



ERPs reveal individual differences in morphosyntactic processing

Darren Tanner^{a,*}, Janet G. Van Hell^{b,c}^a Department of Linguistics, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA^b Department of Psychology, Pennsylvania State University, University Park, PA 16802, USA^c Behavioural Science Institute, Radboud University Nijmegen, Nijmegen, The Netherlands

ARTICLE INFO

Article history:

Received 26 June 2013

Received in revised form

28 December 2013

Accepted 3 February 2014

Available online 11 February 2014

Keywords:

ERPs

N400

P600

LAN

Morphosyntax

Individual differences

Familial sinistrality

ABSTRACT

We investigated individual differences in the neural substrates of morphosyntactic processing among monolingual English speakers using event-related potentials (ERPs). Although grand-mean analysis showed a biphasic LAN-P600 pattern to grammatical violations, analysis of individuals' ERP responses showed that brain responses varied systematically along a continuum between negativity- and positivity-dominant ERP responses across individuals. Moreover, the left hemisphere topography of the negativity resulted from component overlap between a centro-parietal N400 in some individuals and a right hemisphere-dominant P600 in others. Our results show that biphasic ERP waveforms do not always reflect separable processing stages within individuals, and moreover, that the LAN can be a variant of the N400. These results show that there are multiple neurocognitive routes to successful grammatical comprehension in language users across the proficiency spectrum. Our results underscore that understanding and quantifying individual differences can provide an important source of evidence about language processing in the general population.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Successful language comprehension requires the rapid integration of multiple information sources. The meanings of incoming lexical items must be accessed, morphosyntactic cues must be identified and linked together to form a syntactic representation of the sentence, and all of this information must be integrated into a coherent semantic representation at the sentence and discourse levels. Decades of research have now shown that these processes occur incrementally, as the linguistic input unfolds over time (e.g., Rayner & Clifton, 2009). One particular focus in neurocognitive research on language comprehension has been identifying the neural mechanisms supporting morphosyntactic integration (i.e., the processing of grammatical rules or constraints). Indeed, a number of recent neurocognitive models of language comprehension based on recordings of event-related brain potentials (ERPs) have been put forth to explain how morphosyntactic processes unfold in real time (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2008; Friederici, 2002; Friederici & Weissenborn, 2007; Hagoort, 2003; Molinaro, Barber, & Carreiras, 2011; Ullman, 2004).

The validity of these models rests upon the assumptions that proficient, literate native speakers of a language show a relatively homogenous profile of brain responses during language comprehension, and that the grand mean response reflects this normative brain response across individuals. However, some recent research has begun to show neurocognitive processing differences among native speakers of a language, and characterizing these individual differences and their theoretical consequences has become an increasingly important goal (Pakulak & Neville, 2010; Prat, 2011). In the study reported here, we use novel metrics to quantify individual variation in language-related ERP effects, which show that qualitative individual differences in brain responses exist among proficient monolinguals processing morphosyntactic dependencies with little semantic content. This is a linguistic domain and population where individual differences in ERPs have not previously been reported. Moreover, we show that, while failure to account for individual differences in brain responses can lead to spurious conclusions about language processing in the general population, understanding and quantifying these differences can provide an important source of evidence regarding the nature of language processing mechanisms.

Recordings of brain activity using ERPs have been useful in identifying the nature and time course of language comprehension processes, as different ERP components have been reliably associated with the processing of different types of linguistic information.

* Correspondence to: Department of Linguistics, 4080 Foreign Languages Building, MC 168, 707 S Mathews Ave., Urbana, IL 61801, USA. Tel.: +1 217 244 5841.

E-mail address: dstanner@gmail.com (D. Tanner).

For example, the processing of meaningful stimuli (including words) has been shown to elicit a negative-going component prominent over centro-parietal scalp regions with a peak around 400 ms after stimulus presentation (the N400 component). The amplitude of this peak co-varies with a number of factors, such as a given word's frequency or conceptual integratability into a sentence or discourse context (the N400 effect: Hagoort, Hald, Bastiaansen, & Petersson, 2004; Kutas & Hillyard, 1980, 1984; Lau, Phillips, & Poeppel, 2008; Van Berkum, Hagoort, & Brown, 1999). On the other hand, a variety of morphosyntactic anomalies, such as agreement and tense violations, frequently elicit a biphasic pattern characterized by a left anterior negativity (LAN) between 300 and 500 ms followed by a broadly distributed positivity with a centro-parietal maximum beginning around 500 ms (the P600 effect: Friederici, Hahne, & Mecklinger, 1996; Hagoort, Brown, & Groothusen, 1993; Molinaro et al., 2011; Osterhout & Mobley, 1995). Overall this differential pattern of neural responses to linguistic manipulations suggests that lexical and morphosyntactic processes are in many circumstances neurocognitively distinct, as violations of each elicit a characteristic pattern of brain responses.

While the exact functional interpretation of the N400 and LAN/P600 effects is still being debated (see e.g., Bornkessel-Schlesewsky & Schlewsky, 2008; Brouwer, Fitz, & Hoeks, 2012; Kim & Osterhout, 2005; Kuperberg, 2007; Kutas & Federmeier, 2011; Van de Meerendonk, Kolk, Vissers, & Chwilla, 2010), some neurocognitive models of syntactic processing ascribe different processes to the two phases of the LAN-P600 complex (Batterink & Neville, 2013; Friederici & Weissenborn, 2007; Hagoort, 2003; Molinaro et al., 2011; Pakulak & Neville, 2010; Ullman, 2004). Although the exact details of these syntactic processing models differ, a common feature of them is the assumption that the LAN reflects automatic detection of syntactic violations during first pass parses, while the P600 reflects later controlled attempts to reanalyze or unify the ungrammatical parse.

An important implication of these syntactic processing models is that morphosyntactic violations should elicit biphasic LAN-P600 responses in most or all individuals. If the LAN is a singular component reflecting the detection of anomalies, detection should be a prerequisite for reanalysis. Extrapolating to the context of individual differences, this would predict that the extent to which individuals differ in their neural responses to morphosyntactic violations, the magnitude of any individual's P600 effect (reflecting reanalysis or continued attempts to unify the initial failed parse) should be a function of the strength of that individual's detection of the anomaly (indexed by the LAN). However, while P600s are nearly uniformly elicited in studies of morphosyntactic processing, the presence and scalp topography of LANs have been extremely variable across studies. While many studies have reported typical LAN effects between approximately 300 and 500 ms, others have reported syntactic negativities preceding the P600 over bilateral frontal sites (e.g., Gouvea, Phillips, Kazanina, & Poeppel, 2010; Hagoort, Wassenaar, & Brown, 2003), left temporal sites (e.g., Kaan & Swaab, 2003a; Rodriguez-Fornells, Clahsen, Lleó, Zaake, & Münte, 2001), right temporal sites (e.g., Osterhout & Nicol, 1999), or broadly distributed negativities with a right frontal maximum (e.g., Dillon, Nevins, Austin, & Phillips, 2012; Silva-Pereyra & Carreiras, 2007). Despite this variability in topography, many researchers have presumed that these disparate negativities (sometimes referred to more broadly as anterior negativities, or ANs) reflect the same basic underlying process indexed by the canonical LAN. Additionally, some studies of morphosyntactic processing have reported large P600 effects, but failed to find any earlier negativity (e.g., Allen, Badecker, & Osterhout, 2003; Nevins, Dillon, Malhotra, & Phillips, 2007; Osterhout, McKinnon, Bersick, & Corey, 1996), while others have shown that the presence of the LAN may be modulated by presentation modality (visual

versus auditory: Hagoort & Brown, 2000) or participant task (acceptability judgment versus passive reading: Osterhout & Mobley, 1995).

Some work has attempted to explain some of the apparent variability in the LAN. One suggestion is that the presence or absence of LAN effects may be a function of the morphological richness of a language: sentence comprehension in languages with relatively free word order and rich inflectional systems (e.g., German and Italian) may require stronger engagement of automatic morphosyntactic processing mechanisms than sentence comprehension in languages with fixed word order and residual inflectional systems (e.g., English: Friederici & Weissenborn, 2007). A second suggestion is that methodological considerations like choice of reference site for ERP analysis may play a crucial role in the presence or absence of a LAN (Molinaro et al., 2011). Molinaro and colleagues argue that LAN effects are most likely to occur with linked or averaged mastoid references, as opposed to left mastoid references, which may disproportionately subtract out left hemisphere effects like the LAN. However, even these explanations fail to capture all of the variability: LAN effects have been reported in languages with impoverished inflectional systems (English) using left mastoid references (Coulson, King, & Kutas, 1998; Osterhout & Mobley, 1995), whereas others have failed to find a LAN in morphologically rich languages (Hindi) with linked mastoid references (Nevins et al., 2007). Thus, despite the centrality of the LAN to numerous models of sentence comprehension as an integral index of failure in morphosyntactic processing, the enormous variability in scalp topography across studies suggests that it may not reflect a single underlying neurocognitive process with a consistent neuroanatomical source. Moreover, as P600 effects have been found in the absence of earlier LAN or other negativities, the syntactic processes indexed by the P600 may not crucially depend on the earlier detection of an anomaly, as indexed by the LAN.

An important remaining issue is therefore resolving the functional nature of the LAN and the factors related to its presence or absence. One possibility that has received little attention is the role that individual variability in ERP responses may play (though see Osterhout, McLaughlin, Kim, Greewald, & Inoue, 2004). Some studies have shown that biphasic negative-positive grand mean ERP waveforms can sometimes be a result of averaging over individuals who show different ERP response profiles. Individual differences in brain responses have been reported to anomalous content words in garden path sentences (e.g., *The boat sailed down the river sank*), where some individuals showed a P600 effect and others an N400 effect (Osterhout, 1997). The result after averaging was a statistically reliable biphasic response in the grand mean that was not representative of most individuals' brain responses. More recent research has shown that violations of verb-argument animacy constraints (*The box is biting...*) elicited an N400 in individuals with lower verbal working memory (WM) span, but a P600 in participants with higher verbal WM span (Nakano, Saron, & Swaab, 2010; see also Oines, Miyake, & Kim, 2012). Others have shown that interactions between sentence complexity and individual differences in cognitive control (as measured by a color-word Stroop task) can modulate the polarity of ERP responses (negative- vs. positive-going) to sentences containing conflicts between world knowledge and syntactic ordering of constituents (Ye & Zhou, 2008). In these cases, the linguistic anomalies were signaled by both semantic (e.g., lexical associations, animacy, world knowledge) and syntactic (e.g., inflectional morphology, syntactic position) information. The results suggest that some individuals may focus more on lexical information and show N400s while others focus more on combinatorial information and show P600s, and moreover, that these individual differences can be mediated by WM or cognitive control. Importantly,

traditional ERP grand averages in any of the above-mentioned ERP studies would be misleading in terms of the actual distribution of brain responses in the population being sampled and would have shown either null effects or biphasic negative–positive responses (see Kos, Van den Brink, & Hagoort, 2012; Nieuwland & Van Berkum, 2008; Zhang et al. 2013, for additional evidence that individual differences can give rise to non-representative grand mean waveforms).

