



Research report

How right is left? Handedness modulates neural responses during morphosyntactic processing

Sarah Grey^{a,*}, Darren Tanner^{d,e}, Janet G. van Hell^{b,c}^a Department of Modern Languages and Literatures, Fordham University, Faber Hall 556, Bronx, NY 10458, USA^b Department of Psychology, Pennsylvania State University, 140 Bruce V. Moore Building, University Park, PA 16802, USA^c Center for Language Science, Pennsylvania State University, 140 Bruce V. Moore Building, University Park, PA 16802, USA^d Department of Linguistics, University of Illinois at Urbana-Champaign, 707 S. Mathews Avenue, Urbana, IL 61801, USA^e Beckman Institute for Advanced Science and Technology, University of Illinois at Urbana-Champaign, 707 S. Mathews Avenue, Urbana, IL 61801, USA

ARTICLE INFO

Article history:

Received 6 April 2016

Received in revised form 15 May 2017

Accepted 21 May 2017

Available online 26 May 2017

Keywords:

Syntax

Event-related potentials

Handedness

Individual differences

ABSTRACT

Most neurocognitive models of language processing generally assume population-wide homogeneity in the neural mechanisms used during language comprehension, yet individual differences are known to influence these neural mechanisms. In this study, we focus on handedness as an individual difference hypothesized to affect language comprehension. Left-handers and right-handers with a left-handed blood relative, or familial sinistrals, are hypothesized to process language differently than right-handers with no left-handed relatives (Hancock and Bever, 2013; Ullman, 2004). Yet, left-handers are often excluded from neurocognitive language research, and familial sinistrality in right-handers is often not taken into account. In the current study we used event-related potentials to test morphosyntactic processing in three groups that differed in their handedness profiles: left-handers (LH), right-handers with a left-handed blood relative (RH FS+), and right-handers with no reported left-handed blood relative (RH FS−; both right-handed groups were previously tested by Tanner and Van Hell, 2014). Results indicated that the RH FS− group showed only P600 responses during morphosyntactic processing whereas the LH and RH FS+ groups showed biphasic N400-P600 patterns. N400s in LH and RH FS+ groups are consistent with theories that associate left-handedness (self or familial) with increased reliance on lexical/semantic mechanisms during language processing. Inspection of individual-level results illustrated that variability in RH FS− individuals' morphosyntactic processing was remarkably low: most individuals were P600-dominant. In contrast, LH and RH FS+ individuals showed marked variability in brain responses, which was similar for both groups: half of individuals were N400-dominant and half were P600-dominant. Our findings have implications for neurocognitive models of language that have been largely formulated around data from only right-handers without accounting for familial sinistrality or including left-handers, and moreover highlight that there is systematic – and often ignored – variability in language processing outcomes in neurologically healthy populations.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Individual differences are known to influence ERP patterns in language processing (e.g., Nakano et al., 2010; Pakulak and Neville, 2010) and one pertinent yet under-studied individual difference is handedness. Though the majority of humans are right-handed, approximately 10% of the world population is left-handed (Perelle and Ehrman, 1994). Neurocognitive research often uses left-handedness as an exclusionary criterion for participation in studies on language and other domains (Willems et al., 2014).

This means that around a tenth of worldwide language users are under-represented, or not represented at all, in much of our knowledge on the neurocognition of language. The tendency to exclude left-handers from neuroscientific language research stems primarily from the association of left-handedness with more variable patterns of cerebral specialization for language. Whereas right-handers tend to have language lateralized to the left cerebral hemisphere (e.g., Knecht et al., 2000; Mazoyer et al., 2014), some left-handers show more bilateral activity while others show reverse lateralization to the right hemisphere (Knecht et al., 2000; Mazoyer et al., 2014; Pujol et al., 1999; Sommer et al., 2002; Szaflarski et al., 2002). As a consequence, it is generally assumed that left-handers are more variable than right-handers and they

* Corresponding author.

E-mail address: sgrey4@fordham.edu (S. Grey).

are excluded to reduce the amount of noise in the study sample (Willemms et al., 2014). However, although many neurocognitive theories of language (and cognition more generally) assume some degree of uniformity of neurocognitive architecture across individuals (e.g., Coltheart, 2001), it is becoming increasingly clear that cognitive and neurocognitive models of language need to account for the ways in which individuals vary.

One key consequence of this exclusionary approach with regard to left-handedness and presumed heterogeneity is that it leaves out a considerable portion of the population, resulting in neurocognitive models that do not necessarily provide population-wide explanatory reach. In addition, the *inclusionary* approach with respect to right-handers may also not be warranted because it is not clear that right-handers are as homogeneous in their language processing as researchers implicitly assume. Mounting research is beginning to show that gradations in handedness, among other variables, can have profound impacts on individual variation in language processing in otherwise neurologically typical individuals. For example, fMRI research indicates that degree of right-handedness is related to different patterns of semantic memory activation during grammatical processing (Newman et al., 2014). Also, familial sinistrality in right-handers (having a left-handed blood relative, which occurs in approximately half of right-handers; Bever et al., 1989; Hancock and Bever, 2013) has been associated, like left-handers, with increased variability in hemispheric lateralization (Josse and Tzourio-Mazoyer, 2004; see also Bathurst and Kee, 1994; Kee et al., 1983; McKeever et al., 1983; Steinmetz et al., 1991). Likewise, recent ERP research has found differences in processing of semantic and grammatical information for right-handers with familial sinistrality and those without (Kos et al., 2012; Lee and Federmeier, 2015; Tanner and Van Hell, 2014). The exclusion of left-handers and the inclusion of all right-handers without taking familial sinistrality into account therefore gives rise to neurocognitive models of language that substantially underestimate the amount of normal, individual-level variation across the population in the neural organization of language and in real-time language processing systems.

Although it is common practice to use left- and right-handedness as exclusion/inclusion criteria in neurocognitive research on language, there are at least two consequences of this approach. First, by excluding left-handers from their studies researchers are effectively losing information that left-handers contribute to the landscape of our theories and knowledge about the neurocognition of language (Willemms et al., 2014). Second, by including but not identifying right-handers with familial sinistrality, who may show greater variability in laterality and processing signatures than right-handers without familial sinistrality, researchers are losing insights from another potentially distinctive group by mixing them with non-familial sinistrals. As approximately half of right-handers are familial sinistrals, together with the 10% of the left-handed population, this amounts to more than half of the population that is largely excluded (left-handers) or ignored (right-handed familial sinistrals) in neurocognitive research on language. This affects the explanatory reach of most current (neuro)cognitive theories of real-time language comprehension that have been proposed in the past decade (e.g., Friederici et al., 2004; Kutas and Federmeier, 2011; Osterhout et al., 2012; Ullman, 2004, 2015). Moreover, there is increasing evidence of substantial inter-individual variability in normal language processing in populations that are typically assumed to be relatively homogeneous (e.g., literate, monolingual, right-handers; Hancock and Bever, 2013; Lee and Federmeier, 2015; Pakulak and Neville, 2010; Prat and Just, 2011; Tanner and Van Hell, 2014). Research is needed to identify the factors that underlie this individual variation in language processing.

In the present study, we build on work by Tanner and Van Hell (2014) and investigate the role of handedness in modulating neural responses during grammatical processing. Though not the primary scope of their paper, an analysis of individual difference factors revealed differences in morphosyntactic processing in right-handers with and without familial sinistrality. Here, we investigate this phenomenon in more detail. In particular, we contrast ERPs elicited by morphosyntactic violations in newly-collected data from left-handers to the two groups of right-handers that were tested by Tanner and Van Hell. We focus on between-group differences associated with handedness and also report the type and extent of inter-individual variability within the groups. To our knowledge, no other study has explicitly compared these three groups using neurocognitive measures, despite the methodological and theoretical importance of handedness, and individual differences more generally, on language research.

1.1. Handedness and language

As discussed above, handedness can have implications for cortical lateralization of language, and there are reasons to believe that handedness (possibly as a consequence of laterality differences) can modulate the types of information attended to during real-time comprehension. For example, behavioral research suggests that handedness can impact the relative balance of reliance on lexical/semantic and grammatical aspects of language during comprehension (e.g., Bever et al., 1989; Townsend et al., 2001; Ullman et al., 2017) and there are two theoretical accounts for these effects of handedness. Broadly, both accounts associate left-handedness with increased reliance on or access to lexical/semantic information and right-handedness with greater reliance on or access to morphosyntactic information during sentence processing (Bever et al., 1989; Hancock and Bever, 2013; Townsend et al., 2001; Ullman, 2004; Ullman et al., 2017).

Specifically, Bever and colleagues propose that right-handers with familial sinistrality (RH FS+) rely more on lexical/semantic information than non-familial sinistrals, that is, right-handers with no reported left-handed blood relative (RH FS−). RH FS− individuals are instead predicted to rely more on morphosyntactic¹ information than their RH FS+ peers. In a set of behavioral studies, support for this account of differential reliance as a function of familial sinistrality was indeed borne out (Bever et al., 1989; Townsend et al., 2001). Townsend et al., 2001, for example, tested a group of RH FS+ and RH FS− adults on word probe and association probe tasks while they listened to sentence fragments. Participants heard a fragment such as *I liked calling up my aunt each night* which was followed by a brief tone and then a word probe (e.g., *up*) or an association probe (e.g., *talking with a relative*; examples taken from Townsend et al., 2001). Results showed that RH FS+ adults had the fastest response times, which the authors interpreted as support for their prediction that RH FS+ individuals focus on words and semantics during sentence comprehension. The results also showed that only the RH FS− group showed a significant effect of the serial position of the target word (e.g., *up*) which supported the authors' hypothesis that comprehension processes in RH FS− adults emphasize rule-governed language processes, such as the order of words and their syntactic relationships.

Ullman's declarative/procedural (DP) model of language (Ullman, 2001, 2004, 2013, 2015) posits that the declarative memory system is involved in the learning and processing of lexical/semantic information, and that the procedural memory system is involved in learning and processing rule-like aspects of language

¹ We use the term *morphosyntax* (and its derivations) broadly to cover grammatical aspects of syntax (e.g., word order) as well as lexically-marked grammatical features (e.g., *is/are*) and morphologically-marked features (e.g., *walk/walk + ing*).

across morphosyntax, non-lexical semantics, and phonology (see also Paradis, 1994, 2009). With respect to handedness, Ullman hypothesizes that left-handers and RH FS+ individuals, who tend to be less left-hemisphere dominant for language and motor functions, have less efficient procedural memory (which is left hemisphere dominant). Therefore, one prediction borne out of the DP model is that left-handers and FS+ right-handers should rely more on lexical/semantic information (which depends on declarative memory) during morphosyntactic processing in order to make up for the less efficient procedural memory ability. In contrast, FS–right-handers, who are assumed to be left-hemisphere dominant for language and motor functions, should have strong procedural memory and therefore should show greater engagement of morphosyntactic (procedural memory-related) information during grammatical processing as compared to their left-handed (self or familial) peers. Support for these predictions has been found in a recent behavioral study on storage and composition that compared left- and right-handers (Ullman et al., 2017).

Though these accounts predict notable effects of left-handedness (self or familial) on grammatical processing, there is very little research that has empirically tested whether aspects of grammatical information are processed differently across individuals as a function of left-handedness. Not surprisingly, then, there are a number of gaps in our current knowledge. First, most research has in fact only included right-handers in their sample, as outlined above (but see Ullman et al., 2017). Second, nearly all of the studies on handedness and grammatical processing employed exclusively behavioral measures of processing (e.g., Bever et al., 1989; Townsend et al., 2001; Ullman et al., 2017; but see Lee and Federmeier, 2015; Newman et al., 2014; Tanner and Van Hell, 2014), which may not fully capture qualitative differences in how information is used in real-time. These gaps have left us with remarkably little knowledge of grammatical processing in left-handers and how it compares to that of right-handers (with or without familial sinistrality). This also has implications for neurocognitive theories of language that have been largely formulated around data from only right-handers, who may themselves show marked patterns of individual differences in language processing patterns, where at least some of the variance appears to be accounted for by familial sinistrality (cf. Tanner and Van Hell, 2014).

To address these gaps, we examined ERPs during morphosyntactic processing in three groups of neurologically healthy adults who differed in their handedness profiles: (1) left-handers (LH), (2) right-handers with a left-handed blood relative (RH FS+), and (3) right-handers with no reported left-handed blood relative (RH FS–). In particular, we expand on earlier data by reanalyzing the right-handers' data from Tanner and Van Hell (2014) with an explicit focus on the inter-individual distribution and variability of the ERP correlates of morphosyntactic processing in the two groups of right-handers identified in (but not analyzed in detail by) Tanner and Van Hell (2014) and, importantly, we add a new set of ERP data from left-handed individuals.

1.2. ERPs and language

Neurocognitive measures of language processing, and in particular ERPs, not only provide uniquely disambiguating insight into group- and individual-level differences, but are also capable of elucidating qualitative differences in how information is processed (e.g., Morgan-Short et al., 2012a,b; Tanner et al., 2014; Tanner and Van Hell, 2014). ERPs are especially well-suited for investigating the effects of handedness on morphosyntactic processing, and whether handedness modulates reliance on lexical/semantic versus grammatical information during language processing (as suggested by Bever and colleagues

and Ullman and colleagues), given that there are two well-studied ERP components that have shown reliable associations with these two types of processing, respectively: the N400 and P600.

