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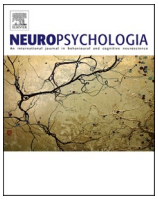

Patterns of hemispheric asymmetry provide evidence dissociating the semantic and syntactic P600

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ABSTRACT

To understand how neural networks in the left (LH) and right (RH) cerebral hemispheres contribute to different aspects of language comprehension, in two experiments we measured event-related potentials (ERPs) as right-handed participants read sentences, some of which contained morphosyntactic and thematic role violations. Replicating prior work (Kuperberg et al., 2006), in Experiment 1 thematic role violations elicited both an N400 and a (semantic) P600 effect. Morphosyntactic violations elicited effects that differed as a function of participants' familial sinistrality (the presence [FS+] or absence [FS-] of a left-handed biological relative): FS+ participants showed a (syntactic) P600 effect whereas FS- participants showed a biphasic N400 and P600 response. To assess whether this difference reflects different underlying patterns of lateralization, in Experiment 2 target words were presented using visual half-field (VF) presentation. Indeed, for morphosyntactic violations, the FS- group elicited an asymmetric pattern, showing a P600 effect only with LH-biased presentation and an N400 effect in both VFs (cf. Lee and Federmeier, 2015). In contrast, FS+ participants showed a bilateral (N400-only) response pattern. This provides further evidence of FS-based differences in hemispheric contributions to syntactic processing. Strikingly, we found that, when lateralized, thematic role violations did not elicit a P600 effect, suggesting that this effect requires contributions from both hemispheres. The different response patterns for morphosyntactic and thematic role animacy violations across FS and VF also point to a processing difference in the comprehension mechanisms underlying the semantic and syntactic P600, which had heretofore been assumed to be variants of the same component.

1. Introduction

Successful language comprehension requires the dynamic coordination of neural networks distributed across the two cerebral hemispheres. As evidence has accumulated that both hemispheres of the brain contribute to the comprehension of word and sentence-level meaning (e.g., Weems and Zaidel, 2004; review by Federmeier et al., 2008), new questions have arisen as to how processing differs across the two networks and what contributions are made by each hemisphere. Because language processing is rapid, and the critical processes for comprehension are often covert, event related potentials (ERPs) have proven an especially useful measure for addressing such questions, as they permit temporally precise, continuous monitoring of brain activity associated with comprehension, yielding functionally well-characterized dependent measures of various aspects of cognitive and linguistic processing. In particular, hemispheric asymmetries in comprehension can be revealed by recording brain activity in conjunction with the visual half-field (VF) paradigm, wherein stimuli are presented outside of foveal vision in either the left (LVF) or right visual field (RVF), biasing initial stimulus processing to the hemisphere contralateral to presentation VF (Beaumont, 1983).

Much of the ERP work on language lateralization has focused on semantic processing as revealed by effects on the N400, a negative-going component that peaks around 400 ms after stimulus onset and is known to index the access of semantic information (Kutas and Hillyard, 1980; reviewed in Kutas and Federmeier, 2011). This work has shown that both hemispheres rapidly access word meaning information in a manner that is shaped by context. However, the hemispheres differ in their use of information about language sequences and event structure (see review in Federmeier, 2022). For example, Federmeier and Kutas (1999) showed that the predictive preactivation of likely upcoming words and concepts during comprehension is associated with LH processing

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mechanisms (see also Federmeier, 2007). On the other hand, work by Metusalem et al. (2016) has highlighted the RH's sensitivity to the global event structure of discourse. These studies, and other work, show that the ERP/VF method can reveal both similarities and differences in the contributions of LH and RH networks to language comprehension.