Previous studies finding correlations between individual difference measures and ERP responses each focused only on a single cognitive factor (e.g., WM or cognitive control). It may be the case that more than one factor is at play in modulating ERP responses. In the current study we investigate the impact of each of these individual difference variables (WM span and cognitive control), as well as lexical processing speed (Barca & Pezzulo, 2012) and language proficiency (Pakulak & Neville, 2010) on ERP responses. We also explore whether familial left-handedness (familial sinistrality) affects ERP responses. Behavioral evidence suggests that right-handed individuals with left-handed blood relatives are more sensitive to lexical and semantic information than right-handers with no left-handed relatives, who are more sensitive to syntactic and sequential information (Bever, Carrithers, Cowart, & Townsend, 1989; Townsend & Bever, 2001; Townsend, Carrithers, & Bever, 2001). This finding has potentially important implications for studies of individual differences using ERPs, in that familial sinistrality may be associated with greater dominance of N400 effects relative to P600 effects, though no research to date has directly investigated this possibility.

Moreover, no research to date has investigated whether individual differences in N400/P600 responses exist among monolinguals processing core morphosyntactic anomalies with little semantic content. Some recent evidence bearing on this final point has shown individual differences in the N400/P600 continuum in the processing of core morphosyntax, but in the context of second language (L2) processing. Tanner, Inoue, and Osterhout (in press) and Tanner, McLaughlin, Herschensohn, and Osterhout (2013) have shown in both novice L2 learners and highly proficient bilinguals that violations of subject–verb number agreement can elicit N400 effects in some individuals and P600s in others. In these L2 studies grand mean waveforms showed biphasic responses, which did not accurately represent any individual's ERP response profile. This suggests that considerable variability in the neurocognitive substrates of morphosyntactic processing exists among even highly proficient bilinguals, a population that has been otherwise shown to have language-related ERP signatures indistinguishable from monolinguals (Friederici, Steinhauer, & Pfeifer, 2002; Morgan-Short, Steinhauer, Sanz, & Ullman, 2012; Steinhauer, White, & Drury, 2009). One might therefore expect that similar variability could be present among monolinguals processing violations of core morphosyntactic constraints in their L1. However, it remains to be seen to what extent this variability exists, how it impacts grand mean waveforms, or what individual difference factors are related to it. Although the LAN and N400 effects are typically distinguished based on characteristic scalp distributions (Hagoort et al., 2003), it is nonetheless possible that some aspects of LAN-like negativities could be accounted for in terms of an N400-like component (cf. Service, Helenius, Maury, & Salmelin, 2007), with the biphasic grand mean response being driven at least partly by individual differences.

Our goal here was to investigate individual differences among monolingual native English speakers processing violations of core morphosyntactic constraints in English. We focus on the ERP correlates to violations of two salient English morphosyntactic rules: subject–verb agreement and verb tense constraints. Based on neurocognitive models of morphosyntactic processing (Batterink & Neville, 2013; Friederici, 2002; Friederici &

Weissenborn, 2007; Hagoort, 2003; Hahne & Jescheniak, 2001; Molinaro et al., 2011; Pakulak & Neville, 2010; Ullman, 2004), one prediction is that morphosyntactic violations should elicit biphasic LAN-P600 responses in all (or most) individuals, though the exact scalp topography of the LAN may differ from the canonical left anterior focus. Moreover, if the processes indexed by the LAN reflect a failure of syntactic unification processes or engagement of an automatic anomaly detection system, the degree to which the anomaly is detected should predict the degree to which reanalysis processes are engaged. That is, the magnitude of the negativity and positivity should be highly *positively* correlated across individuals. Alternately, some previous findings suggest that biphasic grand mean ERP responses can be driven at least in part by individual differences, where some individuals show negativity-dominant responses and others show positivity-dominant responses (Nieuwland & Van Berkum, 2008; Osterhout, 1997; Tanner et al., 2013; Tanner et al., press). On this account, the negativity and positivity should be highly *negatively* correlated across individuals, and the scalp topography of the two effects in the grand mean should reflect the extent to which the respective negativity and positivity intersect in time and space.

2. Method

2.1. Participants

Participants were 42 monolingual native English speakers enrolled at a large U.S. university. All participants were strongly right-handed as assessed by an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, and reported no history of neurological impairment. Data from two participants were excluded due to excessive artifact in the raw EEG, leaving 40 participants in the final analysis (12 male; mean age: 19.4 years, range: 18–35). All participants provided informed consent and received course credit for taking part.

2.2. Materials

Critical stimuli were created in two conditions: subject–verb agreement and verb tense. In the agreement condition sentence frames contained a singular noun, followed by a prepositional phrase modifier containing another singular noun, followed by an auxiliary verb that either agreed or disagreed with the singular subject noun in number (*is/are, was/were*), followed by a short predicate (e.g., *The clerk at the clothing boutique was/were severely underpaid and unhappy*). One hundred twenty sentence frames were constructed, with four versions of each sentence. Two of the versions corresponded to the grammatical/ungrammatical sentence pairs reported here; the other two versions were filler sentences, which contained plural nouns embedded within the prepositional phrase. The four versions of each sentence were distributed across four lists in a Latin square design. Each list contained 30 grammatical sentences and 30 ungrammatical sentences, and no participant saw two versions of the same sentence frame.

Critical stimuli in the verb tense condition consisted of 60 grammatical/ungrammatical sentence pairs, where the ungrammatical version of each pair contained a violation of English constraints on verb tense. Grammatical sentences in this condition contained a progressive verb construction consisting of a form of the verb *be* plus a progressive participle; ungrammatical versions contained a bare verb stem (e.g., *The crime rate was increasing/*increase despite the growing police force*). Sentence pairs in this condition were counterbalanced across lists 1 and 2, and again across lists 3 and 4. Each participant saw 30 grammatical and 30 ungrammatical sentences, and no participant saw two versions of the same sentence frame.

Thus, there were 120 critical sentences used in this experiment (30 grammatical agreement, 30 ungrammatical agreement, 30 grammatical tense, 30 ungrammatical tense), which were pseudo-randomized among 120 filler sentences. Sixty filler sentence pairs were the additional two versions of the agreement sentences (above) and sixty pairs contained violations of lexical semantic constraints (e.g., *John wanted to read/*bake a book in his spare time*). The resulting lists each had 240 sentences, half of which contained an anomaly.

2.3. Procedure

Participants were tested in a single session, lasting approximately 2.5 h. Upon arrival to the laboratory, each participant was asked to fill out an abridged version

of the Edinburgh Handedness Questionnaire and a language history questionnaire. Each participant was randomly assigned to one of the stimulus lists and was seated in a comfortable chair. Participants were instructed to relax and minimize movements and blinks while reading and to read each sentence as normally as possible. Each trial consisted of the following events: each sentence was preceded by a blank screen for 500 ms, followed by a fixation cross, followed by a stimulus sentence presented one word at a time. The fixation cross and each word appeared on the screen for 350 ms followed by a 100 ms blank screen between words. Sentence-ending words appeared with a full stop. A “Good/Bad?” response prompt then appeared. Participants were instructed to respond “good” if they felt the sentence was grammatical and semantically coherent, or “bad” if they felt the sentence was ungrammatical, nonsensical, or in any other way anomalous. The left or right hand for the “good” response was counterbalanced across individuals. Participants were asked to respond as quickly as possible, and given feedback to speed up if the response latency was longer than 3000 ms. Between trials participants were given as much time as necessary to blink. Following EEG data collection, participants completed a battery of individual difference measures, including a working memory task (automated operation span task, [Unsworth, Heitz, Schrock, & Engle, 2005](#)), arrow-based flanker task ([Eriksen & Eriksen, 1974](#)), speeded English 132 word/132 nonword lexical decision task, and a 50 question subtest of the Michigan English Language Institute College Entrance Test (MELICET) probing grammatical proficiency.

2.4. Data acquisition and analysis

Continuous EEG was recorded from 30 Ag/AgCl active electrodes attached to an elastic cap (Brain Products ActiCap, Germany) in accordance with the extended 10–20 system ([Jasper, 1958](#): Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, T7, C3, Cz, C4, T8, CP5, CP1, CP2, CP6, P7, P3, Pz, P4, P8, PO9, O1, Oz, O2, PO10). Additional electrodes were placed on each mastoid. Eye movements were monitored with bipolar montages consisting of electrodes placed at the outer canthus of each eye and above and below the left eye. Scalp electrodes were referenced during recording either to an electrode placed on the right mastoid or scalp vertex; during offline data processing all scalp electrodes were re-referenced to the algebraic mean of activity over the left and right mastoids. Impedances at all sites were held under 10 k Ω .

EEG was amplified using a Neuroscan SynampsRT system with a .05–100 Hz bandpass filter, and digitized with a 500 Hz sampling rate. Following re-referencing, an offline 30 Hz half-amplitude low-pass filter (24 dB/octave roll-off) was applied to the continuous EEG data. ERPs, time-locked to the onset of the critical word (underlined in the examples above), were averaged off-line for each participant at each electrode site in each condition, relative to a 200 ms prestimulus baseline. All artifact-free trials were included in the averages. Trials characterized by eye blinks, excessive muscle artifact, or drift were not included in the averages. An average of 4.4% of trials was excluded, and this number did not differ reliably across conditions.

ERP components of interest were quantified using mean amplitude measures in *a priori* time windows. In accordance with previous reports and visual inspection of the data, we computed mean amplitude measures for each condition in the 300–500 ms (N400/LAN) and 500–800 ms (P600) time windows. Within each time window, ANOVAs were computed with grammaticality (grammatical, ungrammatical) and condition (agreement, tense) as repeated measures factors. In order to investigate the topographic distribution of the relevant effects, data from midline and lateral electrodes were treated separately. Data from midline sites included electrode (Fz, Cz, Pz) as an additional repeated measures factor. Data from lateral sites were grouped into four regions of interest (ROIs): left frontal (F7, F3, FC1, FC5), right frontal (F8, F4, FC2, FC6), left posterior (CP5, CP1, P7, P3), and right posterior (CP6, CP2, P8, P4). In addition to grammaticality, ANOVAs over lateral sites included hemisphere (left, right) and anteriority (anterior, posterior) as repeated measures factors. The Greenhouse–Geisser correction for inhomogeneity of variance was applied to all repeated measures on ERP data with greater than one degree of freedom in the numerator. In such cases, the corrected *p*-value is reported.