The first ERP component, the N400, is a negative-going waveform with a broad centro-parietal distribution that is typically considered an index of lexical/semantic processing in the brain (e.g., Friederici, 2002, 2004; Kaan, 2007; Kutas and Federmeier, 2011; Lau et al., 2008). The amplitude of the N400 covaries with numerous lexical and semantic factors, including the predictability and contextual felicity of a word in a sentential or discourse context, word frequency, and also interpretative relevance of the target (Choudhary et al., 2009; Friederici, 2004; Grey and Van Hell, 2017; Kutas and Federmeier, 2011; Lau et al., 2008; Nieuwland et al., 2007; Nieuwland and Van Berkum, 2006; Van Berkum et al., 1999). Since its discovery, the N400 has been widely accepted as reflecting difficulty in accessing and integrating lexical/semantic information (Kutas and Federmeier, 2011; Kutas and Hillyard, 1980); for an alternative account, see Debruille, 2007; Debruille et al., 2008).

The second neural signature, a positive-going waveform with a predominantly posterior scalp distribution (termed the P600), is typically elicited in response to violations of morphosyntax, for example in word order (Friederici and Mecklinger, 1996; Neville et al., 1991) and subject-verb agreement (Coulson et al., 1998; Kaan, 2002; Osterhout and Mobley, 1995; Silva-Pereyra and Carreiras, 2007; Tanner et al., 2017). Although the exact nature of P600 effects is still being discussed in the literature (e.g., Bornkessel-Schlesewsky and Schlesewsky, 2008; Chow and Phillips, 2013; Coulson et al., 1998; Friederici et al., 2002; Kolk and Chwilla, 2007; Osterhout et al., 2012; van de Meerendonk et al., 2010), more than two decades of research show that the P600 is remarkably sensitive to and reliably elicited by morphosyntactic violations. Despite differences in the exact theoretical descriptions of P600 effects, there is a general agreement that P600s reflect processing of a stimulus in conflict with an expected linguistic representation and a late attempt at conflict resolution or reanalysis, and that the P600 effect reflects a set of processes that are neurocognitively separable from those reflected in the N400 effect (Allen et al., 2003; Bornkessel-Schlesewsky and Schlesewsky, 2008; Chow and Phillips, 2013; DeLong et al., 2014; Kolk and Chwilla, 2007; Kuperberg, 2007; Osterhout and Nicol, 1999; van de Meerendonk et al., 2010).

These two ERP components (N400 and P600) offer a particularly elegant frame for investigating the hypothesized effects of handedness on language and determining whether left-handedness (self or familial) leads to qualitative differences in morphosyntactic processing. In a post hoc examination of right-handed FS– and FS+ groups, Tanner and Van Hell (2014) found that, even among proficient, literate monolinguals, individuals' brain responses to morphosyntactic violations varied along a continuum between N400- and P600-dominance. Importantly, right-handers' familial sinistrality predicted 19% of the variance in individuals' ERP response dominance. That study provides evidence that familial sinistrality affects language processing in right-handers, and also highlights ERPs as a measure that is sensitive to qualitative effects of handedness.

In the current study, we reanalyzed the right-handers' data from Tanner and Van Hell (2014) and explicitly compared this data set to a newly-recruited group of left-handed adults who were tested under the exact same conditions as the previously-tested right-handers. This approach enables us to study similarities or differences in language processing among oft-excluded left-handers, RH FS+ individuals, and RH FS– individuals. The design addresses limitations in previous research that either included only right-handers, or compared right-handers to left-handers but did not

account for familial sinistrality. We tested the following predictions.

First, because left-handedness is not hypothesized to completely *eliminate* the use of morphosyntactic information during processing, we predicted that all three groups would show reliable P600s in response to morphosyntactic violations (i.e., subject-verb agreement and verb tense, see Experimental Procedure). Second, because left-handers and right-handers with familial sinistrality are hypothesized to show heightened reliance on lexical/semantics for processing grammatical information, we predicted that left-handers and right-handers with familial sinistrality would additionally show N400s (together with P600s) in response to morphosyntactic violations. Finally, within the context of [Tanner and Van Hell's \(2014\)](#) findings, we predicted increased inter-individual variability in N400/P600 response dominance across right-handers with familial sinistrality and left-handers.

2. Results

2.1. Behavioral results

During EEG acquisition, participants completed a sentence acceptability judgment task and participants' responses were transformed to *d*-prime scores, which provide an unbiased measure of participants' ability to discriminate between grammatical and ungrammatical items ([Macmillan and Creelman, 2005](#); [Stanislaw and Todorov, 1999](#); [Wickens, 2002](#)). These values were entered into an ANOVA with Condition (subject-verb agreement, verb tense) as the within-subjects factor and Handedness group (LH, RH FS+, RH FS–) as the between-subjects factor. The 2×3 ANOVA showed a main effect for Condition, $F(1,57) = 5.394$, $p = 0.024$, $\eta_p^2 = 0.09$, which was due to discrimination being better for tense than for agreement items (Agreement *d*-prime $M = 3.30$, $SD = 0.84$, 95% CI [3.09, 3.50]; Tense *d*-prime $M = 3.53$, $SD = 0.63$, 95% CI [3.36, 3.68]). There was no main effect of Handedness ($p = 0.193$, $\eta_p^2 = 0.06$), nor an interaction between Condition and Handedness ($p = 0.426$, $\eta_p^2 = 0.03$). Thus, there were no differences among the three handedness groups regarding their performance on the acceptability judgment task, implying there were no differences in behavioral grammatical sensitivity among the three groups. For descriptive information see [Table 1](#).

2.1.1. ERP results across handedness groups

Visual inspection of the waveforms in the three handedness groups suggested that for both tense and agreement violations, the RH FS+ and LH groups showed a biphasic N400–P600 response whereas the RH FS– group showed a robust monophasic P600 response (See [Figs. 1–3](#) for grand mean responses in the LH, RH FS+, and RH FS– groups, respectively. See Appendix [Fig. A1](#) for grand mean ERP waveforms of the three handedness groups combined).

All ERP analyses were conducted on two time windows of interest, 300–500 ms and 500–800 ms. These time windows are representative of the neural patterns of interest (N400 and P600, respectively; for similar time-windows see, e.g., [Osterhout, 1997](#); [Osterhout and Nicol, 1999](#)). Analyses were conducted on data from lateral electrodes that were grouped into four regions of interest (ROIs; for similar approaches to quantification see, e.g., [Chow and Phillips, 2013](#); [Frenzel et al., 2011](#); [Tanner and Van Hell, 2014](#); [Visser et al., 2008](#)): 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) and data from midline sites included Fz, Cz, and Pz. Analyses were conducted separately on lateral and midline sites to examine the topographies of the relevant effects. For lateral sites, mean ERP amplitudes were entered into separate ANOVAs for each time window, with Grammaticality (grammatical, ungrammatical), Condition (agreement, tense), Hemisphere (left, right), and Anterior/posterior (anterior, posterior) as within-subjects factors. For midline sites, ANOVAs included Grammaticality, Condition, and Electrode (Fz, Cz, Pz) as within-subjects factors. We report Greenhouse-Geisser corrected *p*-values for data with more than one degree of freedom in the numerator. First, we report analyses across all 60 participants with the factor of Handedness (LH, RH FS+, RH FS–) as a between-subjects factor. Then, we report ANOVAs within each handedness group to more closely analyze each group's ERP effects. We also briefly present results from follow-up comparisons of the left-handed group with each the two right-handed groups (RH FS+, RH FS–).

The results from an omnibus ANOVA in the 300–500 ms time-window are in [Table 2](#). There were several interactions with the factor of Handedness and these are examined in greater detail in the sections below. In the midline sites, follow-up analysis on the Grammaticality \times Electrode interaction showed an anterior negativity over both conditions, Fz: $F(1,57) = 6.983$, $p = 0.011$, $\eta_p^2 = 0.11$ (*n.s.* at Cz and Pz). Follow-up analysis on the four-way Grammaticality \times Condition \times Hemisphere \times Anterior/posterior interaction for lateral sites showed that verb tense violations elicited a negativity with a left, anterior distribution, $F(1,57) = 12.368$, $p = 0.001$, $\eta_p^2 = 0.18$, which appeared to be driven by the LH and RH FS+ groups (see [Figs. 1 and 2](#)).

The results from an omnibus ANOVA in the 500–800 ms time-window are in [Table 2](#). In the midline, follow-up analysis on the Grammaticality \times Condition \times Electrode interaction showed that violations of subject-verb agreement and verb tense elicited a robust P600 effect and that the effect was stronger in posterior than anterior midline and stronger for subject-verb agreement than tense violations (Agreement Fz: $F(1,59) = 8.543$, $p = 0.005$, $\eta_p^2 = 0.13$; Cz: $F(1,59) = 53.874$, $p < 0.001$, $\eta_p^2 = 0.47$; Pz: $F(1,59) = 95.969$, $p < 0.001$, $\eta_p^2 = 0.62$. Tense Fz: $F(1,59) = 20.947$, $p < 0.001$, $\eta_p^2 = 0.26$; Cz: $F(1,59) = 41.547$, $p < 0.001$, $\eta_p^2 = 0.41$; Pz: $F(1,59) = 54.298$, $p < 0.001$, $\eta_p^2 = 0.48$). In the lateral analysis, follow-up analysis on significant interactions showed that violations of agreement and tense led to a robust and broadly distributed

Table 1
Descriptive information on acceptability judgment task performance for agreement and tense conditions.

	Tense			Agreement		
	<i>M</i>	<i>SD</i>	95% CI	<i>M</i>	<i>SD</i>	95% CI
LH <i>n</i> = 20	3.33	.59	[3.07, 3.58]	3.09	.82	[2.71, 3.43]
RH FS+ <i>n</i> = 20	3.67	.67	[3.36, 3.94]	3.28	.79	[2.92, 3.62]
RH FS– <i>n</i> = 20	3.59	.58	[3.35, 3.83]	3.53	.88	[3.12, 3.92]

Notes. Values represent means, standard deviations, and 95% confidence intervals.

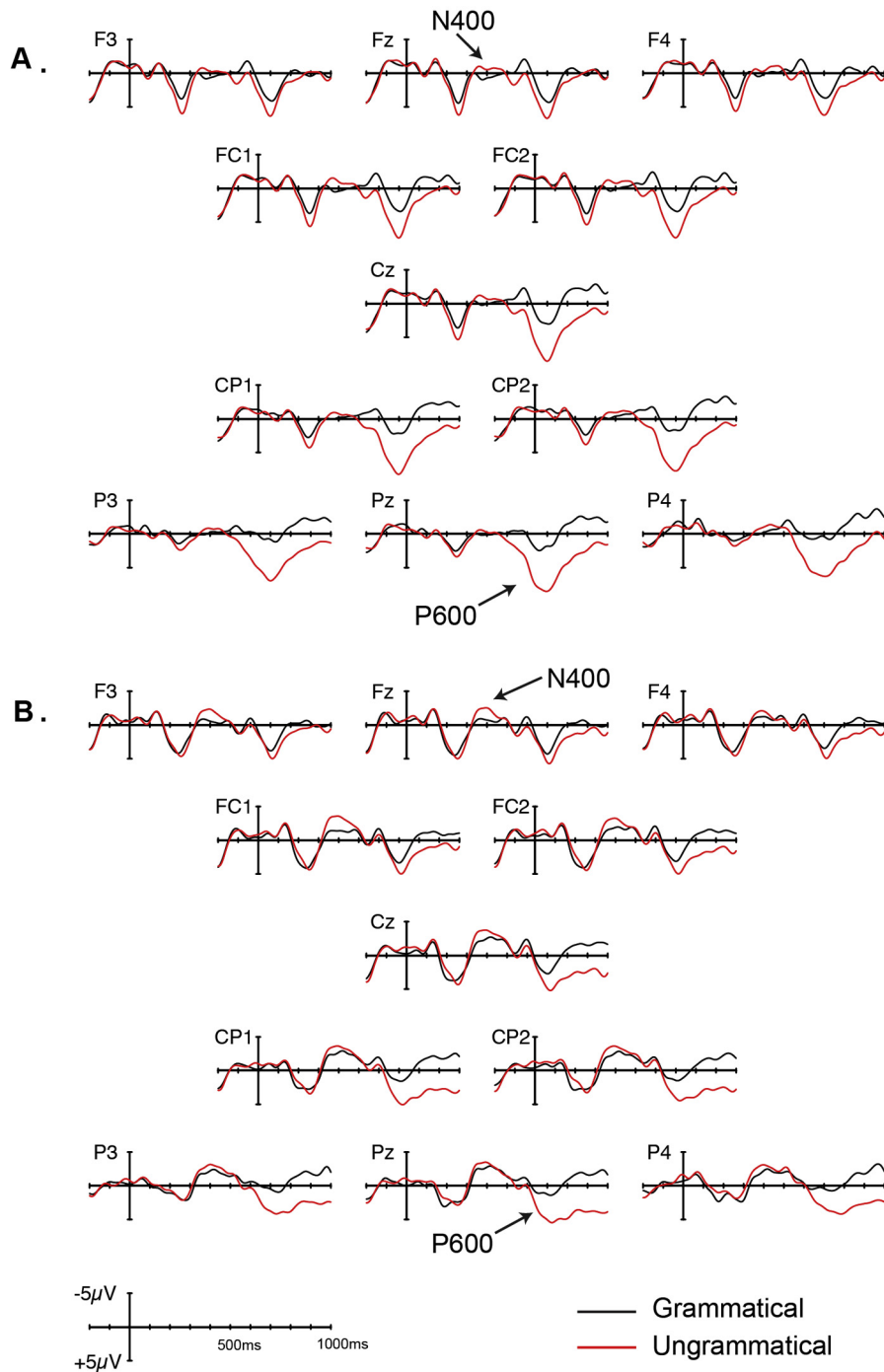


Fig. 1. Grand mean ERP waveforms from the left-handed participants (LH; $n = 20$) over 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the agreement condition; panel B shows ERP responses in the tense condition. These and all subsequent waveforms were filtered with a 15 Hz low-pass filter for presentation purposes only. Waveforms depict 200 ms of prestimulus and 1000 ms of poststimulus activity. Onset of the critical verb is indicated by the vertical calibration bar. Negative voltage is plotted up.