Of course, language comprehension requires more than simply accessing meaning, as words and concepts must be linked together to form structured linguistic and conceptual representations. The processing of language syntax has been strongly linked to left-lateralized brain networks (Indefrey et al., 2001; Friederici et al., 2003; Tyler and Marslen-Wilson, 2008; Tyler et al., 2010). Indeed, studies measuring behavioral responses (e.g., lexical decisions) in VF paradigms have sometimes been taken to suggest that the RH is mostly insensitive to sentence structure (Arambel and Chiarello, 2006; Faust and Chiarello, 1998). However, results from some patient and fMRI studies have instead suggested that the RH may not only be capable of appreciating at least some aspects of syntax, but may also make unique contributions to the processing of some kinds of discourse structures and to the ability to repair certain grammatical errors or misparses (De Renzi et al., 1991; Meyer et al., 2000; Schneiderman and Saddy, 1988; Sherratt and Bryan, 2012).

In the ERP signal, syntactic processing has been linked to modulations on a post-N00, posteriorly-distributed positivity known as the P600. The P600 has been observed to a wide range of syntactic anomalies and dispreferred syntactic structures in multiple languages (e.g., Friederici et al., 1996; Hahne and Friederici, 1999; Kaan et al., 2000; Osterhout and Holcomb, 1992). Although the specificity of the P600 to language and to syntax more specifically is disputed (see discussion in Leckey and Federmeier, 2020), it provides a useful functional marker of structural processing difficulties in language. Therefore, to assess the ability of the two hemispheres to appreciate basic aspects of phrase structure, Lee and Federmeier (2015) presented young adults with two-word phrases, the second of which was lateralized. The phrases consisted of a function word (either 'to' or 'the') followed by a target, which was either a noun or a verb. These targets were either syntactically congruent ('to' paired with a verb, as in 'to go' or 'the' paired with a noun as in 'the sofa') or incongruent (paired with the incorrect function word: 'to sofa' or 'the go').[1] Given the large literature attesting to the LH's ability to appreciate syntax, Lee and Federmeier (2015) expected to see a P600 effect for incongruent versus congruent phrases when presentation was biased to the LH (i.e., in the RVF), and this was indeed the case. The key question, then, was whether the RH was also capable of eliciting this response. What Lee and Federmeier (2015) found was that the RH can elicit a P600, but that the tendency for it to do so is modulated by familial sinistrality.

Familial sinistrality separates those individuals who have at least one biological relative that is left-handed (FS+) from those who do not (FS-). It thus categorizes people (in the Lee and Federmeier study, all right-handed themselves) as a function of a possible genetic tendency toward left-handedness. Handedness and familial sinistrality have both long been linked to variability in patterns of language lateralization (e.g. Luria, 1970; McKeever and VanDeventer, 1977). Whereas people who are strongly right-handed are typically left lateralized for language functioning, left handers are less likely to be so (Knecht et al., 2000; Pujol et al., 1999), and people who show less of a hand preference in motor tasks also show a more bilateral pattern for speech representation (Flowers and Hudson, 2013). Similarly, among right-handed individuals, the presence of familial sinistrality has been associated with reductions in processing asymmetries (for a review, see Lee, 2018). Lesion studies have found that FS+ patients recover from language deficits associated with LH strokes more readily than do their FS- counterparts (Hecaen and Sauget, 1971), but, on the other hand, that they are also more likely to have linguistic deficits as a result of RH stroke damage (Brown and Hécaen, 1976), attesting to their higher likelihood to be RH dominant or bilateral in their language functioning (Annett, 1994). These differences in asymmetry have also been seen in neurally healthy individuals; for example, in a fMRI study using dichotic listening, FS+ participants showed more RH lateralization for language tasks than did FS- participants (Hund-Georgiadis et al., 2002). Similarly, in an imaging study that asked participants to listen to a story, the FS+ group showed reduced asymmetry in language areas compared to the FS– group (Tzourio-Mazoyer et al., 2010).

The results of the Lee and Federmeier (2015) study were consistent with this pattern, in showing an asymmetrical response pattern for the FS- group but a symmetrical one for the FS+ group. For FS- participants, the expected P600 effect was elicited only when initial processing was directed to the LH. The RH did respond differently to the grammatical and ungrammatical phrases, but showed only an N400 effect (more negative responses to the ungrammatical pairings compared to the grammatical ones) – a pattern that has sometimes been linked to lower proficiency (e.g., McLaughlin et al., 2010). Notably, however, for those who were FS+, P600 effects were observed bilaterally. These findings indicate that the RH is, under some conditions, capable of eliciting a P600 response.