3. Results

Participants were very accurate in detecting the morphosyntactic violations in both agreement and tense conditions (Agreement condition: grammatical mean proportion correct=.95, SE=.01, Ungrammatical mean=.92, SE=.01, *d*-prime=3.40, SE=.13; Tense condition: grammatical mean=.93, SE=.02, Ungrammatical mean=.97, SE=.01,

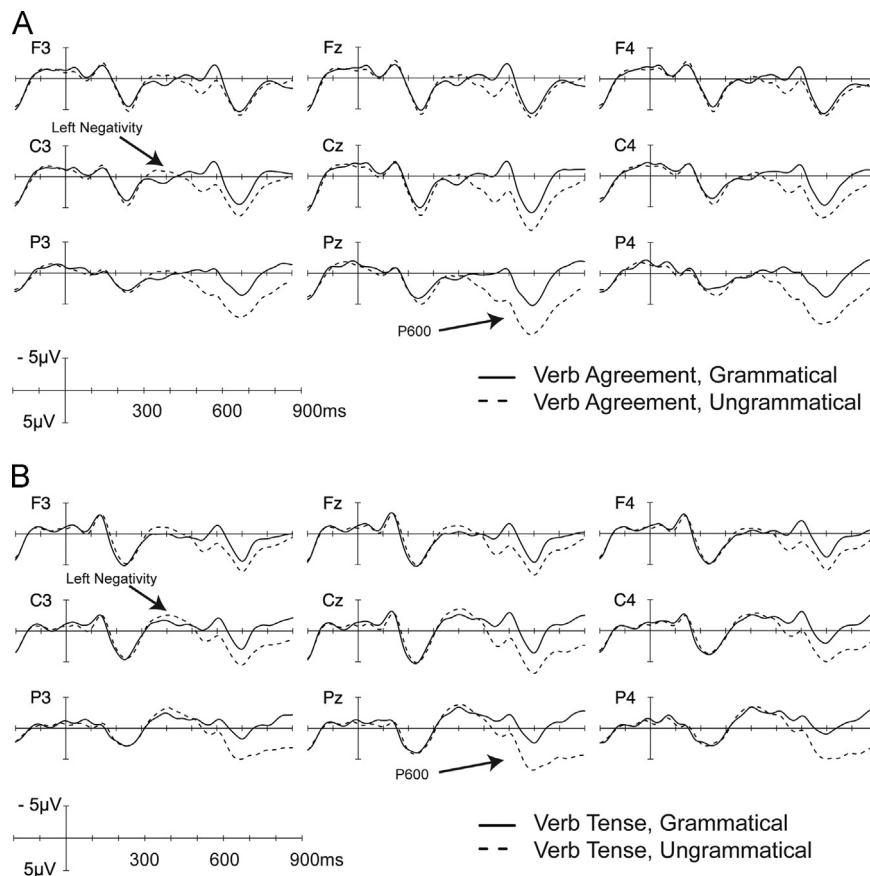


Fig. 1. Grand mean waveforms from nine representative electrodes for grammatical (solid line) and ungrammatical (dashed line) verbs in the agreement (panel A) and tense (panel B) conditions. Onset of the verb is indicated by the vertical calibration bar; each tick mark represents 100 ms of time. Negative voltage is plotted up. ERPs were filtered with a 15 Hz low-pass filter for plotting purposes only in these and all subsequent waveforms.

Table 1

F-statistics from the omnibus grand mean ANOVA on mean amplitude measures in the 300–500 ms and 500–800 ms time windows.

	300–500 ms	500–800 ms
<i>Midline</i>		
Gram. (1, 39)	–	55.154***
Gram. × Cond. (1, 39)	–	–
Gram. × Elec. (2, 78)	–	30.033***
Gram. × Cond. × Elec. (2, 78)	–	9.926***
<i>Lateral</i>		
Gram. (1, 39)	–	45.480***
Gram. × Cond. (1, 39)	–	–
Gram. × Ant. (1, 39)	–	24.297***
Gram. × Hem. (1, 39)	16.887***	7.000*
Gram. × Cond. × Ant. (1, 39)	–	18.085***
Gram. × Cond. × Hem. (1, 39)	–	–
Gram. × Ant. × Hem. (1, 39)	–	–
Gram. × Cond. × Ant. × Hem. (1, 39)	–	–

Degrees of freedom are reported in parentheses. Gram.=Grammaticality; Cond.=Condition; Elec.=Electrode; Ant.=Anteriority; Hem.=Hemisphere.

*** $p < .001$.

* $p < .05$.

d -prime = 3.63, $SE = .10$). Grand mean ERP waveforms from the agreement and tense conditions are presented in Fig. 1. In both conditions, visual inspection of the waveforms showed that, relative to grammatical verbs, ungrammatical verbs elicited a large, widely-distributed positivity with a posterior maximum (a P600). The positivity, however, was preceded by a small negativity with a predominantly left hemisphere scalp distribution. Table 1 reports results from the omnibus ANOVA. In the 300–500 ms time window a significant grammaticality by hemisphere interaction was found over lateral sites. Relative to well-formed controls, brain responses to ungrammatical verbs were more negative going over the left hemisphere (ungrammatical minus grammatical amplitude difference = $-.592 \mu V$, $SE = .029$) than over the right hemisphere (amplitude difference = $-.039 \mu V$, $SE = .035$). In the 500–800 ms time window, the positivity to ungrammatical verbs was reliable over a widespread portion of the scalp. The interaction between grammaticality and hemisphere over lateral sites showed that the positivity was larger over the right hemisphere (ungrammatical minus grammatical amplitude difference = $2.420 \mu V$, $SE = .057$) than over the left hemisphere (amplitude difference = $2.021 \mu V$, $SE = .049$). The interaction between electrode/anteriority and grammaticality indicated that the positivity had a parietal maximum, but this was qualified by a further interaction with condition. Follow-up ANOVAs showed that the interaction was significant in both the agreement condition (midline: Gram. × Elec. $F(2, 78) = 46.102$, $p < .001$; lateral: Gram. × Ant. $F(1, 39) = 37.200$, $p < .001$) and tense condition (midline: Gram. × Elec. $F(2, 78) = 8.823$, $p = .002$; lateral: not significant). This shows that the effect was posteriorly distributed in both conditions, but that this distribution was most pronounced and systematic in the agreement condition.

In sum, grand mean analyses showed that violations of morphosyntactic constraints elicited a classic pattern of ERP effects in both the tense and agreement conditions. Ungrammatical verbs elicited a large P600 effect, which was preceded by a negativity over left hemisphere electrodes. Although the left negativity did not show an anterior scalp distribution (which would have been evidenced by an additional interaction with anteriority), it falls within the range of left negativities that have been interpreted as LAN effects in previous literature (e.g., Kaan & Swaab, 2003a; Rodriguez-Fornells et al., 2001).

However, visual inspection of individual waveforms showed that the biphasic LAN-P600 response was not characteristic of most participants' actual ERP responses. Instead, most individuals

showed only a P600 response, while some showed a small biphasic response, and others showed a centrally-distributed N400-like negativity. To investigate individuals' brain response profiles, we computed mean activity over a large centro-parietal ROI (C3, Cz, C3, CP1, CP2, P3, Pz, P4), where N400 and P600 effects are typically largest. Within this ROI we calculated each individual's N400 effect magnitude (grammatical minus ungrammatical condition in the 300–500 ms window) and P600 effect magnitude (ungrammatical minus grammatical condition in the 500–800 ms window) separately for the agreement and tense conditions. The effect magnitudes in each condition were significantly negatively correlated across individuals (agreement: $r = -.589$, $p < .001$; tense: $r = -.601$, $p < .001$; Fig. 2) and showed a continuous distribution between N400-dominance, biphasic, and P600-dominance. That is, individuals who showed a large P600 effect tended to show little negativity, and vice versa.¹ We further quantified each individual's response dominance in both conditions by fitting the individual's least squares distance from the equal effect sizes lines (the dashed line in Fig. 2) in both the agreement and tense conditions using perpendicular offsets (the Response Dominance Index, RDI; see Tanner et al., in press). RDI values near zero reflect relatively equal-sized N400 and P600 effects, whereas more negative or positive values reflect relative dominance of a negativity or positivity across both time windows, respectively. The equation for how the RDI was derived is given in (1), where N400 and P600 refer to mean amplitude between 300–500 ms and 500–800 ms, respectively, averaged within the centro-parietal ROI (C3, Cz, C4, CP1, CP2, P3, Pz, P4).

$$RDI = \frac{(P600_{Ungram} - P600_{Gram}) - (N400_{Gram} - N400_{Ungram})}{\sqrt{2}} \quad (1)$$

Individuals' RDI scores in the agreement and tense conditions were positively correlated, $r = .425$, $p = .006$. This indicates that individuals tended to show similar polarity responses (N400 or P600) in both conditions.

To demonstrate these differential effects and investigate their scalp topographies, we averaged ERPs for those individuals who showed negativity and positivity-dominant effects in the agreement and tense conditions separately (e.g., those above/to the left of and below/to the right of the dashed lines in Fig. 2, respectively). Waveforms averaging across individuals who showed a negativity-dominance in each condition are presented in Fig. 3; waveforms averaging across individuals who showed a positivity-dominance in each condition are presented in Fig. 4. ANOVA results testing effects for each condition in the negativity- and positivity-dominant groups separately are presented in Tables 2 and 3. As can be seen, those in the negativity-dominant groups showed reliable, broadly-distributed negativities between 300 and 500 ms with no marked hemispheric asymmetries (N400 effects), while those in the positivity-dominant groups showed large P600 effects, with little preceding negativity. Importantly, the positivity in these individuals showed an onset in the 300–500 ms window that was fully significant over midline sites in the agreement condition, and marginally so in the tense condition ($p = .051$). This early positivity was also reliable over right (but not left) hemisphere sites in both conditions (see Table 4). Topographic maps showing the scalp topographies of the grand mean effects between 300–500 ms and 500–800 ms, as well as topographies of the effects in each of the positivity- and negativity-dominant groups for each condition are presented in

¹ As an additional analysis, we computed the correlation at each scalp electrode site independently. Results showed that the effects were similarly negatively correlated across the entire scalp in both conditions. However, here we focus on results from the centro-parietal ROI for brevity, as this ROI is representative of effects that were topographically widespread.

