836.

McClelland, J. L., & Patterson, K. (2002). Rules or connections in past-tense inflections: What does the evidence rule out? *Trends in Cognitive Sciences, 6*, 465–472.

Morris, J., & Holcomb, P. J. (2005). Event-related potentials to violations of inflectional verb morphology in English. *Cognitive Brain Research, 25*, 963–981.

Münte, T. F., Heinze, H. J., & Mangun, G. R. (1993). Dissociation of brain activity related to syntactic and semantic aspects of language. *Journal of Cognitive Neuroscience, 5*, 335–344.

Newman, A. J., Ullman, M. T., Pancheva, R., Waligura, D. L., & Neville, H. J. (2007). An ERP study of regular and irregular English past tense inflection. *NeuroImage, 34*(1), 435–445. http://dx.doi.org/10.1016/j.neuroimage.2006.09.007.

Oh, T. M., Tan, K. L., Ng, P., Berne, Y. I., & Graham, S. (2011). The past tense debate: Is phonological complexity the key to the puzzle? *NeuroImage, 57*, 271–280.

Opitz, A., Regel, S., Müller, G., & Friederici, A. D. (2013). Neurophysiological evidence for morphological underspecification in German strong adjective inflection. *Language, 89*(2), 231–264.

Papoutsi, M., Stamatakis, E. A., Griffiths, J. D., Marslen-Wilson, W. D., & Tyler, L. K. (2011). Is left fronto-temporal connectivity essential for syntax? Effective connectivity, tractography and performance in left-hemisphere damaged patients. *NeuroImage, 58*, 656–664.

Penke, M., & Krause, M. (2002). German noun plurals: A challenge to the dual-mechanism model. *Brain and Language, 81*, 303–311.

Penke, M., & Westermann, G. (2006). Broca's area and inflectional morphology: Evidence from Broca's aphasia and computer modeling. *Cortex, 42*, 563–576.

Penke, M., Weyerts, H., Gross, M., Zander, E., Münte, T. F., & Clahsen, H. (1997). How the brain processes complex words: An event-related potential study of German verb inflections. *Cognitive Brain Research, 6*(1), 37–52.

Picton, T. W. (1992). The P300 wave of the human event-related potential. *Journal of Clinical Neurophysiology, 9*, 456–479.

Pinker, S. (1999). *Words and rules: The ingredients of language*. New York: HarperCollins.

Pinker, S., & Prince, A. (1988). On language and connectionism: Analysis of a parallel distributed processing model of language acquisition. *Cognition, 28*, 73–193.
Pinker, S., & Ullman, M. T. (2002). The past and future of the past tense. *Trends in Cognitive Sciences, 6*(11), 456–463.
Regel, S., Opitz, A., Mueller, G., & Friederici, A. D. (2015). The past tense debate revisited: Electrophysiological evidence for subregularities of irregular verb inflection. *Journal of Cognitive Neuroscience, 27*(9), 1870–1885.
Rodriguez-Fornells, A., Clahsen, H., Lleo, C., Zaake, W., & Münte, T. F. (2001). Event-related brain responses to morphological violations in Catalan. *Cognitive Brain Research, 11*, 47–58.
Rumelhart, D., & McClelland, J. L. (1986). *On learning the past tenses of English verbs. Parallel distributed processing: Explorations in the microstructure of cognition*. Cambridge: MIT Press.
Sahin, N. T., Pinker, S., & Halgren, E. (2006). Abstract grammatical processing of nouns and verbs in Broca's area: Evidence from fMRI. *Cortex, 42*, 540–562.
Simon, G. G., Bernard, C., Largy, P., Lalonde, R., & Rebai, M. (2004). Chronometry of visual word recognition during passive and lexical decision tasks: An ERP investigation. *International Journal of Neuroscience, 114*(11), 1401–1432.
Tanner, D., Morgan-Short, K., & Luck, S. J. (2015). How inappropriate high-pass filters can produce artifactual effects and incorrect conclusions in ERP studies of language and cognition. *Psychophysiology, 52*(8), 997–1009. http://dx.doi.org/10.1111/psyp.12437.
Tyler, L. K., Cheung, T. L. P., Devereux, B. J., & Clarke, A. (2013). Syntactic computations in the language network: Characterizing dynamic network properties using representational similarity analysis. *Frontiers in Psychology, 4*, 1–19.
Tyler, L. K., de Mornay-Davies, P., Anokhina, R., Longworth, C., Randall, B., & Marslen-Wilson, W. D. (2002). Dissociations in processing past tense morphology: Neuropathology and behavioral studies. *Journal of Cognitive Neuroscience, 14*(1), 79–94.
Tyler, L. K., Randall, B., & Marslen-Wilson, W. D. (2002). Phonology and neuropsychology of the English past tense. *Neuropsychologia, 40*, 1154–1166.
Tyler, L. K., Stamatakis, E. A., Post, B., Randall, B., & Marslen-Wilson, W. D. (2005). Temporal and frontal systems in speech comprehension: An fMRI study of past tense processing. *Neuropsychologia, 43*, 1963–1974.
Ullman, M. T. (2001). A neurocognitive perspective on language: The declarative/procedural model. *Nature Reviews Neuroscience, 2*, 717–726.
Ullman, M. T., Corkin, S., Coppola, M., Hickok, G., Growdon, J. H., Koroshetz, W. J., et al. (1997). A neural dissociation within language: Evidence the mental dictionary is part of declarative memory, and that grammatical rules are processed by the procedural system. *Journal of Cognitive Neuroscience, 9*(2), 266–276. http://dx.doi.org/10.1162/jocn.1997.9.2.266.
Ullman, M. T., Pancheva, R., Love, T., Yee, E., Swinney, D., & Hickok, G. (2005). Neural correlates of lexicon and grammar: Evidence from the production, reading, and judgment of inflection in aphasia. *Brain and Language*, 185–238.
Weyerts, H., Penke, M., Dohrn, U., Clahsen, H., & Munte, T. F. (1997). Brain potentials indicate differences between regular and irregular German plurals. *NeuroReport, 8*(4), 957–962.
Wiese, B. (2008). Form and function of verbal ablaut in contemporary standard German. In R. Sackmann (Ed.), *Explorations in integrational linguistics. Four essays on German, French, and Guaraní* (pp. 97–151). Amsterdam; Philadelphia: John Benjamins.