This FS-based pattern of processing for phrase structure violations has been replicated in a pair of studies with Mandarin speakers, who read two-word phrases that consisted of a centrally presented syntactic cue for either a noun (classifier) or a verb (adverb) followed by the lateralized presentation of an unambiguous noun or verb. Again, FS- individuals as a group elicited an asymmetric response pattern, with a P600 effect seen only for violations presented in the RVF (N400 effects were observed in both VFs; Yeh et al., 2022). In contrast, FS+ individuals showed bilateral P600 effects (Weng and Lee, 2020). In both studies, analyses of individual differences showed that, in addition to the overall FS-based effect pattern difference, the size of the RH P600 effect within each group was predicted by the strength of interhemispheric inhibition, such that stronger inhibition yielded more asymmetric response patterns. This suggests that the hemispheres may share a similar capacity to appreciate phrase structure, but that the LH may tend to inhibit the RH during on-line processing, to a degree that is modulated by FS status. Further support for this view comes from a study using the materials and procedures from Lee and Federmeier (2015) with healthy older FS- adults, which found a bilateral P600 effect (Leckey and Federmeier, 2017). Thus, although FS- individuals do not elicit a RH P600 when young, changes that occur with normal aging seem to release that capability, perhaps because of age-related alterations in inhibition across the corpus callosum.

The impact of both familial sinistrality and age reveal that it isn't as simple as addressing whether or not the RH 'can' appreciate syntax; instead, by delineating the circumstances under which these capabilities are apparent, we can learn more about what processing in each network is like and the mechanisms involved in determining what networks are recruited by different comprehenders during normal processing. In turn, comparisons across different types of language structures can provide important insights into the similarity or differences in the neural networks involved in various aspects of language processing, As reviewed above, thus far studies looking at RH syntactic processing using ERPs have primarily focused on phrase structure. One additional study (Kemmer et al., 2014) examined the processing of grammatical number agreement. That study found that both hemispheres elicited P600s to number agreement errors on reflexive pronouns (i.e., errors that were lexically marked: 'the grateful niece asked themselves') but that there was a P600 response to morphologically marked violations (e.g., 'industrial scientists develops many new products') only in the RVF. The P600 pattern to these violations was thus similar to that seen for phrase structure violations in FS- individuals, but, as Kemmer et al. (2014) did not take FS status into account, more work is needed to be able to determine how consistent these patterns are across types of syntactic

[1] Throughout the paper, target words in examples are underlined and other manipulated words are italicized.

manipulations.

Beyond basic syntactic manipulations like phrase structure and agreement, there is a growing literature linking the P600 to aspects of processing that were initially thought to be more semantic in nature. The effect pattern that has come to be termed the "semantic P600" was first reported by Kuperberg et al. (2003) in a study that measured ERPs to verbs in normal control sentences (e.g., "For breakfast the boys would only eat toast and jam"), sentences with a pragmatic violation (e.g., "For breakfast the boys would only bury toast and jam"), and sentences with thematic role animacy violations (e.g., "For breakfast the *eggs* would only eat toast and jam"). Given that both violation types could be characterized as "semantic" in nature, the authors expected to observe a larger N400 at the critical verb in those sentences compared to controls. Pragmatic violations indeed elicited an N400 effect, but thematic role violations instead elicited a post-N400 positivity, with characteristics similar to the syntactic P600. This pattern was replicated in a subsequent experiment (Kuperberg et al., 2006) that also included a morphosyntactic violation condition (e.g., "For breakfast the boys would only eats toast and jam"). These morphosyntactic number agreement violations yielded the expected syntactic P600, which could then be compared within-subjects to the semantic P600, highlighting the similarity in timing and scalp distribution of these two positivities.