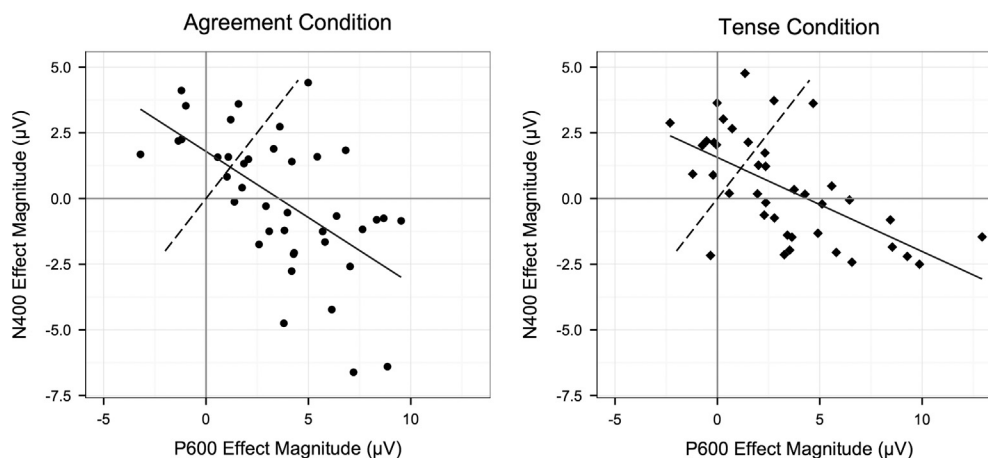


Fig. 2. Scatterplots showing the relationship between N400 and P600 effect magnitudes across individuals for the agreement (left panel) and tense (right panel) conditions, averaged within a centro-parietal ROI (C3, Cz, C4, CP1, CP2, P3, Pz, P4). The solid lines indicate the best-fit line from the correlation analysis for each condition. The dashed lines represent equal N400 and P600 effect magnitudes: individuals above/to the left of the dashed line showed primarily an N400 effect to agreement violations, while individuals below/to the right of the dashed line showed primarily a P600 effect.

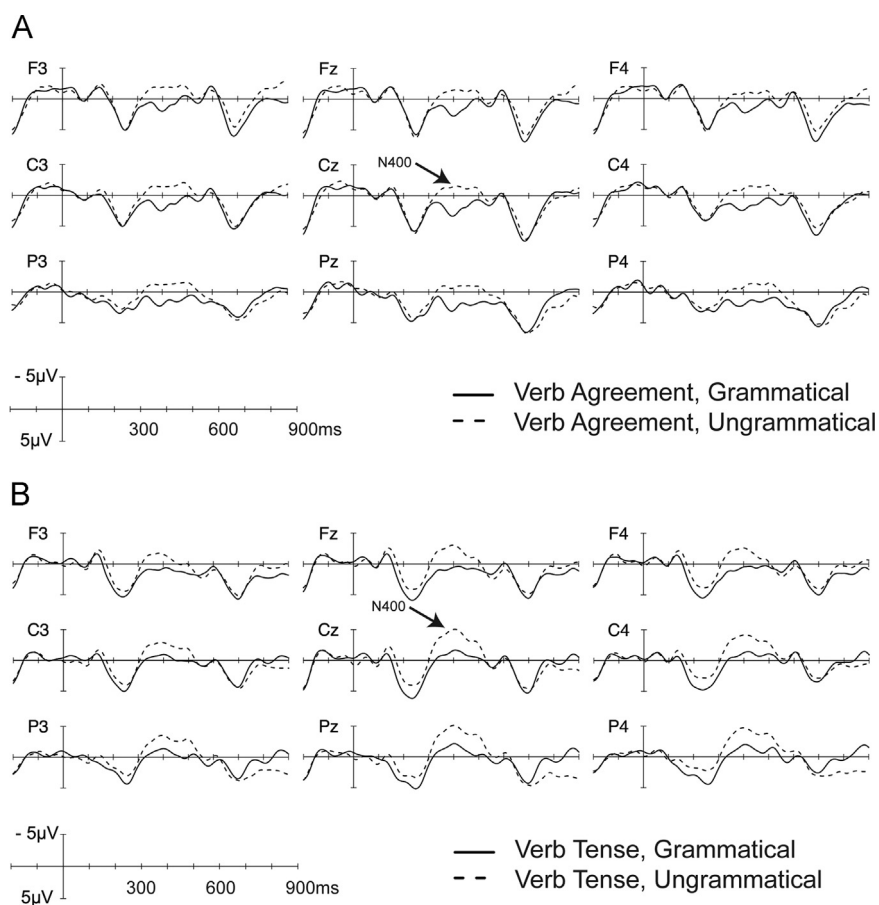


Fig. 3. Waveforms from nine representative electrodes for grammatical (solid line) and ungrammatical (dashed line) verbs for those showing a negativity dominance in the agreement (panel A; $n=9$) and tense (panel B; $n=13$) conditions. Onset of the verb is indicated by the vertical calibration bar; each tick mark represents 100 ms of time. Negative voltage is plotted up.

Fig. 5. Overall these results show that morphosyntactic violations elicited N400 effects in some individuals, biphasic N400–P600 in some individuals, and P600 effects in most individuals (see [Appendix](#)). However, to the extent that the positivity showed a right hemisphere onset in the earlier time window in some individuals, it canceled out the N400 seen in others, such that the grand mean response across all individuals reflected the

spatiotemporal intersection of the centralized N400 and right hemisphere-dominant P600 effects. Thus, the left negativity (LAN effect) seen in the grand mean seems to be an artifact of this spatiotemporal overlap.

To explore what factors related to the relative dominance of N400 versus P600 effects across individuals, we correlated a series of individual difference measures previously shown to affect

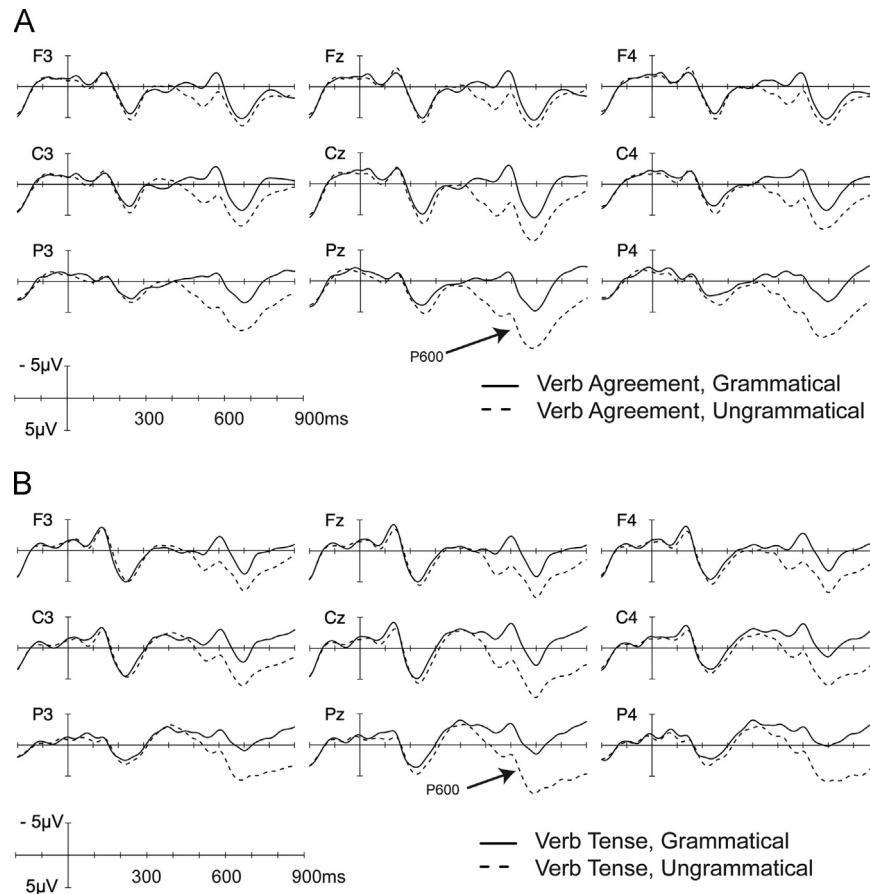


Fig. 4. Waveforms from nine representative electrodes for grammatical (solid line) and ungrammatical (dashed line) verbs for those showing a positivity dominance in the agreement (panel A; $n=31$) and tense (panel B; $n=27$) conditions. Onset of the verb is indicated by the vertical calibration bar; each tick mark represents 100 ms of time. Negative voltage is plotted up.

Table 2

F-statistics from the ANOVA on mean amplitude measures in the 300–500 ms and 500–800 ms time windows for participants who showed a negativity dominance the agreement ($n=9$) and tense ($n=13$) conditions.

	Time window			
	Agreement condition		Tense condition	
	300–500 ms	500–800 ms	300–500 ms	500–800 ms
<i>Midline</i>				
Gram.	39.086*** (1, 8)	–	65.398*** (1, 12)	–
Gram. \times Elec.	–	–	–	–
<i>Lateral</i>				
Gram.	20.202** (1, 8)	–	102.649*** (1, 12)	–
Gram. \times Ant.	–	–	–	–
Gram. \times Hem.	–	–	–	–
Gram. \times Ant. \times Hem.	–	–	–	–

Degrees of freedom are reported in parentheses.

Gram.=Grammaticality; Elec.=Electrode; Ant.=Anteriority; Hem.=Hemisphere.

*** $p < .001$.

** $p < .01$.

language processing with individuals' N400 and P600 magnitudes, as well as individuals' RDI measures in both the tense and agreement conditions. We included participants' operation span measures, flanker effect sizes, MELICET proficiency scores, lexical processing speed, and familial left-handedness in the correlation analyses (see Section 1 for a justification). Means and distribution statistics for each measure are provided in Table 5.

Of these measures, only familial sinistrality showed a reliable relationship with participants' ERP response profiles (all other

$ps > .24$). Twenty participants reported having at least one close blood relative (parent, grandparent, or sibling) who was left-handed (henceforth +FS participants), while 20 reported no left-handed blood relatives (–FS participants). A 2×2 ANOVA on RDI values with condition (agreement, tense) as a repeated measures factor and FS (+FS, –FS) as a between-subjects factor showed a main effect of FS, $F(1, 38)=9.097$, $p=.005$, partial- $\eta^2=.193$, but no effect of condition, $F=1.268$, and no interaction, $F < 1$. Individuals with left-handed family members showed significantly lower

Table 3
F-statistics from the ANOVA on mean amplitude measures in the 300–500 ms and 500–800 ms time windows for participants who showed a positivity dominance the agreement ($n=31$) and tense ($n=27$) conditions.