P600 effect in both conditions and that the effect was stronger in posterior than anterior sites (Anterior: $F[1,57] = 24.418$, $p < 0.001$, $\eta_p^2 = 0.30$; Posterior: $F[1,57] = 88.379$, $p < 0.001$, $\eta_p^2 = 0.61$), and stronger for subject-verb agreement than for tense (Agreement: $F[1,57] = 72.783$, $p < 0.001$, $\eta_p^2 = 0.56$; Tense: $F[1,57] = 55.967$, $p < 0.001$, $\eta_p^2 = 0.50$).

The results from this analysis indicate that tense violations elicited a biphasic N400-P600 response whereas agreement violations elicited a robust monophasic P600. The biphasic patterns,

however, appeared to be driven by ERPs in the left-handers and right-handers with familial sinistrality (see Figs. 1 and 2) rather than the right-handers with no familial sinistrality (see Fig. 3). Indeed, the ANOVA produced several significant interactions with the factor of Handedness. The following sections present a closer examination of each group's ERP patterns.

2.1.2. ERPs in the left-handers

To examine morphosyntactic processing for each group in more detail, ERP patterns within each handedness group were analyzed

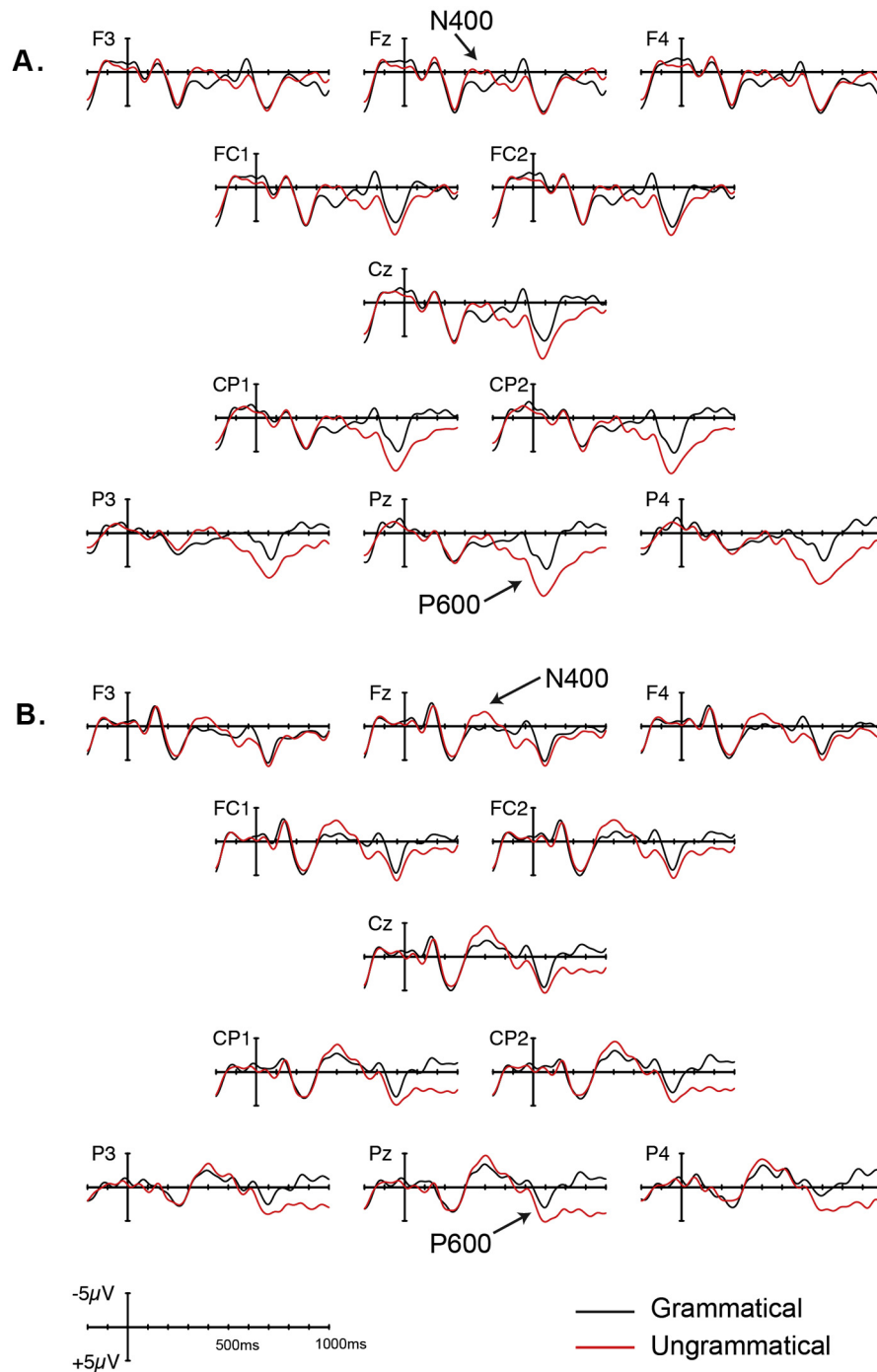


Fig. 2. Grand mean ERP waveforms from the right-handed participants with familial sinistrality (RH FS+; $n = 20$) over 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the agreement condition; panel B shows ERP responses in the tense condition. RH FS+ data come from participants originally tested by [Tanner and Van Hell \(2014\)](#).

with ANOVAs in each time window (300–500 ms and 500–800 ms) with Grammaticality (grammatical, ungrammatical), Condition (agreement, tense), and Electrode (Fz, Cz, Pz) as within-subjects factors in the midline analysis. For lateral sites, ANOVAs included Grammaticality, Condition, Hemisphere (left, right), and Anterior/posterior (anterior, posterior) as within-subjects factors. Waveforms for the left-handed group are depicted in [Fig. 1](#).

In the 300–500 ms time window, midline results for the left-handers showed a main effect of Grammaticality, $F(1,19) = 6.100$, $p = 0.023$, $\eta_p^2 = 0.24$, with no additional significant interactions (all

$ps > 0.10$). This effect for grammaticality was due to violations of agreement and tense eliciting a negativity; that is, an N400 effect (see [Fig. 1](#)): Agreement violation $M \mu V = -2.74$, $SE = 0.545$, 95% CI $[-1.414, 0.867]$, correct $M \mu V = 0.096$, $SE = 0.538$, 95% CI $[-1.029, 1.221]$; Tense violation $M \mu V = -2.196$, $SE = 0.556$, CI $[-3.359, -1.033]$, correct $M \mu V = -1.435$, $SE = 0.407$, CI $[-2.286, -0.584]$. This N400 effect was reflected in the lateral analysis as well, with the ANOVA showing a significant main effect of Grammaticality, $F(1,19) = 5.432$, $p = 0.031$, $\eta_p^2 = 0.22$ (all other main effects and interactions, $p > 0.10$).

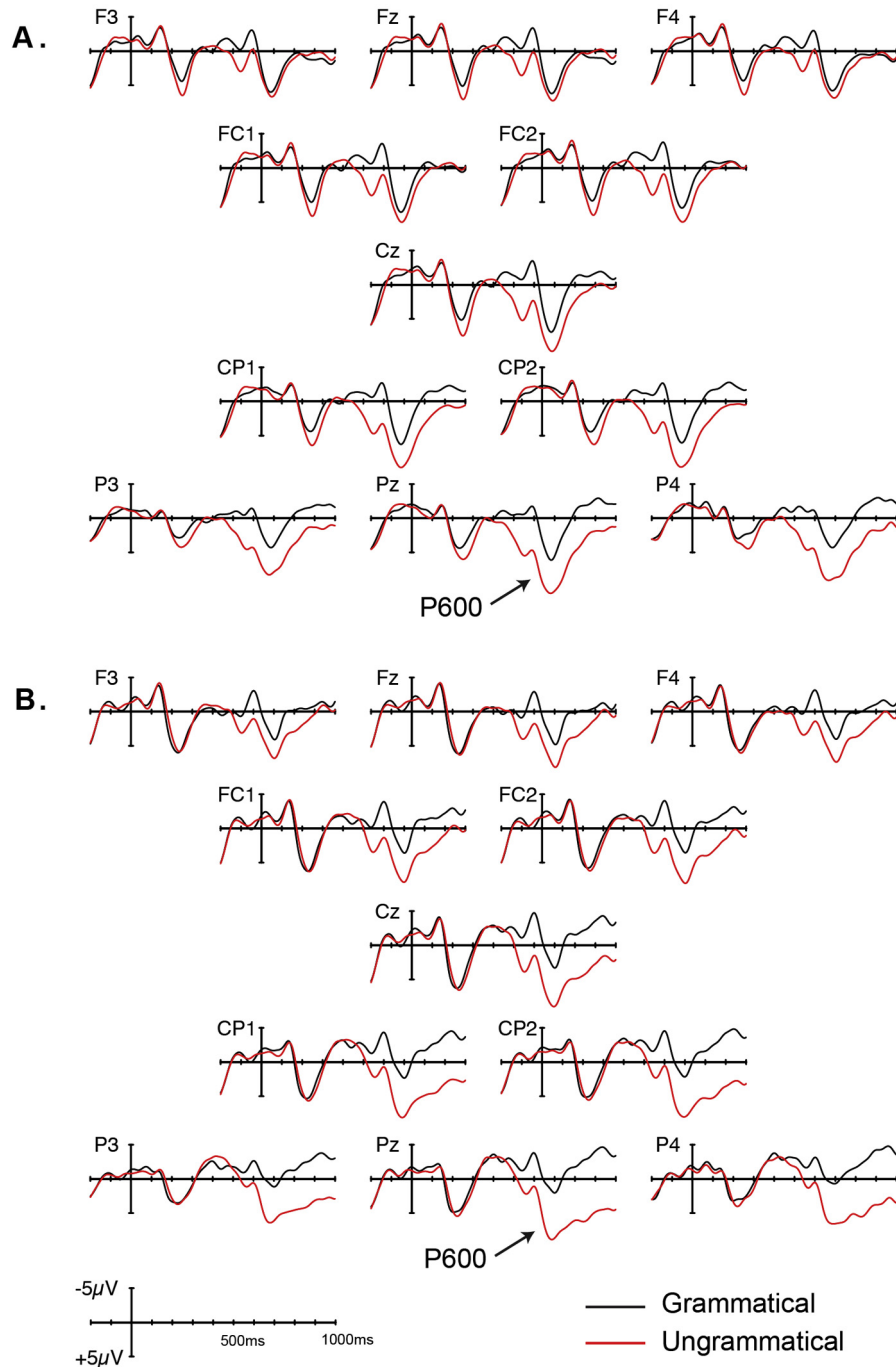


Fig. 3. Grand mean ERP waveforms from the right-handed participants without familial sinistrality (RH FS–; $n = 20$) over 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the agreement condition; panel B shows ERP responses in the tense condition. RH FS– data come from participants originally tested by [Tanner and Van Hell \(2014\)](#).

In the 500–800 ms time-window, the midline ANOVA showed no significant main effects or interactions (all p s > 0.10). The lateral ANOVA revealed a significant Grammaticality \times Condition \times Anterior/posterior interaction, $F(1,19) = 6.356$, $p = 0.002$, $\eta_p^2 = 0.40$ (all other outcomes, $p > 0.10$). Follow-up analysis within each condition showed a significant Grammaticality \times Anterior/posterior interaction ($p < 0.001$, $\eta_p^2 = 0.50$) for agreement, which was due to violations eliciting a significant positivity in the posterior region, $F(1,19) = 17.586$, $p < 0.001$, $\eta_p^2 = 0.48$ (Agreement violation $M \mu V = 3.417$, $SE = 0.811$, 95% CI [1.721, 5.114], correct $M \mu V = -0.128$, $SE = 0.513$, 95% CI [–1.202, 0.946]; anterior region,

$p = 0.072$). Follow-up analysis for the tense condition showed a main effect of Grammaticality, $F(1,19) = 4.655$, $p = 0.044$, $\eta_p^2 = 0.20$, also due to a positivity in response to violations (Tense violation $M \mu V = 1.321$, $SE = 0.381$, 95% CI [0.523, 2.120]; correct $M \mu V = 0.259$, $SE = 0.445$, 95% CI [–0.673, 1.190]. Results for the left-handed group, in sum, indicate that morphosyntactic violations (agreement and tense) elicited a biphasic N400–P600 pattern (see [Fig. 1](#)).