The semantic P600 has now been observed in a number of studies across multiple languages, often elicited using some kind of implausible thematic role assignment (Kim and Osterhout, 2005; Van Herten, Kolk and Chwilla, 2005; Stroud and Phillips, 2012; Chow and Phillips, 2013). A variety of theoretical perspectives on the nature of the semantic P600 have been put forward, emphasizing links to processes involved in integrating newly accessed information into the emerging mental model of the sentence (Brouwer et al., 2012) and/or adjudicating conflict among the representations built from multiple language processing streams, such as those involved in semantic versus combinatorial analyses (Kuperberg, 2007). What these and other theories (e.g., Bornkessel-Schlesewsky and Schlesewsky, 2008; Van Herten, Chwilla and Kolk, 2006) have in common is that they group the semantic and syntactic variants of the P600 together, assuming them to be the "same" component. Notably, this is an assumption that has not been empirically assessed (see discussion in Leckey and Federmeier, 2020), but that could be tested by looking at patterns of lateralization.

In the present paper, therefore, we provide this test in a pair of experiments, while also more generally examining how LH and RH networks are recruited during the processing of different language structures. We use the stimuli from the Kuperberg et al. (2006) study, focusing on morphosyntactic (number agreement) violations that would be expected to yield a syntactic P600 effect and thematic role animacy violations that elicit a semantic P600 effect.[2]

In Experiment 1, we replicate the Kuperberg et al. (2006) study in a sample that recruits both FS- and FS+ individuals, to assess if there are differences in the response patterns that are dependent on FS. Because in previous work with lateralized phrase structure violations (Lee and Federmeier, 2015; Yeh et al., 2022), it was the FS- group that showed asymmetric patterns (only N400 in the RH; P600 selective to the LH), we predicted that this group might be more likely to show a biphasic response pattern to the morphosyntactic violations in the present study. In Experiment 2, then, we again sample from both FS profiles while also lateralizing the target verb to probe hemispheric biases. If, as is typically assumed, the semantic and syntactic P600 are variants of the same component, then we should observe parallel impacts of FS and VS on the effect patterns for these violation types. Thus, for example, in the FS- group, we expect that the syntactic P600 to the morphosyntactic violations may be lateralized to the LH, as it was for the phrase structure violations in Lee and Federmeier (2015). Accordingly, if the same network underlies the semantic and syntactic P600, we should find an identical pattern of FS-based lateralization for the thematic role violations. Effects of familial sinistrality and, in Experiment 2, lateralization, thus provide a useful testing ground to see if these two language-related positivities do, indeed, consistently pattern together.

2. Methods, central presentation

2.1. Participants

ERP data were recorded from 54 young adult participants, recruited from the University of Illinois and the local community around Champaign-Urbana and either paid in cash or given class credit for their participation. All participants gave written informed consent prior to engaging in the study. Participants were all monolingual speakers of English, had normal or corrected-to-normal vision, and were screened for history of psychiatric disorders and serious head injury. They were all right-handed as assessed by the Edinburgh inventory (mean score 0.83; range 0.38–1; Oldfield, 1971). All participants completed a familial sinistrality assessment (Bishop, 1980) and were designated to one of two groups based on their resulting profile. The FS+ group was made up of participants who reported an immediate biological family member (parent, sibling, grandparent) who was left-handed (handedness assessment for FS+ group: mean score 0.86; range 0.38–1). The FS- group consisted of participants who reported exclusively right-handed biological relatives (handedness assessment for FS- group: mean score 0.81; range 0.48–1). Participants with family members who were ambidextrous or who had, at some point, been forced to write with their non-dominant hand were in not included in the sample. ERP data for 6 of the participants were excluded from analysis due to excessive artifact contamination. The final FS- group consisted of 24 participants (13 females and 11 males) with a mean age of 19.7 years (range 18–24) and the FS+ group was made up of 24 participants (15 females and 9 males) with a mean age of 19.9 years (range 18–29) .[3]