	Time window			
	Agreement condition		Tense condition	
	300–500 ms	500–800 ms	300–500 ms	500–800 ms
<i>Midline</i>				
Gram.	4.772* (1, 30)	95.015*** (1, 30)	4.168+ (1, 26)	69.564*** (1, 26)
Gram. \times Elec.	–	45.542*** (2, 60)	–	9.731** (2, 52)
<i>Lateral</i>				
Gram.	–	75.215*** (1, 30)	–	64.902*** (1, 26)
Gram. \times Ant.	–	42.999*** (1, 30)	–	–
Gram. \times Hem.	13.065*** (1, 30)	8.811** (1, 30)	15.657*** (1, 26)	9.726** (1, 26)
Gram. \times Ant. \times Hem.	–	4.841* (1, 30)	–	–

Degrees of freedom are reported in parentheses. Gram.=Grammaticality; Elec.=Electrode; Ant.=Anteriority; Hem.=Hemisphere.

*** $p < .001$.

** $p < .01$.

* $p < .05$.

+ $p < .06$.

Table 4
Mean amplitude differences in the 300–500 ms time window depicting the ungrammaticality effect size and standard errors for the ungrammatical minus grammatical condition over the left and right hemispheres for participants in the positivity-dominant groups. Units are in μV .

	Left hemisphere		Right hemisphere	
	Amplitude difference	SE	Amplitude difference	SE
Agreement condition ($n=31$)	.068	.332	.759	.318
Tense condition ($n=27$)	–.238	.198	.706	.262

mean RDI values, indicating significantly less positivity-dominance in their brain responses (mean = 1.009 μV , SE = .608), than those without left-handed family members (mean = 3.603 μV , SE = .608). Thus, familial sinistrality accounted for approximately 19% of the variance in individuals' N400 or P600 response dominance.

4. Discussion

We investigated individual differences in neural responses to morphosyntactic violations. Grand mean analyses showed a reliable left hemisphere (LAN-like) negativity followed by a large P600 effect for both subject–verb agreement violations and verb tense violations. This is similar to biphasic LAN-P600 effects, which are frequently reported to morphosyntactic violations. However, further analysis showed that this biphasic LAN-P600 response was not characteristic of most individuals' ERP responses. Instead, individuals' brain responses varied along a continuum between negativity-dominant, biphasic, and positivity-dominant. Additionally, the negativity seen in the negativity-dominant groups did not have the left hemisphere distribution that surfaced in the grand mean waveforms, but a central scalp distribution, much more similar to N400 effects typically reported to lexical semantic violations. The P600 in the positivity dominant groups showed an onset already during the 300–500 ms time window, but with a right hemisphere preponderance. The left hemisphere scalp topography of the negativity in the grand mean thus reflected the intersection across individuals of the two effects (N400 and P600) in time and space: the right hemisphere distribution of the P600 effect in most individuals canceled out

the central and right portions of the N400 seen in others, leaving only a left hemisphere negativity in the grand mean.

We found this pattern of individual differences in response to core morphosyntactic violations, which have been argued to consistently elicit biphasic LAN-P600 violations across individuals (see Molinaro et al., 2011, for a recent defense of this position). Others have reported individual differences in N400 versus P600 effects for violations where both semantic and syntactic information provided cues to the anomalies (Nakano et al., 2010; Oines et al., 2012; Ye & Zhou, 2008); however, our results show that such individual differences are additionally found in response to linguistic anomalies with little semantic content. Furthermore, we found similar profiles of individual differences for both agreement and tense violations, despite differences in the length and structure of the two types of sentences.

The N400/P600 response dominance continuum reported here is reminiscent of that reported in L2 speakers (Tanner et al., 2013; Tanner et al., in press). In novice L2 learners, individuals' N400/P600 response dominance to morphosyntactic violations seems to be especially malleable, such that continued L2 instruction can trigger a shift from N400- to P600-dominance within learners (McLaughlin et al., 2010). However, taken in context with the continuum being found in proficient, immersed L2 speakers (Tanner et al., in press) and the proficient monolinguals studied here, the combined findings suggest that the N400/P600 response dominance continuum is not restricted to novice language learners. These findings lend themselves to the overall conclusion that there is substantial, but systematic variability in how individuals engage core aspects of the language processing network, and that similar differences are found in individuals across the language proficiency spectrum (see Prat, 2011, for a review of hemodynamic studies).

4.1. The LAN and the N400

In the present data, we found little evidence for a LAN component that co-occurred with a P600 and that was topographically separable from the N400 effect. Based on models arguing that the LAN reflects detection of anomalies and the P600 reanalysis, we predicted that the magnitude of the earlier negativity and the P600 should be *positively* correlated across individuals. Instead, the magnitude of the negativity (LAN/N400) and following positivity (P600) were *negatively* correlated across individuals. This suggests that the earlier negativity does not

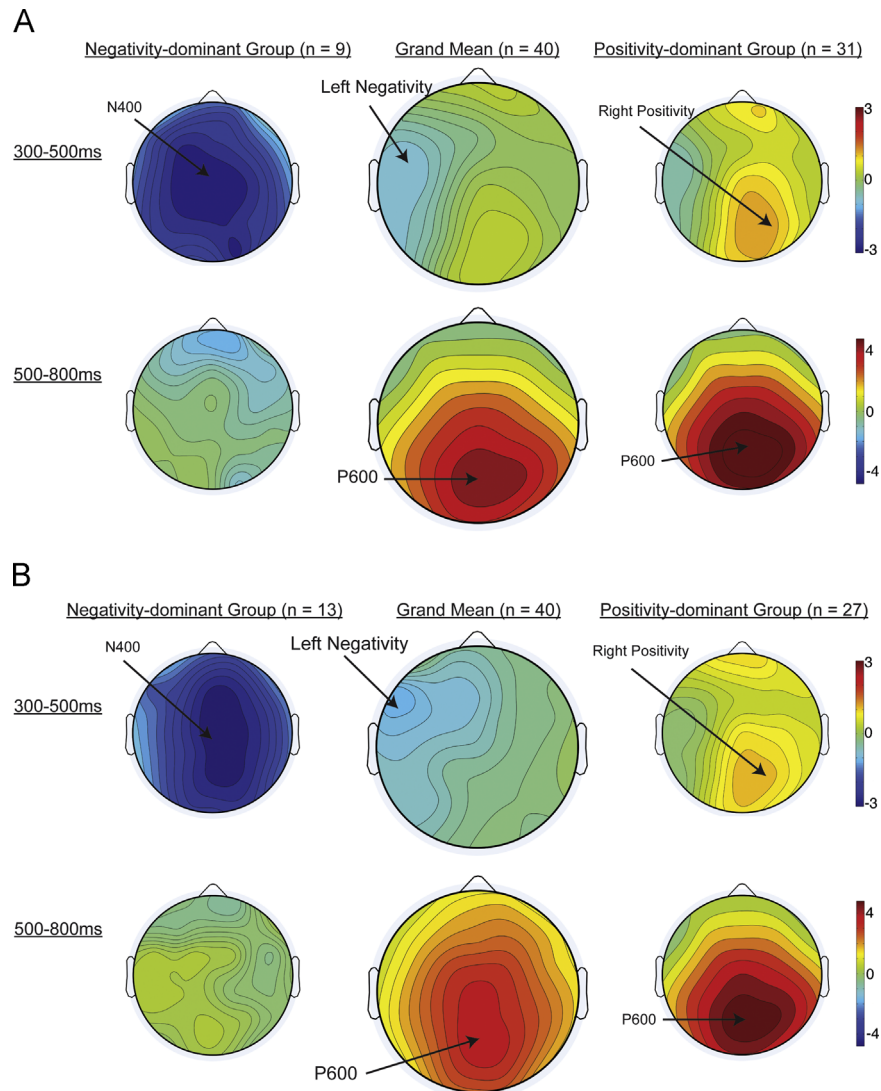


Fig. 5. Topographic maps indicating the scalp distribution of effects for the agreement (panel A) and tense (panel B) conditions. Maps depict activity in the ungrammatical minus grammatical conditions, averaged within the 300–500 ms and 500–800 ms time windows. Maps showing effect topographies in the grand mean analysis are presented in the center column; maps showing effect topographies for participants in the negativity- and positivity-dominant groups are shown in the left and right columns, respectively. Calibration scales show $\pm 3 \mu\text{V}$ for the 300–500 ms time window and $\pm 4.8 \mu\text{V}$ for the 500–800 ms time window.

Table 5

Distributional statistics for individual difference measures included in the correlation analyses.

Measure	Mean	Std. Dev.	Range
OSpan (max 75)	57.68	14.0	16–74
Flanker effect (ms)	54.19	23.0	–3.8–109.6
MELICET (max 50)	45.13	3.1	37–49
LDT lexicality effect (ms)	87.62	66.5	–1.3–247.4
Familial sinistrality	.50	.5	0–1

Note: OSpan=Automated operation span partial storage score; Flanker Effect=mean reaction time (RT) incongruent minus mean RT congruent for correct trials; MELICET=total score on MELICET proficiency test; LDT Lexicality Effect=mean RT nonword minus mean RT word for correct trials (Barca & Pezzulo, 2012); Familial Sinistrality=self-report of left-handed blood relative: 0=no left-handed relatives, 1=left-handed relative (parent, grandparent, or sibling).

trigger reanalysis of the morphosyntactic anomalies. These results are inconsistent with predictions made by neurocognitive models of syntactic comprehension holding that biphasic LAN-P600 effects should occur within individuals, that the two components index separable stages in grammatical processing (e.g., the

detection of anomalies followed by reanalysis), and moreover, that the LAN reflects an automatic process (Batterink & Neville, 2013; Friederici, 2002; Friederici & Weissenborn, 2007; Molinaro et al., 2011; Pakulak & Neville, 2010; Ullman, 2004).

As discussed in Section 1, studies of morphosyntactic anomalies in sentence context nearly uniformly elicit reliable P600 effects, though there is remarkable variability in both the presence and scalp topographies of negativities ((L)AN components). Our results suggest that some of the cross-study variability in the LAN-P600 complex is explainable in terms of the N400/P600 response continuum reported here. Some reported grand mean LAN effects (or other ANs) may reflect the residual N400 effects after being averaged with a P600, which onsets in the same time window. This was found to be the case in the present data. The finding of reliable P600s but inconsistent (L)ANs in the broader literature is a natural consequence of individual differences in the response dominance continuum reported here. Repeated sampling from a population showing individual differences in the N400/P600 response continuum would by chance produce varying degrees of LAN/N400 and P600 in the grand mean. As the majority of participants in this study showed positivity-dominance in ERP

responses to morphosyntactic violations, nearly any sampling distribution would show a reliable P600. However, grand mean negativities preceding the P600 would only become reliable if a sufficient number of participants showing N400s were included in the sample.

In the present study we demonstrated that a grand mean response with a biphasic LAN-like negativity followed by a P600 can result from averaging across individuals who show primarily either an N400 or P600 effect. Note, however, that approximately 35% of the participants showed some degree of biphasic response across conditions (i.e., those in the upper right quadrants in Fig. 2). This suggests that both responses (LAN/N400 and P600) can co-occur within individuals. To the extent that a given individual shows a biphasic response to morphosyntactic violations, the scalp distribution of each phase will reflect the extent to which the two components intersect in time and space. That is, biphasic LAN-P600 effects within an individual could reflect component overlap between an N400 and P600 in the same way we have demonstrated across individuals.