2.1.3. ERPs in the RH FS+ group

ERP waveforms for the right-handed group with familial sinistrality are depicted in [Fig. 2](#). The midline ANOVA 300–500 ms pro-

duced a significant main effect of Grammaticality, $F(1,19) = 24.312$, $p < 0.001$, $\eta_p^2 = 0.56$, and significant Grammaticality \times Electrode interaction, $F(2,38) = 8.947$, $p = 0.005$, $\eta_p^2 = 0.32$. Follow-up analysis on the interaction showed that violations elicited stronger effects, at central and posterior than anterior sites, and in the form of more negative ERPs, i.e., an N400 effect: at Pz, $F(1,19) = 27.191$, $p < 0.001$, $\eta_p^2 = 0.59$ (Agreement violation $M \mu V = 1.189$, $SE = 0.719$, 95% CI $[-0.315, 2.269]$, correct $M \mu V = 1.590$, $SE = 0.537$, 95% CI $[0.466, 2.713]$; Tense violation $M \mu V = -2.952$, $SE = 0.439$, 95% CI $[-3.870, -2.033]$, correct $M \mu V = -2.172$, $SE = 0.532$, 95% CI $[-3.287, -1.058]$); at Cz, $F(1,19) = 25.335$, $p < 0.001$, $\eta_p^2 = 0.57$ (Agreement violation $M \mu V = 1.020$, $SE = 0.787$, 95% CI $[-0.628, 2.668]$, correct $M \mu V = 1.696$, $SE = 0.597$, CI $[0.446, 2.945]$; Tense violation $M \mu V = -2.955$, $SE = 0.413$, 95% CI $[-3.820, -2.090]$, correct $M \mu V = -1.561$, $SE = 0.408$, 95% CI $[-2.415, -0.706]$); at Fz, $F(1,19) = 4.559$, $p = 0.046$, $\eta_p^2 = 0.19$ (Agreement violation $M \mu V = 0.458$, $SE = 0.566$, CI $[-0.726, 1.642]$, correct $M \mu V = 1.696$, $SE = 0.643$, CI $[0.350, 3.042]$; Tense violation $M \mu V = -1.080$, $SE = 0.650$, CI $[-2.441, 0.280]$, correct $M \mu V = 0.401$, $SE = 0.707$, CI $[-0.1080, 1.882]$). This N400 effect was also reflected in lateral analysis, which produced a main effect of Grammaticality ($F[1,19] = 14.417$, $p = 0.001$, $\eta_p^2 = 0.43$) as well as Grammaticality \times Hemisphere ($F[1,19] = 23.697$, $p < 0.001$, $\eta_p^2 = 0.56$) and Grammaticality \times Anterior/posterior ($F[1,19] = 5.449$, $p = 0.031$, $\eta_p^2 = 0.22$) interactions. Follow-up analysis indicated the N400 was dominant in posterior, right hemisphere regions: posterior, $F(1,19) = 25.375$, $p < 0.001$, $\eta_p^2 = 0.57$ (n.s. in anterior); right hemisphere, $F(1,19) = 27.019$, $p < 0.001$, $\eta_p^2 = 0.59$ ($p = 0.054$ in left hemisphere). See Fig. 2.

In the 500–800 ms window, the midline ANOVA showed a main effect of Grammaticality, $F(1,19) = 4.752$, $p = 0.042$, $\eta_p^2 = 0.20$, as well as interactions for Grammaticality \times Electrode, $F(2,38) = 9.694$, $p = 0.002$, $\eta_p^2 = 0.34$, and Grammaticality \times Condition \times Electrode, $F(2,38) = 8.890$, $p = 0.003$, $\eta_p^2 = 0.32$. Follow-up analysis within each condition showed that agreement violations elicited a positivity at central-posterior regions: at Pz, $F(1,19) = 30.396$, $p < 0.001$, $\eta_p^2 = 0.62$ (Agreement violation $M \mu V = 5.430$, $SE = 0.828$, 95% CI $[3.697, 7.164]$; correct $M \mu V = 1.280$, $SE = 0.711$, 95% CI $[-0.208, 2.767]$); at Cz, $F(1,19) = 18.932$, $p < 0.001$, $\eta_p^2 = 0.50$ (Agreement violation $M \mu V = 3.940$, $SE = 0.777$, 95% CI $[2.313, 5.567]$, correct $M \mu V = 1.145$, $SE = 0.828$, CI $[-0.589, 2.878]$); n.s. at Fz. This pattern was also present in the tense condition, with slightly smaller F -values and effect sizes: at Pz, $F(1,19) = 14.644$, $p = 0.001$, $\eta_p^2 = 0.44$ (Tense violation $M \mu V = 2.548$, $SE = 0.579$, 95% CI $[1.336, 3.761]$, correct $M \mu V = -0.145$, $SE = 0.575$, 95% CI $[-1.348, 1.059]$); at Cz, $F(1,19) = 10.164$, $p = 0.005$, $\eta_p^2 = 0.349$ (Tense violation $M \mu V = 2.183$, $SE = 0.637$, 95% CI $[0.849, 3.517]$, correct $M \mu V = 0.228$, $SE = 0.526$, 95% CI $[-0.873, 1.330]$); at Fz $p = 0.055$. The lateral analysis also showed this P600 pattern, with the ANOVA showing significant interactions for Grammaticality \times Hemisphere ($F[1,19] = 14.549$, $p = 0.001$, $\eta_p^2 = 0.43$), Grammaticality \times Anterior/posterior ($F[1,19] = 8.484$, $p = 0.009$, $\eta_p^2 = 0.31$), and Grammaticality \times Condition \times Anterior/posterior ($F[1,19] = 7.649$, $p = 0.012$, $\eta_p^2 = 0.29$). Follow-up analysis with Hemisphere showed that the P600 was right-hemisphere dominant, $F(1,19) = 11.925$, $p = 0.003$, $\eta_p^2 = 0.39$ (n.s. in left hemisphere). Follow-up analysis within each condition indicated that agreement violations elicited a significant main effect in the posterior region ($F(1,19) = 24.242$, $p < 0.001$, $\eta_p^2 = 0.56$; n.s. at anterior). This was also true for the tense condition, with slightly smaller F -values and effect sizes: posterior, $F(1,19) = 12.278$, $p = 0.002$, $\eta_p^2 = 0.39$ (n.s. at anterior).

Thus, results for this right-handed group with familial sinistrality echo the results observed for the left-handed group: a biphasic N400-P600 pattern in response to morphosyntactic violations (see Fig. 2).

2.1.4. ERPs in the RH FS– group

ERPs for right-handers with no familial sinistrality are shown in Fig. 3. The midline ANOVA 300–500 ms showed a main effect of Grammaticality, $F(1,19) = 6.961$, $p = 0.016$, $\eta_p^2 = 0.27$, and Grammaticality \times Electrode interaction, $F(1,19) = 26.105$, $p < 0.001$, $\eta_p^2 = 0.58$. Follow-up analysis indicated that violations elicited more positive ERPs, in central-posterior sites: at Pz, $F(1,19) = 28.063$, $p < 0.001$, $\eta_p^2 = 0.60$ (Agreement violation $M \mu V = 1.073$, $SE = 0.566$, 95% CI $[-0.111, 2.257]$, correct $M \mu V = -0.176$, $SE = 0.393$, 95% CI $[-1.0, 0.647]$; Tense violation $M \mu V = -2.170$, $SE = 0.563$, 95% CI $[-3.348, -0.991]$; correct $M \mu V = -2.416$, $SE = 0.364$, 95% CI $[-3.178, -1.654]$); at Cz, $F(1,19) = 8.625$, $p = 0.008$, $\eta_p^2 = 0.31$ (Agreement violation $M \mu V = 0.369$, $SE = 0.675$, 95% CI $[-1.044, 1.782]$; correct $M \mu V = -0.663$, $SE = 0.550$, 95% CI $[-1.813, 0.488]$; Tense violation $M \mu V = -1.822$, $SE = 0.466$, 95% CI $[-2.797, -0.846]$, correct $M \mu V = -2.129$, $SE = 0.384$, 95% CI $[-2.933, -1.325]$; n.s. at Fz. This is the onset of the large P600 response in this group (see Fig. 3). The lateral analysis mirrored this midline pattern. The ANOVA showed a significant main effect of Grammaticality ($F[1,19] = 3.695$, $p = 0.070$, $\eta_p^2 = 0.16$) as well as a significant interaction for Grammaticality \times Hemisphere \times Anterior/posterior ($F[1,19] = 11.463$, $p = 0.003$, $\eta_p^2 = 0.38$). Follow-up analysis showed that the onset of the P600 was bilateral, but with some right-hemisphere dominance, as indicated by F -values and effect sizes: posterior, right-hemisphere, $F(1,19) = 24.555$, $p < 0.001$, $\eta_p^2 = 0.56$; posterior, left-hemisphere, $F(1,19) = 12.382$, $p = 0.002$, $\eta_p^2 = 0.40$.

In the 500–800 ms time window, the midline analysis showed significant interactions for Grammaticality \times Condition ($F[1,19] = 4.444$, $p = 0.049$, $\eta_p^2 = 0.19$) and Grammaticality \times Electrode ($F[2,38] = 12.261$, $p = 0.001$, $\eta_p^2 = 0.39$). Follow-up analysis within each condition showed that tense violations elicited stronger P600 effects than agreement, as indicated by F -values and effect sizes: Tense, $F(1,19) = 50.730$, $p < 0.001$, $\eta_p^2 = 0.73$ (Tense violation $M \mu V = 4.553$, $SE = 0.652$, 95% CI $[3.187, 5.918]$, correct $M \mu V = -0.670$, $SE = 0.389$, 95% CI $[-1.484, 0.143]$); Agreement, $F(1,19) = 28.391$, $p < 0.001$, $\eta_p^2 = 0.60$ (Agreement violation $M \mu V = 4.458$, $SE = 0.689$, 95% CI $[3.017, 5.900]$, correct $M \mu V = 0.792$, $SE = 0.539$, 95% CI $[-0.336, 1.920]$). Follow-up analysis at each midline site showed that the P600 was significant only at electrode Pz, $F(1,19) = 8.057$, $p = 0.011$, $\eta_p^2 = 0.298$ (n.s. at Cz and Fz). The lateral analysis also followed this pattern, with the ANOVA producing significant interactions for Grammaticality \times Condition ($F[1,19] = 7.011$, $p = 0.016$, $\eta_p^2 = 0.27$) and Grammaticality \times Anterior/posterior ($F[1,19] = 12.877$, $p = 0.002$, $\eta_p^2 = 0.40$) (There was also a marginally significant Grammaticality \times Hemisphere \times Anterior/posterior interaction, $p = 0.052$). Follow-up analysis within each condition again showed stronger P600 effects for tense ($F[1,19] = 47.543$, $p < 0.001$, $\eta_p^2 = 0.71$) than for agreement ($F[1,19] = 22.177$, $p < 0.001$, $\eta_p^2 = 0.54$) and in the posterior region only ($F[1,19] = 8.987$, $p = 0.007$, $\eta_p^2 = 0.32$; n.s. in anterior). Thus, results for this right-handed group with no familial sinistrality show that, rather than a biphasic N400-P600 response to morphosyntactic violations, these right-handers showed a robust monophasic P600 pattern (see Fig. 3).

Table 2

F-statistics from the grand average ANOVAs on mean amplitudes in the 300–500 ms and 500–800 ms time windows across the three Handedness groups.

	df	300–500 ms	500–800 ms
<i>Midline</i>			
Gram.	1, 57	–	80.139***
Gram. × Cond.	1, 57	–	–
Gram. × Electrode	2, 114	4.008*	61.988***
Gram. × Hand.	1, 57	4.694*	3.92*
Gram. × Cond. × Electrode	2, 114	–	8.261*
Gram. × Hand. × Cond.	1, 57	–	4.062*
Gram. × Hand. × Electrode	4, 114	–	–
Gram. × Hand. × Cond. × Elec.	4, 114	–	–
<i>Lateral</i>			
Gram.	1, 57	5.288*	62.687***
Gram. × Cond.	1, 57	–	–
Gram. × Hand.	2, 57	4.553*	3.373*
Gram. × Hand. × Cond.	2, 57	–	4.541*
Gram. × Hemi.	1, 57	10.756*	38.908***
Gram. × Hemi × Cond.	1, 57	–	–
Gram. × Hemi × Hand.	2, 57	3.613*	15.487***
Gram. × Hand. × Cond. × Hemi.	2, 57	–	–
Gram. × Antpost	1, 57	–	50.969***
Gram. × Cond. × Antpost	1, 57	–	17.546***
Gram. × Hand. × Antpost	2, 57	–	–
Gram. × Hand. × Cond. × Antpost	2, 57	–	–
Gram. × Hemi. × Antpost	1, 57	–	28.923***
Gram. × Cond. × Hemi. × Antpost	1, 57	4.710*	–
Gram. × Hand. × Hemi. × Antpost	2, 57	–	17.911***
Gram. × Hand. × Cond. × Hemi. × Antpost	2, 57	–	–

Note. Gram. = Grammaticality; Cond. = Condition; Hand. = Handedness group; Elec. = Electrode; Hemi. = Hemisphere; Antpost = Anterior/posterior; df = degrees of freedom. * $p < 0.05$; *** $p < 0.001$.

2.1.5. Comparing LH group with FS+ and FS– groups

To further examine how ERP patterns for the left-handed group compare with patterns for the two right-handed groups (FS+ and FS–), ANOVAs were conducted in each time window (300–500 ms and 500–800 ms) that included the factors Grammaticality, Condition, and Electrode as within-subjects factors and the two-level factor of Handedness (LH, RH FS+ in one set of ANOVAs; LH, RH FS– in the other set of ANOVAs). Lateral analysis contained the within-subjects factors of Grammaticality, Condition, Hemisphere, and Anterior/posterior. For reasons of brevity and clarity, here we report significant main effects of Grammaticality and significant interactions with Handedness, since each group's distributional effects are already reported in the preceding sections (Sections 2.1.2–2.1.4).