2.2. Materials

We used the materials from Kuperberg et al. (2006). These consisted of four sentence types. Control sentences, which contained no violations (e.g., 'After catching the ball, the boy would throw it very quickly.'), were used as a base to create three types of violations: thematic role animacy violations, non-thematic role pragmatic violations, and morphosyntactic violations. Thematic role animacy violations were created by replacing the animate noun with a contextually-related inanimate one (e.g., "After catching the ball, the *cheers* would throw it very quickly"). Morphosyntactic violations were produced by violating subject-verb agreement (e.g., "After catching the ball, the boy would throws it very quickly"). Finally, non-thematic role pragmatic violations were created by replacing the verb with a pragmatically anomalous one taken from a sentence within one of the other lists (e.g., "After catching the ball, the boy would choose it very quickly"). See Kuperberg et al. (2006) for more details about stimulus properties and norming. Using this sentence set, four lists were created, such that each sentence frame and critical verb appeared once per list, and, across lists, all verbs were used in all conditions. Participants were randomly assigned to one of the four lists.

[2] As in Kuperberg et al. (2006), pragmatic violations were also included. Based on prior work, these were expected to yield N400 effects in both FS groups and both hemispheres (see, e.g., Federmeier and Kutas, 1999; Kutas et al., 1988), and were thus of less theoretical interest. Results from this condition are presented in the Supplemental Materials.

[3] We thus increased the sample size for each FS group compared to the original Kuperberg et al. (2003, 2006) studies, which had 15 and 20 participants, respectively.

2.3. Procedures

Participants completed the experiment while seated 100 cm from a CRT monitor within an electrically shielded booth. They were given written and verbal instructions as to how to complete the task. A centrally positioned red square served as a fixation point to reduce lateral eye movements. Participants were asked to maintain fixation on this spot throughout the experiment and to minimize blinks during the time when the sentence appeared on the screen. Each sentence was preceded by a series of four plus signs appearing in the center of the screen for 500 ms to make participants aware that a trial was about to begin (see Fig. 1 for a schematic of the procedure). After a stimulus onset asynchrony (SOA) ranging randomly between 1000 and 1500 ms (to reduce the contribution of slow potentials to the average ERP), the sentence was presented in the center of the screen one word at a time. Each word was on the screen for 200 ms with an interstimulus interval of 300 ms. The order of presentation for the sentences was randomized with the constraint that no more than two of a particular sentence type would be presented consecutively.

To motivate participants to read attentively, we asked them to judge each sentence for global "correctness." After each sentence, the word "OKAY?" appeared in the center of the screen in red, and at this point the participant was asked to press a response button in one hand for "yes" if they felt that the sentence was error-free and a button in the other hand for "no" if they had detected any kind of error (i.e., in grammar or in meaning) at some point in the sentence. Designated response hand was counterbalanced across participants. The "OKAY?' prompt remained on the screen until a response was made with a button press. Following the response there was a further interval of 2500 ms to allow participants to relax and blink before the next trial began. To prevent tiredness and attentional lapses, the experiment was divided into four equal blocks, and participants were permitted to take a break between each of the blocks.

2.4. EEG recording parameters

The electroencephalogram (EEG) was recorded from twenty-six silver/silver-chloride electrodes attached to a cap that was placed on the head. The twenty-six electrodes were Midline Prefrontal (MiPf), Left and Right Medial Prefrontal (LMPf and RMPf), Left and Right Lateral Prefrontal (LLPf and RLPf), Left and Right Medial Frontal (LMFr and RMFr), Left and Right Mediolateral Frontal (LDFr and RDFr), Left and Right Lateral Frontal (LLFr and RLFr), Midline Central (MiCe), Left and Right Medial Central (LMCe and RMCe), Left and Right Mediolateral Central (LDCe and RDCe), Midline Parietal (MiPa), Left and Right Mediolateral Parietal (LDPa and RDPa), Left and Right Lateral Temporal (LLTe and RLTe), Midline Occipital (MiOc), Left and Right Medial Occipital (LMOc and RMOc), and Left and Right Lateral Occipital (LLOc and RLOc). All of these scalp electrodes were referenced on-line to the left mastoid and re-referenced off-line to the average of the right and the left mastoids. The vertical electrooculogram (EOG) was monitored by an electrode placed on the left infraorbital ridge and the horizontal EOG was monitored by two electrodes placed on the outer canthus of each eye. Electrode impedances were kept below 5 kΩ. The continuous EEG was amplified using Sensorium amplifiers through a bandpass filter of 0.02–100 Hz and recorded at a sampling rate of 250 Hz.