This account of the LAN/N400 relationship is also consistent with ERP evidence implicating the degree of lexical access difficulty and discourse processing in modulating the size and topography of the LAN/N400 preceding the P600. ERP studies have shown that negativities preceding the P600 are larger and can have a more central, N400-like scalp distribution when morphosyntactic information interfaces with other aspects of language processing known to modulate the N400. This occurs, for example, when morphosyntax is discourse-dependent (e.g., person versus number agreement: Mancini, Molinaro, Rizzi, & Carreiras, 2011), when accessing morphosyntactic information requires deep lexical access (e.g., gender agreement with phonologically opaque nouns: Molinaro, Vespignani, & Job, 2008), or when it has semantic reference (e.g., gender agreement with animate, biologically-gendered nouns versus inanimate nouns with only syntactic gender: Deutsch & Bentin, 2001). This evidence from the broader literature shows that the semantic consequences of a morphosyntactic dependency can influence the relative magnitude of N400 or P600 effects seen in grand mean waveforms. A morphosyntactic anomaly will elicit relatively more N400-effect, co-occurring with the P600, when it requires deeper lexical, semantic, or discourse processing (e.g., Deutsch & Bentin, 2001; Mancini et al., 2011; Molinaro et al., 2008; cf. Nakano et al., 2010; Oines et al., 2012; Ye & Zhou, 2008), but correspondingly less N400 and more P600 when there are fewer or no semantic consequences.

Moreover, a recent study using magnetoencephalography (MEG) showed that morphosyntactic LAN and semantic N400 components had the same generator in the left anterior temporal lobe (Service et al., 2007). The crucial distinguishing feature was that the N400 showed an additional right hemisphere generator. All of this evidence is consistent with the hypothesis that, in certain cases – as was the case in the present data – the LAN may be a variant of the N400 component. The presence and relative magnitude of the LAN/N400 component in grand mean waveforms will therefore be a function of the linguistic cues mediating the morphosyntax (e.g., how discourse-, semantically-, or lexically-dependent the morphosyntactic relationship is), the individuals in the sample (e.g., individuals' relative reliance on lexical or combinatorial cues, see below), or an interaction between the two. Our findings therefore suggest that a degree of caution must be taken when interpreting biphasic grand mean responses, as the biphasic nature of the response may be caused by component overlap, either within or across individuals.

4.2. Individual differences in morphosyntactic processing

A substantial amount of previous ERP research has shown that the processes indexed by N400 and P600 effects, while not

necessarily language-specific, are crucial for language comprehension, and reflect activity in a core language processing network. Previous evidence suggesting individual differences in engagement of this network during morphosyntactic processing mostly examined second language learners and bilinguals. However, the data reported here show that similar differences also exist among proficient monolinguals processing morphosyntax in their native language. Our participants were sampled from a proficient, literate, university student population, similar to those frequently used in other ERP studies of monolingual language processing. In most individuals morphosyntactic violations elicited primarily P600 effects, which is the ERP response most classically associated with this type of anomaly. However, a substantial subset of individuals showed dominance of N400 effects, which have most frequently been associated with semantic anomalies, while some individuals showed a combination of both effects to varying degrees.

Note, however, that some recent findings show that the relationship between semantic and syntactic processing and the N400 and P600 components is not a strict one-to-one mapping. Notably, N400 effects have now been reported for some outright morphosyntactic violations (e.g., Nieuwland, Martin, & Carreiras, 2013; Severens, Jansma, & Hartsuiker, 2008), and P600 effects have been reported in some fully grammatical, but semantically anomalous sentences (e.g., Hoeks, Stowe, & Doedens, 2004; Kim & Osterhout, 2005; Kim & Sikos, 2011; Kuperberg, Kreher, Sitnikova, Caplan, & Holcomb, 2007; Van de Meerendonk et al., 2010; Van Herten, Chwilla, & Kolk, 2006). While a definitive account of the functional interpretation of the two effects remains elusive in the broader literature at this time, some nuanced generalizations can be made. The amplitude of the N400 component has been shown to reflect strength of predictions at the lexical and semantic levels, where N400 amplitude is inversely related to the predictability of a given item (DeLong, Urbach, & Kutas, 2005; Federmeier & Kutas, 1999; Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007; Federmeier, 2007; Wlotko & Federmeier, 2012). The P600 effect, on the other hand, is elicited by a broad range of manipulations, including morphosyntactic anomalies, grammatical but difficult-to-parse syntactic dependencies, exceptionally strong semantic violations, and violations of verb argument combinatorial constraints, particularly those involving animacy (Frenzel, Schlesewsky, & Bornkessel-Schlesewsky, 2011; Kaan, Harris, Gibson, and Holcomb 2000; Kaan & Swaab, 2003b; Osterhout, Holcomb, & Swinney, 1994; Paczynski & Kuperberg, 2012; Van de Meerendonk et al., 2010; see Kuperberg, 2007; Osterhout, Kim, & Kuperberg, 2012; Van Petten & Luka, 2012, for recent reviews). Kuperberg (2007) suggests that the N400 reflects semantic access from long-term memory (see also Kutas & Federmeier, 2011), whereas the P600 may index engagement of a general combinatorial processing stream, which is sensitive both to morphosyntactic information as well as mismatches between the output of semantic and morphosyntactic analyses. With regard to our data, this might suggest that N400-dominant individuals rely primarily on word- or morphological-form-based predictions of upcoming items (e.g., predicting *is* versus *are* or the presence of the progressive *-ing* morpheme on a verb following the auxiliary verb *was*), while those showing P600-dominance rely primarily on combinatorial morphosyntactic constraints (see Tanner et al., *in press*, for further discussion). Importantly though, our findings of individual differences in the N400/P600 continuum in response to core morphosyntactic violations nonetheless provide further evidence for the lack of a one-to-one relationship between semantics and the N400 on the one hand, and morphosyntax and the P600 on the other.

We found that familial sinistrality (FS) was reliably associated with individuals' N400/P600 response dominance. Participants

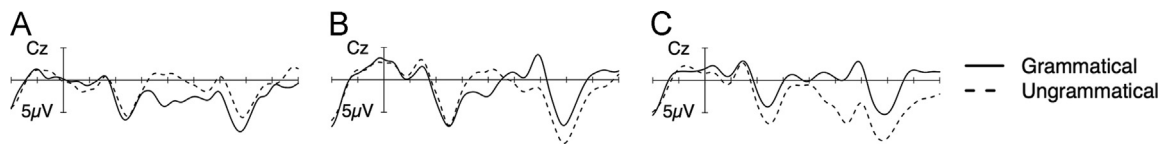


Fig. A1. Waveforms depicting averages over individuals from the agreement condition in three quadrants of Fig. 2 (left panel). Those showing negativities in both time windows are depicted in A ($n=5$); those showing biphasic N400/P600 responses are depicted in B ($n=14$); those showing positivities across both time windows are depicted in C ($n=21$). Midline vertex electrode Cz is shown. Onset of the verb is indicated by the vertical calibration bar; each tick mark represents 100 ms of time. Negative voltage is plotted up.

who were themselves right-handed, but who reported having a close left-handed blood relative (+FS) showed less positive-going ERP responses to morphosyntactic violations. Previous research has found a more bilateral, rather than left-lateralized, cortical representation of language in +FS individuals (Kee, Bathurst, & Hellige, 1983; McKeever, Seitz, Hoff, Marino, & Diehl, 1983; see Hancock & Bever, 2013, for a recent overview). ERP research has additionally shown that the N400 component in individuals with no left-handed blood relatives (−FS) shows a marked right hemisphere dominance, but shows no hemispheric asymmetries in +FS individuals (Kutas, Van Petten, & Besson, 1988), and this is consistent with the hypothesis of greater bilaterality in +FS individuals. Work by Bever and colleagues (Bever et al., 1989; Hancock & Bever, 2013; Townsend et al., 2001) goes further in hypothesizing that this distributed cortical network in +FS individuals can influence the use of linguistic cues during language comprehension. They propose that +FS individuals will show more sensitivity to lexical and semantic relationships, while −FS individuals will show more sensitivity to syntactic and sequential information. Our results are consistent with Bever and colleagues' hypothesis. +FS participants in our study showed less overall dominance of the P600 effect (associated with combinatorial analysis) and greater dominance of the N400 effect (associated with semantic access and lexical predictions). While it is possible that our findings of individual differences are related to differences in cortical networks associated with language processing (e.g., left-lateralized versus bilateral), ERPs' limited spatial resolution makes definitive conclusions about this regarding our data impossible. Note, however, that some MEG findings localizing N400 effects have noted individual differences in hemispheric contribution to the effects, even among right-handers. Whereas N400 generators have been localized to the left hemisphere in most studies (see Lau et al., 2008; Van Petten & Luka, 2006, for reviews; though see Service et al., 2007 for evidence of bilateral generators), some studies report significant right-hemisphere activation in a subset of subjects (Helenius et al. 2002; Helenius, Salmelin, Service, & Connolly, 1998; Pykkänen & McElree, 2007), though these studies do not report participants' familial handedness histories. Future fMRI and MEG research may wish to more precisely document possible differences in cortical localization of language functions for +FS and −FS individuals. Nonetheless, FS alone accounted for approximately 19% of the variance in individuals' response dominance, showing that FS is an important predictor of the neurocognitive mechanisms supporting grammatical comprehension.

Some previous work has implicated working memory (WM) span and cognitive control in predicting ERP response quality to conflicts between semantic and syntactic cues (Nakano et al., 2010; Oines et al., 2012; Ye & Zhou, 2008). Here we showed that similar differences in ERP response quality exist even for processing violations of core morphosyntactic constraints; however, we found no evidence of an association between individual's WM span or cognitive control and relative dominance of the N400 or P600. One possibility is that resolving competition between lexical-semantic and syntactic information is more reliant on WM and cognitive control resources than processing core morphosyntax. Alternately, the lack of influence of WM or cognitive

control in the current study may reflect that the emergence of these effects is sensitive to variability in tasks used across studies, and may emerge only in tasks involving some linguistic processing. Effects of WM on language processing have been found using reading and speaking span tasks (Nakano et al., 2010; Oines et al., 2012) and effects of cognitive control were found using a color-word Stroop task (Ye & Zhou, 2008). These tasks involve some degree of linguistic processing and may be tapping into some of the same linguistic processes measured in the ERP task, giving rise to the correlations (see MacDonald & Christiansen, 2002). We chose WM (operation span, which involves memorizing letters while solving simple arithmetic problems) and cognitive control (arrow-based flanker task) measures that are more language-neutral, thereby providing non-linguistic measures of the same underlying cognitive constructs.