With respect to the LH and RH FS+ ERP effects, the midline ANOVA 300–500 ms showed a main effect of Grammaticality, $F(1,38) = 25.991$, $p < 0.001$, $\eta_p^2 = 0.41$. There were no significant interactions with Handedness: Grammaticality × Handedness, $p = 0.179$; Grammaticality × Condition × Handedness, $p = 0.954$; Grammaticality × Electrode × Handedness, $p = 0.328$; Grammaticality × Condition × Electrode × Handedness, $p = 0.925$. The lateral analysis also reflected this pattern with a main effect of Grammaticality ($F[1,38] = 18.256$, $p < 0.001$, $\eta_p^2 = 0.33$) as well as a four-way Grammaticality × Hemisphere × Anterior/posterior × Handedness interaction ($F[1,38] = 6.494$, $p = 0.015$, $\eta_p^2 = 0.15$), which was driven by the N400 in the RH FS+ being more right-lateralized (see above in Section 2.1.3).

In the 500–800 ms midline analysis the results showed a significant main effect of Grammaticality, $F(1,38) = 7.668$, $p = 0.009$, $\eta_p^2 = 0.17$, and no interactions with Handedness: Grammaticality × Handedness, $p = 0.821$; Grammaticality × Condition × Handedness, $p = 0.334$; Grammaticality × Electrode × Handedness, $p = 0.622$. Grammaticality × Condition × Electrode × Handedness, $p = 0.578$. The lateral analysis showed similar results with a main effect of Grammaticality ($F[1,38] = 7.402$, $p = 0.010$, $\eta_p^2 = 0.16$)

and Grammaticality × Hemisphere × Handedness interaction ($F[1,38] = 7.547$, $p = 0.009$, $\eta_p^2 = 0.17$), due to the right-lateralization of the P600 in the RH FS+ group (see above in Section 2.1.3).

Regarding the LH and RH FS– effects, the midline ANOVA 300–500 ms showed a main effect of Grammaticality, $F(1,38) = 12.699$, $p = 0.001$, $\eta_p^2 = 0.25$ with no interactions for Handedness: Grammaticality × Handedness, $p = 0.717$; Grammaticality × Condition × Handedness, $p = 0.644$; Grammaticality × Electrode × Handedness, $p = 0.125$. Grammaticality × Condition × Electrode × Handedness, $p = 0.737$. The effect of Grammaticality, while overall more negative for violations than correct items (violation $M \mu V = -1.628$, $SE = 0.257$; correct $M \mu V = -0.062$, $SE = 0.309$; due to the N400 in the LH group, see Section 2.1.2), was a positive effect (i.e., more positive to violations than correct) in the RH FS– group and a negative effect (i.e., more negative to violations than correct) in the LH group, see also Sections 2.1.2 and 2.1.4: in LH group, Agreement violation $M \mu V = -0.274$, $SE = 0.547$, Agreement correct $M \mu V = 0.096$, $SE = 0.493$, Tense violation $M \mu V = -2.196$, $SE = 0.498$, Tense correct $M \mu V = -1.435$, $SE = 0.383$; in RH FS– group, Agreement violation $M \mu V = 0.490$, $SE = 0.547$, Agreement correct $M \mu V = -0.560$, $SE = 0.493$, Tense violation $M \mu V = -1.362$, $SE = 0.498$, Tense correct $M \mu V = -1.519$, $SE = 0.383$. This effect of grammaticality reflects the onset of the P600 in the RH FS– group (see Section 2.1.4) and the N400 effect in the LH group (see Section 2.1.2). The lateral analysis showed a main effect of Grammaticality ($F[1,38] = 9.127$, $p = 0.004$, $\eta_p^2 = 0.19$), and a significant Grammaticality × Hemisphere × Anterior/posterior × Handedness interaction ($F[1,38] = 12.287$, $p = 0.001$, $\eta_p^2 = 0.24$), due to the slight right-hemisphere dominance of the P600 effect in the RH FS– group (see Section 2.1.4).

In the 500–800 ms time-window the midline ANOVA with LH and RH FS– groups showed a main effect of Grammaticality ($F[1,38] = 4.339$, $p = 0.044$, $\eta_p^2 = 0.10$) and a Grammaticality × Condition × Handedness interaction ($F[1,38] = 6.432$, $p = 0.015$,

$\eta_p^2 = 0.15$ (all other outcomes *n.s.*). This interaction was due to tense violations eliciting stronger P600 effects than agreement violations for the RH FS– group, as indicated by *F*-values and effect sizes, see Section 2.1.4. The lateral analysis showed a significant effect for Grammaticality ($F[1,38] = 5.616$, $p = 0.023$, $\eta_p^2 = 0.13$). This analysis also showed interactions for Grammaticality \times Condition \times Handedness ($F[1,38] = 8.026$, $p = 0.007$, $\eta_p^2 = 0.17$), due to the RH FS– group showing a stronger P600 for tense than agreement violations (with no such distinction in the LH group, see Sections 2.1.2 and 2.1.4), and a Grammaticality \times Hemisphere \times Anterior/posterior \times Handedness ($F[1,38] = 5.643$, $p = 0.023$, $\eta_p^2 = 0.13$) due to the marginal interaction for Hemisphere and Anterior/posterior observed in the RH FS– group (see Section 2.1.4).

To summarize, analyses conducted across the three handedness groups (Section 2.1.1) and those conducted in comparisons of the left-handers with each of the two right-handed groups (FS+, FS–, this section) as well as analyses conducted within each of the handedness groups (Sections 2.1.2–2.1.4) indicate that morphosyntactic violations elicited biphasic N400–P600 patterns in left-handers and right-handers with familial sinistrality, whereas the same violations elicited a monophasic P600 response in right-handers without familial sinistrality. In the following section, we examine whether these group-level patterns were sustained when considering individual-level ERP patterns.

2.1.6. Individual-level ERP analyses

Although at the group-level we observed biphasic N400–P600 patterns in the left-handed (self or familial) groups, biphasic patterns can often be an artefact of averaging across individuals who show predominantly N400 or P600 responses, rather than true biphasic responses uniformly within each individual (e.g., Tanner et al., 2014, 2013; Tanner and Van Hell, 2014; Osterhout, 1997). To examine patterns of individual variability across the three handedness groups, we calculated each participant's N400 and P600 effect magnitudes for the agreement and tense conditions. Effect magnitudes were calculated over a centro-parietal ROI that included electrodes C3, Cz, C4, CP1, CP2, P3, Pz, and P4 (where N400 and P600 effects are typically largest). We used these N400 and P600 effect magnitudes to then calculate each individual's relative response dominance for N400 or P600 effects for each of the two conditions. This calculation, called a Response Dominance Index (RDI), is made by fitting the individual's least squares distance from the equal effect sizes line (the dashed line in Fig. 4) with perpendicular offsets. The equation for calculating the RDI value is given in (1) below. An RDI value near zero indicates relatively equally-sized N400 and P600 effects, whereas a more negative value (above and to the left of the dashed line in Fig. 4) indicates that an individual is more N400-dominant in their processing of the target morphosyntactic structure. Conversely, a more positive value (below and to the right of the dashed line in Fig. 4) indicates a P600-dominant response (see also Tanner et al., 2014; Tanner and Van Hell, 2014).

$$(1) \text{RDI} = \frac{(P600_{\text{Ungrammatical}} - P600_{\text{Grammatical}}) - (N400_{\text{Grammatical}} - N400_{\text{Ungrammatical}})}{\sqrt{2}}$$

As can be seen from Fig. 4, which presents the RDI scatter plots of the three handedness groups, the RH FS– right-handers showed only a small amount of individual variability in response dominance, with nearly all participants being P600-dominant (below and to the right of the dashed line; Fig. 4) for the agreement and tense conditions. In contrast, both the LH and RH FS+ groups showed patterns of substantial variation that were similar for both groups, with a much larger proportion of individuals being

negativity-dominant (above and to the left of the dashed line; Fig. 4) than in the RH FS– group, though some individuals were positivity dominant in LH and RH FS+ groups as well. This demonstrates, on a descriptive level, that the FS+ right-handers show a similar pattern of individual variability as left-handers, and only in the FS– right-handers is individual variation in neural responses to morphosyntax remarkably low.

To investigate these RDI patterns in more detail, we conducted a 2×3 ANOVA with Condition as the within-subjects factor, Handedness as the between-subjects factor, and RDI values as the dependent variable. Results showed a main effect of Condition, $F(1,57) = 4.495$, $p = 0.038$, $\eta_p^2 = 0.07$, and a main effect of Handedness, $F(2,57) = 4.762$, $p = 0.012$, $\eta_p^2 = 0.14$; the Condition \times Handedness interaction was not significant ($p = 0.413$). The main effect of Condition was due to the RDIs for agreement being more positive than those for tense (Agreement RDI $M = 2.63$, $SD = 3.71$, 95% CI [1.66, 3.62]; Tense RDI $M = 1.52$, $SD = 3.42$; 95% CI [0.63, 2.35]).

Tukey HSD post hoc tests showed that the main effect of Handedness was driven by the following pattern. The RDI values for the RH FS– group ($M = 3.60$, $SE = 0.62$, 95% CI [2.35, 4.84]) were more positive than those for the RH FS+ group ($p = 0.013$) and marginally more positive than those for the LH group ($p = 0.071$); the RDI values for the two left-handed groups (RH FS+ and LH) were not different from each other ($p = 0.766$; RH FS+: RDI $M = 1.00$, $SE = 0.62$, 95% CI [–0.23, 2.25]; LH: RDI $M = 1.62$, $SE = 0.62$, 95% CI [0.37, 2.86]). In other words, the two left-handed groups (self and familial) were similar in their response dominance, and both groups were less positivity-dominant (either significantly or marginally) than the right-handers with no familial sinistrality. This effect of handedness accounted for approximately 14% of the variance in N400 or P600 response dominance. Note that this similarity in response dominance between LH and RH FS+ groups is also descriptively supported by the extensive overlap in 95% confidence intervals for RDI values in the LH and RH FS+ groups, whereas RDI confidence intervals overlap very little with the RH FS– group.

This RDI analysis highlights notable individual variation in N400- and P600-dominant individuals as a function of handedness. To further substantiate these differential patterns, we calculated grand average ERP waveforms for the sub-groups of individuals who showed N400-dominant or P600-dominant responses, for agreement and tense. Waveforms averaged across each sub-group are depicted in Fig. 5 (agreement) and Fig. 6 (tense). As can be seen, the grand average waveforms of N400-dominant individuals, when grouped, show large N400 effects while P600-dominant individuals show large P600 effects. Of note is that the N400-dominant sub-groups were composed predominantly of left-handed (self and familial) individuals – N400-dominant agreement sub-group: 6 LH, 6 RH FS+, 3 RH FS–; N400-dominant verb tense sub-group: 8 LH, 11 RH FS+, 2 RH FS– (remainder of participants were in the P600-dominant sub-groups). Overall, these sub-groups' grand mean ERP waveforms reinforce the patterns of individual variability and effects of handedness evidenced in the RDI outcomes (see Fig. 4), and show clear and differentiated ERP patterns at the sub-group level.

2.1.7. Relationships between behavioral and ERP outcomes

Recall that during EEG recording, all participants completed an acceptability judgment task. Although there were no group differences in behavioral performance on this task, i.e., for discriminating between grammatical and ungrammatical morphosyntactic violations (see Section 2.1), the ERP results covered in Sections 2.1.1–2.1.6 show significant differences in the neural correlates

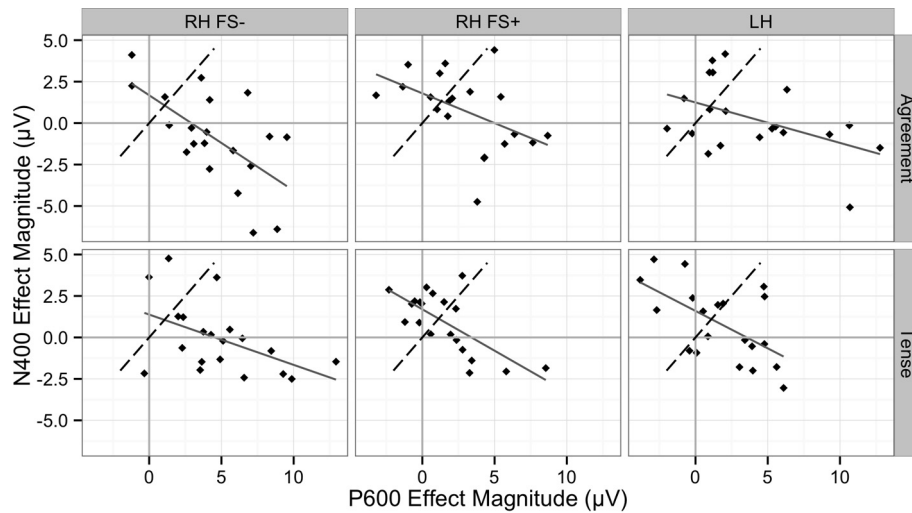


Fig. 4. Plots of individuals' N400/P600 response dominance in the RH FS–, RH FS+, and LH groups, separately for the agreement and tense conditions. Each point represents data from an individual, averaged over centro-parietal electrodes C3, Cz, C4, CP1, CP2, P3, Pz, and P4. The solid lines show the best-fit regression line relating individuals N400 and P600 effect magnitudes; the dashed lines reflect equal N400 and P600 effect magnitudes. Individuals above/to the left of the dashed lines are N400-dominant; individuals below/to the right of the dashed line are P600-dominant. RH FS– and RH FS+ data come from participants' originally tested by [Tanner and Van Hell \(2014\)](#).