Recent research has also shown that, when sampling monolinguals with a wide range of literacy and socioeconomic status levels, language proficiency can shape ERP responses to English phrase structure violations (Pakulak & Neville, 2010). Our results extend these findings in important ways by showing that individual differences in morphosyntactic processing can be seen even among proficient, highly literate monolinguals processing morphosyntactic dependencies. That is, individual differences in the N400–P600 continuum are not restricted to L2 learners or low proficiency monolinguals, but instead seem to be a generalizable property of morphosyntactic processing in individuals across the language proficiency spectrum. Although we did not find a systematic relationship between participants' English proficiency and variability along the N400/P600 response dominance continuum, our results show that marked and systematic variability exists in language processing mechanisms for highly proficient adults speakers, even when processing core morphosyntactic structures in the absence of any semantic cues. Importantly, with proper quantification, ERPs can be highly sensitive to these differences.

Acknowledgments

This research was supported by NSF OISE-0968369 to Judith F. Kroll, Janet G. van Hell, and Paola E. Dussias, and conducted when the first author was a postdoctoral researcher affiliated with the Pennsylvania State University. We would like to thank Sofia Alvarez, Leah Pappas, Catharine Stransky, and Brendan Tomoschuk for their assistance in collecting the data. We would also like to thank two anonymous reviewers for helpful comments on this manuscript.

Appendix

To further depict the continuous nature of individual differences in N400/P600 responses, we computed averaged ERPs in the agreement condition for individuals within three quadrants from Fig. 2. Relative to brain responses in the grammatical control condition, ERP waveforms to anomalous verbs from those in the

upper left quadrant (A; $n=5$) show extended negativities, from those in the upper right quadrant (B; $n=14$) depict biphasic responses, and from those in the lower right quadrant (C; $n=21$) depict extended positivities.

See Fig. A1.

References

- Allen, M., Badecker, W., & Osterhout, L. (2003). Morphological analysis in sentence processing: An ERP study. *Language and Cognitive Processes*, 18, 405–430.
- Barca, L., & Pezzulo, G. (2012). Unfolding visual lexical decision in time. *PLoS One*, 7 (4), e35932, <http://dx.doi.org/10.1371/journal.pone.0035932>.
- Batterink, L., & Neville, H. (2013). The human brain processes syntax in the absence of conscious awareness. *Journal of Neuroscience*, 33, 8528–8533, <http://dx.doi.org/10.1523/JNEUROSCI.0618-13.2013>.
- Bever, T. G., Carrithers, C., Cowart, W., & Townsend, D. J. (1989). Language processing and familial handedness. In: A. M. Galaburda (Ed.), *From Reading to Neurons* (pp. 331–360). Cambridge, MA: MIT Press.
- Bornkessel-Schlesewsky, I., & Schlewsky, M. (2008). An alternative perspective on "semantic P600" effects in language comprehension. *Brain Research Reviews*, 59, 55–73, <http://dx.doi.org/10.1016/j.brainresrev.2008.05.003>.
- Brouwer, H., Fitz, H., & Hoeks, J. (2012). Getting real about semantic illusions: Rethinking the functional role of the P600 in language comprehension. *Brain Research*, 1446, 127–143, <http://dx.doi.org/10.1016/j.brainres.2012.01.055>.
- Coulson, S., King, J. W., & Kutas, M. (1998). Expect the unexpected: Even-related brain response to morphosyntactic violations. *Language and Cognitive Processes*, 13, 21–58.
- DeLong, K. A., Urbach, T. P., & Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience*, 8, 1117–1121, <http://dx.doi.org/10.1038/nn1504>.
- Deutsch, A., & Bentin, S. (2001). Syntactic and semantic factors in processing gender agreement in Hebrew: Evidence from ERPs and eye movements. *Journal of Memory and Language*, 45, 200–224, <http://dx.doi.org/10.1006/jmla.2000.2768>.
- Dillon, B., Nevins, A., Austin, A. C., & Phillips, C. (2012). Syntactic and semantic predictors of tense in Hindi: An ERP investigation. *Language and Cognitive Processes*, 27, 313–344.
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon identification of a target letter in a non-search task. *Perception & Psychophysics*, 16, 142–149.
- Federmeier, K. D. (2007). Thinking ahead: The role and roots of prediction in language comprehension. *Psychophysiology*, 44, 491–505, <http://dx.doi.org/10.1111/j.1469-8986.2007.00531.x>.
- Federmeier, K. D., & Kutas, M. (1999). A rose by any other name: Long-term memory structure and sentence processing. *Journal of Memory and Language*, 41, 469–495, <http://dx.doi.org/10.1006/jmla.1999.2660>.
- Federmeier, K. D., Wlotko, E. W., De Ochoa-Dewald, E., & Kutas, M. (2007). Multiple effects of sentential constraint on word processing. *Brain Research*, 1146, 75–84, <http://dx.doi.org/10.1016/j.brainres.2006.06.101>.
- Frenzel, S., Schlewsky, M., & Bornkessel-Schlesewsky, I. (2011). Conflicts in language processing: A new perspective on the N400–P600 distinction. *Neuropsychologia*, 49, 574–579, <http://dx.doi.org/10.1016/j.neuropsychologia.2010.12.003>.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6, 78–84.
- Friederici, A. D., Hahne, A., & Mecklinger, A. (1996). Temporal structure of syntactic processing: Early and late event-related potential effects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 22, 1219–1248.
- Friederici, A. D., Steinhauer, K., & Pfeifer, E. (2002). Brain signatures of artificial language processing: Evidence challenging the critical period hypothesis. *Proceedings of the National Academy of Sciences USA*, 99, 529–534.
- Friederici, A. D., & Weissenborn, J. (2007). Mapping sentence form onto meaning: The syntax-semantic interface. *Brain Research*, 1146, 50–58, <http://dx.doi.org/10.1016/j.brainres.2006.08.038>.
- Gouvea, A. C., Phillips, C., Kazanina, N., & Poeppel, D. (2010). The linguistic processes underlying the P600. *Language and Cognitive Processes*, 25, 149–188, <http://dx.doi.org/10.1080/01690960902965951>.
- Hagoort, P. (2003). How the brain solves the binding problem for language: A neurocomputational model of syntactic processing. *NeuroImage*, 20, 18–29, <http://dx.doi.org/10.1016/j.neuroimage.2003.1796>.
- Hagoort, P., & Brown, C. M. (2000). ERP effects of listening to speech compared to reading: The P600/SPS to syntactic violations in spoken sentences and rapid serial visual presentation. *Neuropsychologia*, 38, 1531–1549.
- Hagoort, P., Brown, C. M., & Groothusen, J. (1993). The syntactic positive shift as an ERP measure of syntactic processing. *Language and Cognitive Processes*, 8, 439–484.
- Hagoort, P., Hald, L., Bastiaansen, M., & Petersson, K. M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science*, 304, 438–441, <http://dx.doi.org/10.1126/science.1095455>.
- Hagoort, P., Wassenaar, M., & Brown, C. M. (2003). Syntax-related ERP-effects in Dutch. *Cognitive Brain Research*, 16, 38–50.
- Hahne, A., & Jescheniak, J. D. (2001). What's left if the Jabberwock gets the semantics? An ERP investigation into semantic and syntactic processes during auditory sentence comprehension. *Cognitive Brain Research*, 11, 199–212.
- Hancock, R., & Bever, T. G. (2013). Genetic factors and normal variation in the organization of language. *Biolinguistics*, 7, 75–95.
- Helenius, P., Salmelin, R., Service, E., & Connolly, J. F. (1998). Distinct time courses of word and context comprehension in the left temporal cortex. *Brain*, 121, 1133–1142.
- Helenius, P., Salmelin, R., Service, E., Connolly, J. F., Leinonen, S., & Lyytinen, H. (2002). Cortical activation during spoken-word segmentation in nonreading-impaired and dyslexic adults. *Journal of Neuroscience*, 22, 2936–2944.
- Hoeks, J. C. J., Stowe, L. A., & Doedens, G. (2004). Seeing words in context: The interaction of lexical and sentence level information during reading. *Cognitive Brain Research*, 19, 59–73, <http://dx.doi.org/10.1016/j.cogbrainres.2003.10.022>.
- Jasper, H. H. (1958). The ten–twenty system of the International Federation. *Electroencephalography and Clinical Neurophysiology*, 10, 371–375.
- Kaan, E., Harris, A., Gibson, E., & Holcomb, P. J. (2000). The P600 as an index of syntactic integration difficulty. *Language and Cognitive Processes*, 15, 159–201.
- Kaan, E., & Swaab, T. Y. (2003a). Electrophysiological evidence for serial sentence processing: A comparison between non-preferred and ungrammatical continuations. *Cognitive Brain Research*, 17, 621–635.
- Kaan, E., & Swaab, T. Y. (2003b). Repair, revision and complexity in syntactic analysis: An electrophysiological differentiation. *Journal of Cognitive Neuroscience*, 15, 98–110.
- Kee, D. W., Bathurst, K., & Hellige, J. B. (1983). Laterized interference of repetitive finger tapping: Influence of familial handedness, cognitive load and verbal production. *Neuropsychologia*, 21, 617–624.
- Kim, A., & Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from event-related potentials. *Journal of Memory and Language*, 52, 205–225, <http://dx.doi.org/10.1016/j.jml.2004.10.002>.
- Kim, A., & Sikos, L. (2011). Conflict and surrender during sentence processing: An ERP study of syntax-semantics interaction. *Brain and Language*, 118, 15–22, <http://dx.doi.org/10.1016/j.bandl.2011.03.002>.
- Kos, M., van den Brink, D., & Hagoort, P. (2012). Individual variation in the late positive complex to semantic anomalies. *Frontiers in Psychology*, 3(318), <http://dx.doi.org/10.3389/fpsyg.2012.00318>.
- Kuperberg, G. R. (2007). Neural mechanisms of language comprehension: Challenges to syntax. *Brain Research*, 1146, 23–49, <http://dx.doi.org/10.1016/j.brainres.2006.12.063>.
- Kuperberg, G. R., Kreher, D. A., Sitnikova, T., Caplan, D., & Holcomb, P. J. (2007). The role of animacy and thematic relationships in processing active English sentences: Evidence from event-related potentials. *Brain and Language*, 100, 223–237, <http://dx.doi.org/10.1016/j.bandl.2005.12.006>.
- Kutas, M., & Federmeier, K. (2011). Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, 62, 621–647, <http://dx.doi.org/10.1146/annurev.psych.093008.131123>.
- Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic anomaly. *Science*, 207, 203–205.
- Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, 307, 161–163.
- Kutas, M., Van Petten, C. K., & Besson, M. (1988). Event-related potential asymmetries during the reading of sentences. *Electroencephalography and Clinical Neurophysiology*, 69, 218–233.
- Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience*, 9, 920–933, <http://dx.doi.org/10.1038/nrn2532>.
- MacDonald, M. C., & Christiansen, M. H. (2002). Reassessing working memory: Comment on Just and Carpenter (1992) and Waters and Caplan (1996). *Psychological Review*, 109, 35–54, <http://dx.doi.org/10.1037/0033-295X.109.1.35>.
- Mancini, S., Molinaro, N., Rizzi, L., & Carreiras, M. (2011). A person is not a number: Discourse involvement in subject–verb agreement computation. *Brain Research*, 1410, 64–76, <http://dx.doi.org/10.1016/j.brainres.2011.06.055>.
- McKeever, W. F., Seitz, K. S., Hoff, A. L., Marino, M. F., & Diehl, J. A. (1983). Interacting sex and familial sinistrality characteristics influence both language lateralization and spatial ability in right handers. *Neuropsychologia*, 21, 661–668.
- McLaughlin, J., Tanner, D., Pitkanen, I., Frenck-Mestre, C., Inoue, K., Valentine, G., et al. (2010). Brain potentials reveal discrete stages of L2 grammatical learning. *Language Learning*, 60, 123–150.
- Molinaro, N., Barber, H., & Carreiras, M. (2011). Grammatical agreement processing in reading: ERP findings and future directions. *Cortex*, 47, 908–930, <http://dx.doi.org/10.1016/j.cortex.2011.02.019>.
- Molinaro, N., Vespignani, F., & Job, R. (2008). A deeper reanalysis of a superficial feature: An ERP study on agreement violations. *Brain Research*, 1228, 161–176, <http://dx.doi.org/10.1016/j.brainres.2008.06.064>.
- Morgan-Short, K., Steinhauer, K., Sanz, C., & Ullman, M. T. (2012). Explicit and implicit second language training differentially affect the achievement of native-like brain activation patterns. *Journal of Cognitive Neuroscience*, 24, 933–947.
- Nakano, H., Saron, C., & Swaab, T. Y. (2010). Speech and span: Working memory capacity impacts the use of animacy but not of world knowledge during spoken sentence comprehension. *Journal of Cognitive Neuroscience*, 22, 2886–2898, <http://dx.doi.org/10.1162/jocn.2009.21400>.
- Nevins, A., Dillon, B., Malhotra, S., & Phillips, C. (2007). The role of feature-number and feature-type in processing Hindi verb agreement violations. *Brain Research*, 1164, 81–94.
- Nieuwland, M. S., & Van Berkum, J. J. A. (2008). The interplay between semantic and referential aspects of anaphoric noun phrase resolution: Evidence from ERPs. *Brain and Language*, 106, 119–131, <http://dx.doi.org/10.1016/j.bandl.2008.05.001>.
- Nieuwland, M. S., Martin, A. E., & Carreiras, M. (2013). Event-related brain potential evidence for animacy processing asymmetries during sentence comprehension. *Brain and Language*, 126, 151–158, <http://dx.doi.org/10.1016/j.bandl.2013.04.005>.