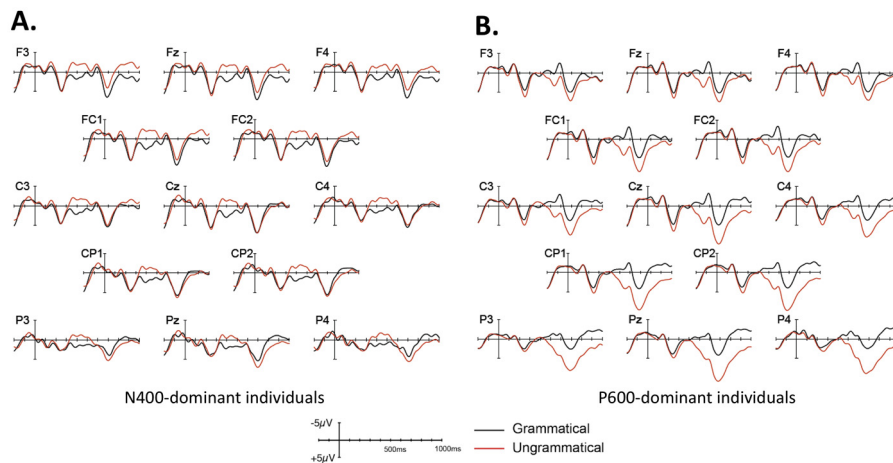


Fig. 5. Grand mean ERP waveforms for the agreement condition over 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the N400-dominant sub-group of individuals ($n = 15$) for agreement; panel B shows ERP responses in the P600-dominant sub-group ($n = 43$) for agreement.

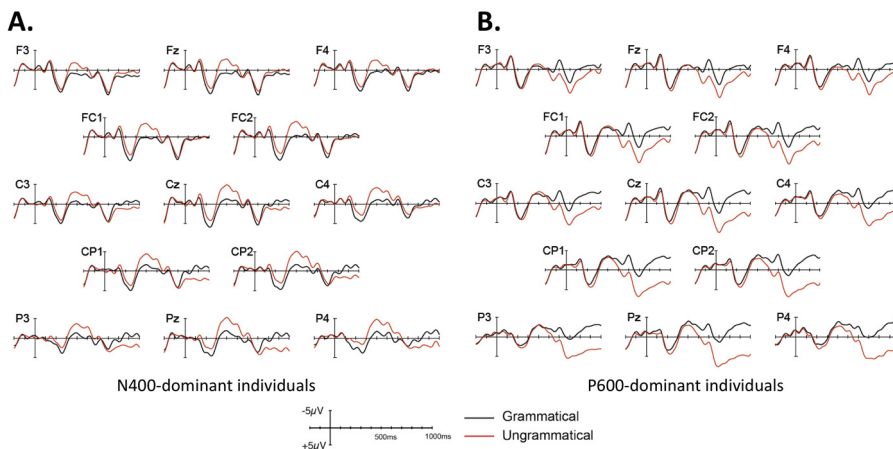


Fig. 6. Grand mean ERP waveforms for the tense condition over 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the N400-dominant sub-group of individuals ($n = 21$) for tense; panel B shows ERP responses in the P600-dominant sub-group ($n = 39$) for tense.

of morphosyntactic processing as a function of left-handedness (self or familial). To investigate whether behavioral performance was related to our individual-level ERP patterns, we ran correlations on the *d*-prime values with N400 and P600 effect magnitudes as well as RDI values for both agreement and tense in each handedness group (note that the small sample size of $n = 20$ in each group precludes drawing strong conclusions about correlations for any group). For the LH group, there was a significant positive correlation (two-tailed) between Tense *d*-prime and Tense P600 effect magnitude, $r = 0.456$, $p = 0.043$, as well as between Agreement *d*-prime and Agreement P600 effect magnitude, $r = 0.461$, $p = 0.041$. This indicates that the better left-handers were at discriminating between grammatical and ungrammatical morphosyntax, the larger their P600 response. In contrast, there were no significant correlations between *d*-prime performance and ERP outcomes for the two right-handed groups (all $ps > 0.10$). Similar positive relationships between better performance on sentence acceptability judgment and P600 effects have been observed in adult second language processing (e.g., Tanner et al., 2013; White et al., 2012) which, like left-handedness, is often associated with heterogeneity in language processing.

3. Discussion

In this study we examined grammatical processing in three groups of adults who differed in their handedness profiles: left-handers (LH), right-handers with at least one left-handed blood relative (RH FS+), and right-handers with no left-handed family members (RH FS–). Informed by theoretical predictions regarding the influence of handedness on grammatical processing and ERP research on language, we predicted that all three groups would show reliable P600s in response to morphosyntactic violations. This prediction was borne out in our results. Additionally, because left-handers and right-handers with familial sinistrality are hypothesized to show increased reliance on lexical/semantics for processing grammatical information (Bever et al., 1989; Townsend et al., 2001; Ullman, 2004; Ullman et al., 2017), we predicted that left-handers and right-handers with familial sinistrality would additionally show N400s (together with P600s) in response to morphosyntactic violations. This prediction was also borne out. Note that the qualitative differences observed in ERPs were found without any corresponding group differences in behavioral sensitivity during the sentence acceptability judgment task.

We additionally predicted increased inter-individual variability in N400/P600 response dominance across right-handers with familial sinistrality (in line with Tanner and Van Hell, 2014) and left-handers. This prediction was supported by our results for individuals' ERP patterns. The analyses of RDI values showed that the apparent biphasic N400-P600 patterns in the LH and RH FS+ groups were driven by heightened variation in N400 and P600 response dominance across participants, rather than consistent biphasic responses in all individuals in these two groups². Across the LH and RH FS+ groups, half of the participants showed N400-dominant responses to morphosyntactic violations and the other

half showed P600-dominant responses. In contrast, FS– right-handers exhibited remarkably little individual variation; nearly all participants in this group were P600-dominant.

These ERP results provide novel insights into the effects of left-handedness on grammatical processing. Previously, supporting evidence for effects of handedness has come from research that included only behavioral measures, or only groups of right-handers (Bever et al., 1989; Lee and Federmeier, 2015; Newman et al., 2014; Tanner and Van Hell, 2014; Townsend et al., 2001; Ullman et al., 2017). Our results demonstrate that the RH FS– individuals showed robust P600s to morphosyntactic violations and that this was consistent across RH FS– individuals, as illustrated with the RDI measure. This lends support to the hypothesis that these individuals rely heavily on or have better access to morphosyntactic mechanisms during grammatical processing (Bever et al., 1989; Hancock and Bever, 2013; Townsend et al., 2001; Ullman et al., 2017). In contrast, the LH and RH FS+ groups showed biphasic N400-P600 patterns which were found to arise from a much larger proportion of the left-handed individuals (both self and familial) showing N400-dominant responses during morphosyntactic processing. This supports an association between left-handedness and increased reliance on processes typically associated with accessing or integrating lexical/semantic information during sentence processing, even when the linguistic construction under consideration involves core morphosyntax (Bever et al., 1989; Hancock and Bever, 2013; Townsend et al., 2001; Ullman et al., 2017). It is important to note here that not all left-handers were N400-dominant: about half of the left-handers (self/familial) were P600-dominant, and showed evidence of relying primarily on cognitive mechanisms classically associated with morphosyntactic processing. Moreover, only in the left-handed group were P600 effect magnitudes significantly correlated with sentence acceptability judgment performance (note that the small sample size of $n = 20$ precludes drawing strong conclusions). Overall, the findings indicate that left-handers (self/familial) show a marked increase in variability regarding the extent to which they recruit morphosyntactic mechanisms compared to their non-left-handed (RH FS–) peers, and this is in line with research showing more variable patterns of language lateralization in these groups (Josse and Tzourio-Mazoyer, 2004; Knecht et al., 2000).

Previous ERP research on left-handers' linguistic processing has studied aspects of language other than morphosyntactic processing as studied here. In some cases, no electrophysiological differences were reported between left- and right-handers (e.g., for phonological processing: Barrett and Rugg, 1989; Rugg, 1985). However, ERP research on semantic processing has shown robust effects of handedness. For instance, Coulson and Lovett (2004) found that late positivities for joke comprehension were more bilaterally distributed in left-handers than in right-handers. Regarding familial sinistrality in right-handers, Kos et al., 2012 found that, although nearly all participants showed N400s to semantic violations, RH FS+ individuals were far less likely to show semantic P600 effects following the N400 than their RH FS– counterparts, suggesting less reliance on the mechanisms associated with P600 effects for right-handers with familial sinistrality. Additionally, in an earlier study on semantic processing, Kutas et al. (1988) found that RH FS+ individuals showed N400s that were more bilaterally distributed than RH FS– individuals, whose N400s exhibited right-hemisphere dominance. Finally, in a recent study on syntactic processing of word class using ERPs and the split visual field paradigm, Lee and Federmeier (2015) found that RH FS– individuals' P600 effects were unilaterally distributed to the left hemisphere whereas RH FS+ P600 effects were bilaterally distributed which indicates increased right hemisphere involvement during syntactic processing in right-handed familial sinistrals.

² Note that the observed negativity in the group-level biphasic response could be interpreted as a left anterior negativity (LAN). Biphasic LAN-P600 patterns have been argued by some researchers to be a hallmark of native morphosyntactic processing (e.g., Molinaro et al. (2011)). However, the analysis in Tanner and Van Hell (2014) demonstrated that what might be interpreted as a LAN-P600 response was instead driven by component overlap in the N400 and P600 responses across individuals (see Molinaro et al. (2015), Tanner (2015) for recent discussions of this issue). A key aspect of this discussion is that ERP component overlap makes interpreting the functional significance of scalp topography, for example in the lateralization of the LAN or bilateral posterior distribution of the N400, difficult, but a lengthy discussion of this topic is outside the scope of the present work.

The results from Kutas et al., 1988 and Kos et al., 2012 provide evidence for effects of handedness on semantic processing, and Coulson and Lovett's (2004) findings suggest that handedness affects higher-level language interpretations as well. The findings from our study support theoretical claims for the effects of handedness on grammatical processing and extend this literature by showing that handedness is a clear determinant of individual variability in grammatical processing: association with left-handedness (either self or familial) corresponded to increased variability in ERP responses and greater likelihood of showing an N400-dominant brain response to grammatical violations; that is, a greater likelihood of relying on lexical/semantic mechanisms while processing core morphosyntax. Furthermore, in the left-handed group only, the size of a P600 effect (the classic correlate of morphosyntactic processing) was related to better grammatical discrimination performance, suggesting that left-handers' overt ability to distinguish grammatical from ungrammatical morphosyntax was related to the magnitude of their morphosyntactic (P600-related) processing.

In this paper we have tested the effects of handedness on lexical/semantic versus grammatical mechanisms during comprehension, using N400 and P600 responses as indices of such mechanisms. There are, of course, various possible routes to successful comprehension, and heuristic versus algorithmic mechanisms are another explanation for how individuals achieve comprehension (e.g., Caramazza and Zurif, 1976; Dwivedi, 2013). Under such an explanation, then, one might speculate that left-handedness (self or familial) promotes greater variability among individuals in the extent to which they employ heuristic or algorithmic processes. Although current discussions of such comprehension processes do not address the possible influence of handedness, it would be interesting to see whether the patterns observed in the current study extend similarly to issues of heuristic versus algorithmic mechanisms.

More fundamentally, our pattern of findings provides an empirical basis for questioning the common tradition to exclude left-handers from neurocognitive language research. The group of left-handers in the present study added insight into both how handedness impacts language processing, as well as the types and range of normal variability in language processing in cognitively and neurologically intact individuals. As pointed out by Willems et al., 2014, and evidenced here, including left-handers in our scope of scientific inquiry has the potential to be highly informative for theoretical models on the neurocognition of language, and perhaps even transformative for language science research. In order to improve the explanatory reach of neurocognitive models of language – models which often ignore individual variability – more research on left-handers and FS+ and FS– right-handers is necessary.

In addition, our findings on right handers with and without left-handed family members indicate that right-handers as a group are less homogeneous than is commonly assumed in neurocognitive research, providing further evidence for robust individual differences in language processing in typically-developing and neurologically-healthy populations. As mentioned in the introduction, approximately 50% of right-handers have a left-handed blood relative and around 10% of the world is left-handed. Given that most neurocognitive studies on language have included only right-handers, this means that about half of a study's sample may have been more highly variable in their response patterns than the other half. In fact, by mixing and not distinguishing RH FS+ and RH FS– participants in a sample, researchers may be losing unique information that RH FS+ individuals could contribute to empirical and theoretical issues in cognitive neuroscience on language. Additionally, in our study the RH FS+ and LH individuals were not only found to be more

variable, but notably showed a highly similar distribution of variation. This suggests that more than half of language users may show systematic variation in language processing that remains largely unexplained in neurocognitive theories of language, and may be more like that of left-handers than of right-handers without left-handed family members.