- Oines, L., Miyake, A., & Kim, A. (2012). Individual differences in verbal working memory predict reanalysis vs. integration in syntax-semantics conflict scenarios. *Poster presented at the Architectures and Mechanisms for Language Processing Conference*, Riva del Garda, Italy.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97–113.
- Osterhout, L. (1997). On the brain response to syntactic anomalies: Manipulations of word position and word class reveal individual differences. *Brain and Language*, 59, 494–522.
- Osterhout, L., Holcomb, P. J., & Swinney, D. A. (1994). Brain potentials elicited by garden-path sentences: Evidence for the application of verb information during parsing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 28, 786–803.
- Osterhout, L., Kim, A., & Kuperberg, G. R. (2012). The neurobiology of sentence comprehension. In: M. Spivey, M. Joannisse, & K. McCrae (Eds.), *The Cambridge handbook of Psycholinguistics* (pp. 365–389). Cambridge: Cambridge University Press.
- Osterhout, L., McKinnon, R., Bersick, M., & Corey, V. (1996). On the language-specificity of the brain response to syntactic anomalies: Is the syntactic positive shift a member of the P300 family? *Journal of Cognitive Neuroscience*, 8, 507–526.
- Osterhout, L., McLaughlin, J., Kim, A., Greewald, R., & Inoue, K. (2004). Sentences in the brain: Event-related potentials as real-time reflections of sentence comprehension and language learning. In: M. Carreiras, & C. Clifton (Eds.), *The on-line study of sentence comprehension: Eyetracking-ERPs, and beyond* (pp. 271–308). New York: Psychology Press.
- Osterhout, L., & Mobley, L. (1995). Event-related brain potentials elicited by failure to agree. *Journal of Memory and Language*, 34, 739–773.
- Osterhout, L., & Nicol, J. (1999). On the distinctiveness, independence, and time course of the brain responses to syntactic and semantic anomalies. *Language and Cognitive Processes*, 14, 283–317.
- Paczynski, M., & Kuperberg, G. R. (2012). Multiple influences of semantic memory on sentence processing: Distinct effects of semantic relatedness on violations of real-world event/state knowledge and animacy selection restrictions. *Journal of Memory and Language*, 67, 426–448, <http://dx.doi.org/10.1016/j.jml.2012.07.003>.
- Pakulak, E., & Neville, H. J. (2010). Proficiency differences in syntactic processing of monolingual native speakers indexed by event-related potentials. *Journal of Cognitive Neuroscience*, 22, 2728–2744.
- Prat, C. S. (2011). The brain basis of individual differences in language comprehension abilities. *Language and Linguistics Compass*, 5, 635–649, <http://dx.doi.org/10.1111/j.1749-818x.2011.00303.x>.
- Pylkkänen, L., & McElree, B. (2007). An MEG study of silent meaning. *Journal of Cognitive Neuroscience*, 19, 1905–1921, <http://dx.doi.org/10.1162/jocn.2007.19.11.1905>.
- Rayner, K., & Clifton, C. (2009). Language processing in reading and speech perception is fast and incremental: Implications for event-related potential research. *Biological Psychology*, 80, 4–9, <http://dx.doi.org/10.1016/j.biopsycho.2008.05.002>.
- Rodriguez-Fornells, A., Clahsen, H., Lleó, C., Zaake, W., & Münte, T. F. (2001). Event-related brain responses to morphological violations in Catalan. *Cognitive Brain Research*, 11, 47–58.
- Service, E., Helenius, P., Maury, S., & Salmelin, R. (2007). Localization of syntactic and semantic brain responses using magnetoencephalography. *Journal of Cognitive Neuroscience*, 19, 1193–1205, <http://dx.doi.org/10.1162/jocn.2007.19.7.1193>.
- Severens, E., Jansma, B. M., & Hartsuiker, R. J. (2008). Morphophonological influences on the comprehension of subject–verb agreement: An ERP study. *Brain Research*, 1228, 135–144, <http://dx.doi.org/10.1016/j.brainres.2008.05.092>.
- Silva-Pereyra, J. F., & Carreiras, M. (2007). An ERP study of agreement features in Spanish. *Brain Research*, 1185, 201–211, <http://dx.doi.org/10.1016/j.brainres.2007.09.029>.
- Steinhauer, K., White, E. J., & Drury, J. E. (2009). Temporal dynamics of late second language acquisition: Evidence from event-related brain potentials. *Second Language Research*, 25, 13–41, <http://dx.doi.org/10.1177/0267658308098995>.
- Tanner, D., Inoue, K., & Osterhout, L. Brain-based individual differences in on-line L2 grammatical comprehension. *Bilingualism: Language and Cognition*, <http://dx.doi.org/10.1017/S1366728913000370>, in press.
- Tanner, D., McLaughlin, J., Herschensohn, J., & Osterhout, L. (2013). Individual differences reveal stages of L2 grammatical acquisition: ERP evidence. *Bilingualism: Language and Cognition*, 16, 367–382, <http://dx.doi.org/10.1017/S1366728912000302>.
- Townsend, D. J., & Bever, T. G. (2001). *Sentence comprehension: The integration of rules and habits*. Cambridge, MA: MIT Press.
- Townsend, D. J., Carrithers, C., & Bever, T. G. (2001). Familial handedness and access to words, meaning, and syntax during sentence comprehension. *Brain and Language*, 78, 308–331, <http://dx.doi.org/10.1006/brln.2001.2469>.
- Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition*, 92, 231–270.
- Unsworth, N., Heitz, R. P., Schrock, J., & Engle, R. W. (2005). An automated version of the operation span task. *Behavior Research Methods*, 37, 498–505.
- Van Berkum, J. J. A., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: Evidence from the N400. *Journal of Cognitive Neuroscience*, 11, 657–671.
- Van de Meerendonk, N., Kolk, H. H. J., Vissers, C. T. W. M., & Chwilla, D. J. (2010). Monitoring in language perception: Mild and strong conflicts elicit different ERP patterns. *Journal of Cognitive Neuroscience*, 22, 67–82.
- Van Herten, M., Chwilla, D. J., & Kolk, H. H. J. (2006). When heuristics clash with parsing routines: ERP evidence for conflict monitoring in sentence perception. *Journal of Cognitive Neuroscience*, 18, 1181–1197, <http://dx.doi.org/10.1162/jocn.2006.18.7.1181>.
- Van Petten, C., & Luka, B. J. (2006). Neural localization of semantic context effects in electromagnetic and hemodynamic studies. *Brain and Language*, 97, 279–293, <http://dx.doi.org/10.1016/j.bandl.2005.11.003>.
- Van Petten, C., & Luka, B. J. (2012). Prediction during language comprehension: Benefits, costs, and ERP components. *International Journal of Psychophysiology*, 83, 176–190, <http://dx.doi.org/10.1016/j.ijpsycho.2011.09.015>.
- Wlotko, E. W., & Federmeier, K. D. (2012). So that's what you meant! Event-related potentials reveal multiple aspects of context use during construction of message-level meaning. *NeuroImage*, 62(1), 356–366, <http://dx.doi.org/10.1016/j.neuroimage.2012.04.054>.
- Ye, Z., & Zhou, X. (2008). Involvement of cognitive control in sentence comprehension: Evidence from ERPs. *Brain Research*, 1203, 103–115, <http://dx.doi.org/10.1016/j.brainres.2008.01.090>.
- Zhang, Y., Li, P., Piao, Q., Liu, Y., Huang, Y., & Shu, H. (2013). Syntax does not necessarily precede semantics in sentence processing: ERP evidence from Chinese. *Brain and Language*, 126, 8–19, <http://dx.doi.org/10.1016/j.bandl.2013.04.001>.