Increasingly, research is demonstrating that there is substantial inter-individual variability in normal language processing and language development. Behavioral evidence has long shown that there are individual differences in normal child language development (e.g., Bates et al., 1995), and there is now evidence that even subtle cognitive differences have consequences for neurocognitive aspects of language comprehension, even among children who fall within the normal range on tests of cognitive and intellectual development (e.g., Hampton Wray and Weber-Fox, 2013). Moreover, there is mounting evidence for marked, systematic individual differences among adult populations that have previously been assumed to be largely homogeneous (e.g., Hancock and Bever, 2013; Pakulak and Neville, 2010; Prat and Just, 2011). The current study contributes to the growing body of evidence for this normal variation and shows that comprehensive neurocognitive models of language must incorporate a degree of flexibility to allow for individual differences such as those documented here and by others, though more research is needed to better understand the full extent and sources of such variation.

Crucially, understanding the range of variation and the factors that underlie it in 'typical' populations is critical in order for researchers to appropriately interpret language processing in special populations that are often characterized as deviating from the norm, for example in the case of child and adult second language learners, individuals with language disorders, aging populations, and, traditionally, left-handers. Our results underscore the fact that the language processing system is flexible and dynamic, and that there are multiple neurocognitive routes to successful language comprehension. The evidence provided here furthers our understanding of the range of variation in neurological healthy young adults, but it is important to note that there is an array of individual differences that must also be accounted for. Though we have provided compelling evidence of effects of handedness as an individual difference in language processing, moving forward it will be important to reconcile the relative contributions of handedness and other influential individual differences in language processing.

4. Experimental procedure

4.1. Participants

Participants were monolingual native English speakers at a large U.S. university. All participants had normal or corrected-to-normal vision and reported no history of neurological impairment. As is typical for neurocognitive language research, participants tested by Tanner and Van Hell (2014) were recruited to be right-handed ($n = 40$; confirmed by an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971). For the present study, we recruited and tested an additional group of 28 left-handers to compare to the right-handers from Tanner and Van Hell (2014). Data from eight participants in the left-handed group were excluded from analysis due to excessive artifact in the raw electroencephalogram (EEG) data, testing-session errors, or failure to follow task instructions. Of the 40 right-handers, 20 reported having a left-handed blood relative³, which resulted in 20 participants within

³ In the left-handers group, eight participants reported having a left-handed blood relative.

each handedness group: non-familial sinistrals (RH FS–; mean age = 19.3 years, range: 18–24, 6 male), familial sinistrals (RH FS+; mean age = 19.5 years, range: 18–35, 7 male) and left-handers (LH; mean age = 19.3 years; range: 18–35, 7 male) for a total of 60 participants included in data analysis.

4.2. Materials

The materials are the same as those used in [Tanner and Van Hell \(2014\)](#). The critical stimuli consisted of two target morphosyntactic structures: subject-verb agreement and verb tense (examples 2 and 3, * marks the point of ungrammaticality).

(2) The clerk at the clothing boutique was/*were severely underpaid and unhappy.

(3) The crime rate was increasing/*increase despite the growing police force.

There were 120 sentences in each target condition, 60 grammatical and 60 ungrammatical. The sentences were counter-balanced across four stimulus lists (Latin-square design) such that each participant saw 30 grammatical and 30 ungrammatical items for each condition but no participant saw two versions of the same sentence in a list. As illustrated in (2), in the agreement condition the sentence structure consisted of a singular noun followed by a prepositional phrase that agreed or disagreed in number with the single subject noun. In the tense condition, illustrated in (3), the sentence structure contained a progressive verb construction with the verb *be* plus a progressive participle or a bare verb stem. There were also 120 filler sentences. Sixty of the filler sentences were either ungrammatical agreement sentences that contained plural nouns in the embedded prepositional phrase, or matched correct sentences (30 of each) and sixty were either lexical/semantic violation sentences, or matched semantically correct sentences (30 of each). Therefore, each experimental list had a total of 240 sentences.

4.3. Procedure

Participants were tested in a single 2.5 h-long session. Following informed consent, each participant filled out a language history questionnaire and the Edinburgh Handedness Inventory ([Oldfield, 1971](#)). Participants were then seated in a comfortable chair in a sound-attenuated chamber and completed a sentence acceptability judgment task while EEG data were recorded.

For the sentence acceptability judgment task, participants were presented with the following instructions: “Your job is to read each sentence silently to yourself (i.e., don’t move your mouth) and decide if you think the sentence is acceptable in English or not. Some of the sentences you read will be good English sentences, and some will be either ungrammatical or have a meaning that is odd or completely implausible. An acceptable (or “good”) sentence is one that is grammatical and makes sense. A “bad” sentence is one that violates some rule of English or has a silly meaning and doesn’t make much sense.” Each trial in the task began with 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. After each sentence, a “Good/Bad?” prompt appeared on the screen and participants indicated with a

button press whether they thought the sentence was grammatical and semantically well-formed (good) or ungrammatical/nonsensical (bad). The response hand (left/right) for the “good” judgment was counter-balanced across participants. During this task, participants were encouraged to relax and read each sentence as naturally as possible; they were also asked to minimize movement and eye blinks while reading each sentence. Between trials participants could take as much time as they needed to blink or rest their eyes. Following this task, participants also completed a battery of memory and language measures that are not discussed here (for more details, see [Tanner and Van Hell, 2014](#)).

4.4. EEG data acquisition and analysis

All parameters for data acquisition and analysis followed those reported in [Tanner and Van Hell \(2014\)](#). Scalp EEG was recorded at a sampling rate of 500 Hz from 32 Ag/AgCl active electrodes (extended 10–20 system, [Jasper, 1958](#); mounted in an elastic cap, Brain Products ActiCap, Germany). EEG was amplified using a Neuroscan Synamps RT system; it was filtered online with 0.05–100 Hz bandpass and off-line with a 30 Hz half-amplitude low-pass filter (24 dB/octave roll-off). Scalp electrodes were referenced online to a vertex reference and re-referenced off-line to the average of activity recorded over the left and right mastoids. Additional electrodes were placed above and below the left eye and at the outer canthus of each eye, both referenced in bipolar montages, in order to screen for ocular artifacts. Impedances at all sites were kept below 10 k Ω .

ERPs, which were time-locked to the onset of the critical word for each sentence, were averaged off-line for both linguistic target conditions in each participant (200 ms prestimulus baseline). Data free of ocular and muscle artifacts were included in the analyses. A total of 5.2%, 4.5%, and 4.4% of trials were excluded due to artifacts in the LH, RH FS+, and RH FS–, respectively.

Author note

The study was conducted while the first author was a postdoctoral researcher at The Pennsylvania State University working with the first and second authors.

Acknowledgments

This data was presented at the 2015 meeting of the Cognitive Neuroscience Society. We thank Michael Ullman for providing information on the Declarative/Procedural model predictions for handedness. We also thank Paige Elinsky, Erika Exton, Sarah Fairchild, and Silviana Lee in the Bilingualism and Language Development lab at Penn State for their assistance in data collection for the left-handed group. We thank two anonymous reviewers for their valuable comments on this work. This research was supported by NSF SMA-1514276 to Sarah Grey and Janet G. van Hell, NSF BCS-1431324 to Darren Tanner, and NSF OISE-0968369, NSF BCS-1349110, and NSF OISE-1545900 to Janet G. van Hell.

Appendix A

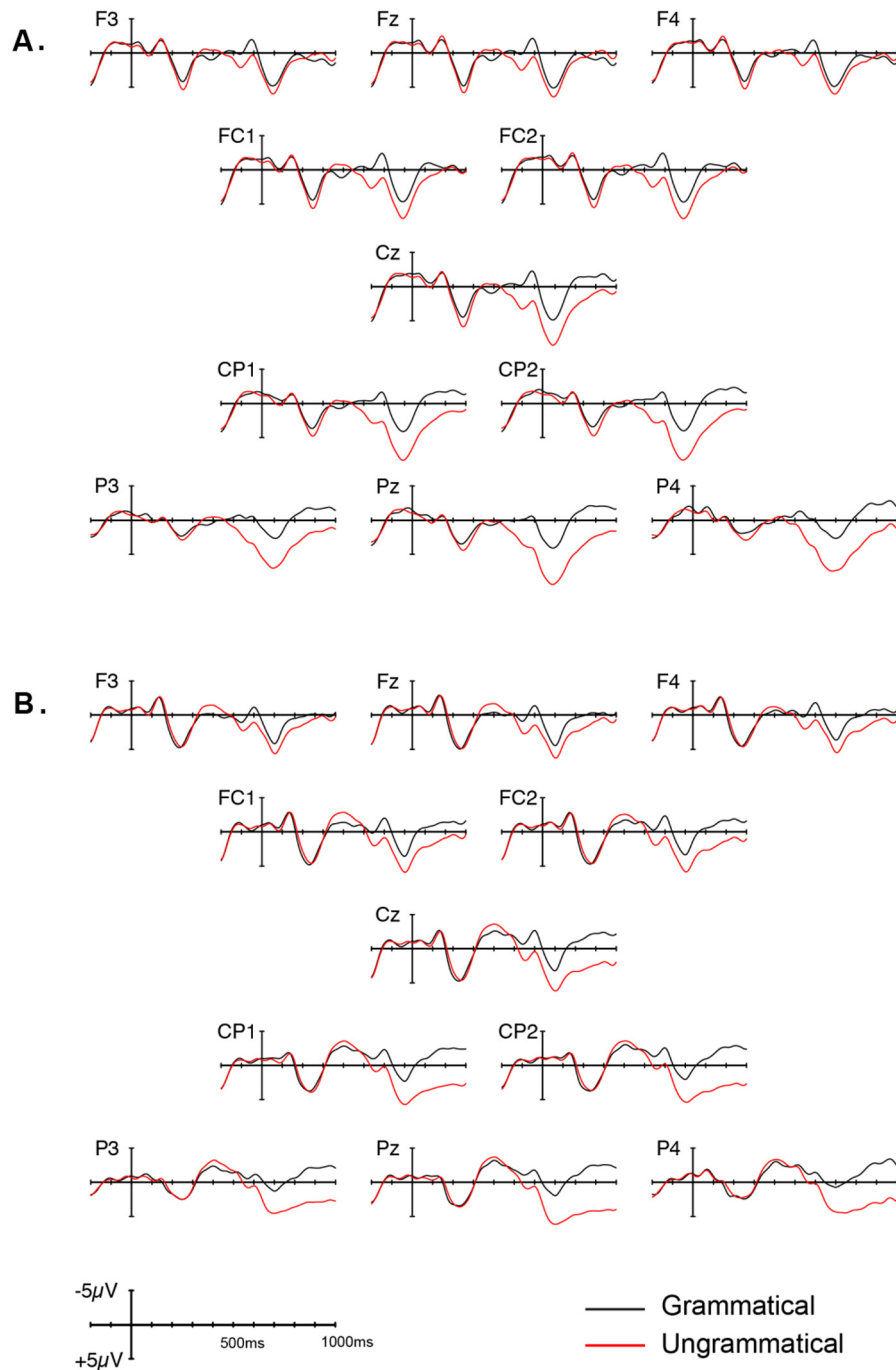


Fig. A1. ERP waveforms averaged from all of the participants ($N = 60$) across the three handedness groups. Figure depicts 11 representative electrode sites for grammatical (black line) and ungrammatical (red line) verbs. Panel A shows ERP responses in the agreement condition; panel B shows ERP responses in the tense condition. Waveforms depict 200 ms of prestimulus and 1000 ms of poststimulus activity. Onset of the critical verb is indicated by the vertical calibration bar. Negative voltage is plotted up.

References

- Allen, M., Badecker, W., Osterhout, L., 2003. Morphological analysis in sentence processing: an ERP study. *Lang. Cogn. Processes* 18 (4), 405–430.
- Barrett, S.E., Rugg, M.D., 1989. Asymmetries in event-related potentials during rhyme-matching: confirmation of the null effects of handedness. *Neuropsychologia* 27 (4), 539–548.
- Bates, E., Dale, P.S., Thal, D., 1995. Individual differences and their implications for theories of language development. In: Fletcher, P., MacWhinney, B. (Eds.), *The Handbook of Child Language*. Wiley-Blackwell, Oxford, UK, pp. 96–151.
- Bathurst, K., Kee, D.W., 1994. Finger-tapping interference as produced by concurrent verbal and nonverbal tasks: an analysis of individual differences in left-handers. *Brain Cogn.* 24 (1), 123–136.
- Bever, T.G., Carrithers, C., Cowart, W., Townsend, D.J., 1989. Language processing and familial handedness. In: Galaburda, A.M. (Ed.), *From Reading to Neurons*. MIT Press, Cambridge, MA, pp. 331–360.
- Bornkessel-Schlesewsky, I., Schlewsky, M., 2008. An alternative perspective on “semantic P600” effects in language comprehension. *Brain Res. Rev.* 59, 55–73.
- Caramazza, A., Zurif, E.B., 1976. Dissociation of algorithmic and heuristic processes in language comprehension: evidence from aphasia. *Brain Lang.* 3 (4), 572–582.
- Choudhary, K.K., Schlewsky, M., Roehm, D., Bornkessel-Schlesewsky, I., 2009. The N400 as a correlate of interpretatively relevant linguistic rules: evidence from Hindi. *Neuropsychologia* 47, 3012–3022.
- Chow, W.-Y., Phillips, C., 2013. No semantic illusions in the “Semantic P600” phenomenon: ERP evidence from Mandarin Chinese. *Brain Res.* 1506, 76–93.
- Coltheart, M., 2001. Assumptions and methods in cognitive neuropsychology. In: Rapp, B. (Ed.), *The Handbook of Cognitive Neuropsychology: What Deficits Reveal About the Human Mind*. Psychology Press, New York, pp. 3–21.

- Coulson, S., Lovett, C., 2004. Handedness, hemispheric asymmetries, and joke comprehension. *Cogn. Brain Res.* 19 (3), 275–288.
- Coulson, S., King, J.W., Kutas, M., 1998. Expect the unexpected: event-related brain response to morphosyntactic violations. *Lang. Cogn. Processes* 13 (1), 21–58.
- Debrulle, J.B., 2007. The N400 potential could index a semantic inhibition. *Brain Res. Rev.* 56, 472–477.
- Debrulle, J.B., Ramirez, D., Wolf, Y., Schaefer, A., Nguyen, T.-V., Bacon, B., Brodeur, M., 2008. Knowledge inhibition and N400: a within- and between-subjects study with distractor words. *Brain Res.* 1187, 167–183.
- DeLong, K.A., Quante, L., Kutas, M., 2014. Predictability, plausibility, and two late ERP positivities during written sentence comprehension. *Neuropsychologia* 61, 150–162.
- Dwivedi, V.D., 2013. Interpreting quantifier scope ambiguity: evidence of heuristic first, algorithmic second processing. *PLoS One* 8 (11), e81461.
- Frenzel, S., Schlesewsky, M., Bornkessel-Schlesewsky, I., 2011. Conflicts in language processing: a new perspective on the N400–P600 distinction. *Neuropsychologia* 49 (3), 574–579.
- Friederici, A.D., 2002. Towards a neural basis of auditory sentence processing. *Trends Cogn. Sci.* 6 (2), 78–84.
- Friederici, A.D., 2004. Event-related brain potential studies in language. *Curr. Neurol. Neurosci. Rep.* 4 (6), 466–470.
- Friederici, A.D., Mecklinger, A., 1996. Syntactic parsing as revealed by brain responses: first-pass and second-pass parsing processes. *J. Psycholinguist. Res.* 25 (1), 157–176.
- Friederici, A.D., Hahne, A., Saddy, D., 2002. Distinct neurophysiological patterns reflecting aspects of syntactic complexity and syntactic repair. *J. Psycholinguist. Res.* 31, 45–63.
- Friederici, A.D., Gunter, T., Hahne, A., Mauth, K., 2004. The relative timing of syntactic and semantic processes in sentence comprehension. *Neuroreport* 15 (1), 165–169.
- Grey, S., Van Hell, J.G., 2017. Foreign-accented speaker identity affects neural correlates of language comprehension. *J. Neurolinguist.* 42, 93–108.
- Hampton Wray, A., Weber-Fox, C., 2013. Specific aspects of cognitive and language proficiency account for variability in neural indices of semantic and syntactic processing in children. *Dev. Cogn. Neurosci.* 5, 149–171.
- Hancock, R., Bever, T.G., 2013. Genetic factors and normal variation in the organization of language. *Biolinguistics* 7, 75–95.
- Jasper, H.H., 1958. The ten-twenty system of the international federation. *Electroencephalogr. Clin. Neurophysiol.* 10, 371–375.
- Josse, G., Tzourio-Mazoyer, N., 2004. Hemispheric specialization for language. *Brain Res. Rev.* 44 (1), 1–12.
- Kaan, E., 2002. Investigating the effects of distance and number interference in processing subject-verb dependencies: an ERP study. *J. Psycholinguist. Res.* 31 (2), 165–193.
- Kaan, E., 2007. Event-related potentials and language processing: a brief overview. *Lang. Linguist. Compass* 1 (6), 571–591.
- Kee, D.W., Bathurst, K., Hellige, J.B., 1983. Lateralized interference of repetitive finger tapping: influence of familial handedness, cognitive load and verbal production. *Neuropsychologia* 21 (6), 617–624.
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., Henningsen, H., 2000. Handedness and hemispheric language dominance in healthy humans. *Brain* 123 (12), 2512–2518.
- Kolk, H., Chwilla, D., 2007. Late positives in unusual situations. *Brain Lang.* 100 (3), 257–261.
- Kos, M., van den Brink, D., Hagoort, P., 2012. Individual variation in the late positive complex to semantic anomalies. *Front. Psychol.* 3.
- Kuperberg, G.R., 2007. Neural mechanisms of language comprehension: challenges to syntax. *Brain Res.* 1146, 23–49.
- Kutas, M., Federmeier, K.D., 2011. Thirty years and counting: Finding meaning in the N400 component of the event-related brain potential. *Annu. Rev. Psychol.* 62, 621–647.
- Kutas, M., Hillyard, S.A., 1980. Event-related brain potentials to semantically inappropriate and surprisingly large words. *Biol. Psychol.* 11 (2), 99–116.
- Kutas, M., Van Petten, C., Besson, M., 1988. Event-related potential asymmetries during the reading of sentences. *Electroencephalogr. Clin. Neurophysiol.* 69 (3), 218–233.
- Lau, E.F., Phillips, C., Poeppel, D., 2008. A cortical network for semantics: (de)constructing the N400. *Nat. Rev. Neurosci.* 9, 920–933.
- Lee, C.-L., Federmeier, K.D., 2015. It's all in the family: brain asymmetry and syntactic processing of word class. *Psychol. Sci.* 26 (7), 997–1005.
- Macmillan, N.A., Creelman, C.D., 2005. *Detection Theory: A User's Guide*. Cambridge University Press, New York, NY.
- Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Percey, G., Tzourio-Mazoyer, N., 2014. Gaussian mixture modeling of hemispheric lateralization for language in a large sample of healthy individuals balanced for handedness. *PLoS One* 9 (6), e101165.
- 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 (6), 661–668.
- Molinero, N., Barber, H.A., Carreiras, M., 2011. Grammatical agreement processing in reading: ERP findings and future directions. *Cortex* 47 (8), 908–930.
- Molinero, N., Barber, H.A., Caffarra, S., Carreiras, M., 2015. On the left anterior negativity (LAN): the case of morphosyntactic agreement. *Cortex* 66, 156–159.
- Morgan-Short, K., Finger, I., Grey, S., Ullman, M.T., 2012a. Second language processing shows increased native-like neural responses after months of no exposure. *PLoS One* 7 (3), e32974.
- Morgan-Short, K., Steinhauer, K., Sanz, C., Ullman, M.T., 2012b. Explicit and implicit second language training differentially affect the achievement of native-like brain activation patterns. *J. Cogn. Neurosci.* 24 (4), 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. *J. Cogn. Neurosci.* 22 (12), 2886–2898.
- Neville, H.J., Nicol, J.L., Barss, A., Forster, K.I., Garrett, M.F., 1991. Syntactically based sentence processing classes: evidence from event-related brain potentials. *J. Cogn. Neurosci.* 3 (2), 151–165.
- Newman, S., Malaia, E., Seo, R., 2014. Does degree of handedness in a group of right-handed individuals affect language comprehension? *Brain Cogn.* 86, 98–103.
- Nieuwland, M.S., Van Berkum, J.J.A., 2006. When peanuts fall in love: N400 evidence for the power of discourse. *J. Cogn. Neurosci.* 18 (7), 1098–1111.
- Nieuwland, M.S., Otten, M., Van Berkum, J.J.A., 2007. Who are you talking about? Tracking discourse-level referential processing with event-related brain potentials. *J. Cogn. Neurosci.* 19 (2), 228–236.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9 (1), 97–113.
- Osterhout, L., 1997. On the brain response to syntactic anomalies: manipulations of word position and word class reveal individual differences. *Brain Lang.* 59 (3), 494–522.
- Osterhout, L., Mobley, L.A., 1995. Event-related brain potentials elicited by failure to agree. *J. Mem. Lang.* 34 (6), 739–773.
- Osterhout, L., Nicol, J., 1999. On the distinctiveness, independence, and time course of the brain responses to syntactic and semantic anomalies. *Lang. Cogn. Processes* 14 (3), 283–317.
- Osterhout, L., Kim, A., Kuperberg, G.R., 2012. The neurobiology of sentence comprehension. In: Spivey, M., Joannisse, M., McCrae, K. (Eds.), *The Cambridge Handbook of Psycholinguistics*. Cambridge University Press, Cambridge, pp. 365–389.
- Pakulak, E., Neville, H.J., 2010. Proficiency differences in syntactic processing of monolingual native speakers indexed by event-related potentials. *J. Cogn. Neurosci.* 22 (12), 2728–2744.
- Paradis, M., 1994. Neurolinguistic aspects of implicit and explicit memory: implications for bilingualism and SLA. In: Ellis, N.C. (Ed.), *Implicit and Explicit Learning of Languages*. Academic Press, London, pp. 392–420.
- Paradis, M., 2009. *Declarative and Procedural Determinants of Second Languages*, vol. 40. John Benjamins Publishing.
- Perelle, J., Ehrman, L., 1994. An international study of human handedness: the data. *Behav. Genet.* 24 (3), 217–227.
- Prat, C.S., Just, M.A., 2011. Exploring the neural dynamics underpinning individual differences in sentence comprehension. *Cereb. Cortex* 21 (8), 1747–1760.
- Pujol, J., Deus, J., Losilla, J.M., Capdevila, A., 1999. Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology* 52 (5), 1038–1038.
- Rugg, M.D., 1985. The effects of handedness on event-related potentials in a rhyme-matching task. *Neuropsychologia* 23 (6), 765–775.
- Silva-Pereyra, J.F., Carreiras, M., 2007. An ERP study of agreement features in Spanish. *Brain Res.* 1185, 201–211.
- Sommer, I.E.C., Ramsey, N.F., Mandl, R.C.W., Kahn, R.S., 2002. Language lateralization in monozygotic twin pairs concordant and discordant for handedness. *Brain* 125 (12), 2710–2718.
- Stanislaw, H., Todorov, N., 1999. Calculation of signal detection theory measures. *Behav. Res. Methods Instrum. Comput.* 31 (1), 137–149.
- Steinmetz, H., Volkman, J., Jäncke, L., Freund, H.J., 1991. Anatomical left-right asymmetry of language-related temporal cortex is different in left- and right-handers. *Ann. Neurol.* 29 (3), 315–319.
- Szaflarski, J.P., Binder, J.R., Possing, E.T., McKiernan, K.A., Ward, B.D., Hammeke, T.A., 2002. Language lateralization in left-handed and ambidextrous people fMRI data. *Neurology* 59 (2), 238–244.
- Tanner, D., 2015. On the left anterior negativity (LAN) in electrophysiological studies of morphosyntactic agreement. *Cortex* 66, 149–155.
- Tanner, D., Van Hell, J.G., 2014. ERPs reveal individual differences in morphosyntactic processing. *Neuropsychologia* 56, 289–301.
- Tanner, D., McLaughlin, J., Herschensohn, J., Osterhout, L., 2013. Individual differences reveal stages of L2 grammatical acquisition: ERP evidence. *Biling. Lang. Cogn.* 16 (2), 367–382.
- Tanner, D., Inoue, K., Osterhout, L., 2014. Brain-based individual differences in on-line L2 grammatical comprehension. *Biling. Lang. Cogn.* 17, 277–293.
- Tanner, D., Grey, S., van Hell, J.G., 2017. Dissociating retrieval interference and reanalysis during sentence comprehension: ERP evidence. *Psychophysiology* 54 (2), 248–259.
- Townsend, D.J., Carrithers, C., Bever, T.G., 2001. Familial handedness and access to words, meaning, and syntax during sentence comprehension. *Brain Lang.* 78 (3), 308–331.
- Ullman, M.T., 2001. The declarative/procedural model of lexicon and grammar. *J. Psycholinguist. Res.* 30 (1), 37–69.
- Ullman, M.T., 2004. Contributions of memory circuits to language: the declarative/procedural model. *Cognition* 92 (1–2), 231–270.
- Ullman, M.T., 2013. Declarative/procedural model of language. In: Pashler, H. (Ed.), *Encyclopedia of the Mind*. Sage Publications, Los Angeles, pp. 224–226.
- Ullman, M.T., 2015. The declarative/procedural model: a neurobiological model of language learning, knowledge, and use. In: Hickok, G., Small, S.A. (Eds.), *The Neurobiology of Language*. Elsevier, pp. 953–968.

- Ullman, M.T., Grey, S., Lovelett, J.T., Gelfand, M.P., Litcofsky, K.A., Pullman, M.Y., Moffa, M., Walenski, M., under revision. The influence of handedness on language: storage versus composition differences in left- and right-handers.
- Van Berkum, J.J.A., Brown, C.M., Hagoort, P., 1999. Early referential context effects in sentence processing: evidence from event-related brain potentials. *J. Mem. Lang.* 41 (2), 147–182.
- 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. *J. Cogn. Neurosci.* 22 (1), 67–82.
- Vissers, C.T.W., Kolk, H.H., Van de Meerendonk, N., Chwilla, D.J., 2008. Monitoring in language perception: evidence from ERPs in a picture – sentence matching task. *Neuropsychologia* 46 (4), 967–982.
- White, E.J., Genesee, F., Steinhauer, K., 2012. Brain responses before and after intensive second language learning: proficiency based changes and first language background effects in adult learners. *PLoS One* 7 (12), e52318.
- Wickens, T., 2002. *Elementary Signal Detection Theory*. Oxford University Press, Oxford.
- Willems, R.M., Van der Haegen, L., Fisher, S.E., Francks, C., 2014. On the other hand: including left-handers in cognitive neuroscience and neurogenetics. *Nat. Rev. Neurosci.* 15 (3), 193–201.