2.5. Data analysis

EEG data were screened for blocking, drift, lateral saccadic eye movements, and blinks, and contaminated trials were excluded from the analysis. Average artifact rejection percentage was 9.3% (range across groups and conditions 8%–11.5%) and an ANOVA with 2 levels of FS (FS- and FS+) and 4 levels of Sentence Type (control, pragmatic violation, morphosyntactic violation, thematic role violation) revealed no difference in artifact rejection rates as a function of group or condition. The data were separated into epochs, which began 200 ms before the onset of the target word and ended 1500 ms after onset. A digital bandpass filter of 0.2–20 Hz was applied to the data.

The primary ERP analysis was carried out on all artifact-free trials. However, to ensure that patterns were not dependent on whether participants did or did not judge the sentence to have contained an error, we also conducted follow-up analyses limited to sentences for which participants' classifications aligned with the experimental condition designations (i.e., control sentences with a "yes" judgment and violation sentences with a "no" judgment). In all cases except those delineated below, analyses on "correct" trials yielded identical patterns and statistical outcomes as those conducted on all trials (and are thus not separately described).

To ascertain the time windows and channels to be analyzed, we examined a single average across all violation types and FS groups. This revealed a spatially widespread negativity, which, as is typical for the N400, peaked around 400 ms after stimulus presentation. Thus, to characterize N400-like effects, we used an analysis window of 300 ms to 500 ms (which matches that used in Kuperberg et al., 2003, 2006) and included all 26 scalp channels.[4] Following the negativity, over posterior electrode sites there was a sustained positive-going response. This matches the P600 distribution typically reported in the literature; it is longer-lasting than the time window used by Kuperberg et al. but a similar, sustained response was found in Lee and Federmeier (2015). The P600 was thus measured from 500 to 1200 ms, using all 15 electrode sites posterior to the midline. Interactions with channel are not reported because they were not of theoretical significance (i.e., we treat each channel array as a single region of interest). ERP results for pragmatic violations, which were of less interest for this study, are reported in the Supplemental Materials.

3. Results, central presentation

3.1. Behavioral data

The behavioral task was implemented to increase the likelihood that participants would attend to the sentences and process them actively. As we are interested in comprehension processes that occur prior to (and that may not be dependent on) any overt response, the behavioral responses were not of particular theoretical interest in this series of studies, but the results are presented for completeness. Participants were fairly unlikely to say that they detected anything wrong with the control sentences, saying "no" to the "OKAY?" prompt only 9.7% of the time. In contrast, they much more often judged that there was an error in the violation sentences: Percentage of "no" responses was 68.3% for pragmatic violations, 86.3% for morphosyntactic violations, and 91.1% for thematic role animacy violations. Note that we did not expect participants to perfectly classify these sentences along experimenter-determined lines, given dialectical variability and the inherent subjectivity of acceptability judgments (especially for semantics). Nevertheless, the notable difference in classification rate between the control sentences and all types of violation sentences attests to participant attentiveness. Critically, the two groups were similar in their behavior: An ANOVA with 2 levels of FS (FS- and FS+) and 4 levels of Sentence

[4] Although negative-going effects in the 300–500 ms time window in response to various morphosyntactic violations are well-attested, there remain questions about whether these are best thought of as modulations of the N400 or of the Left Anterior Negativity (LAN), or whether both N400 and LAN effects are observed under different circumstances (see review by Molinaro et al., 2011). For the current study this distinction is not critical, and by using all scalp electrodes in our analyses in this time window we can capture effects whether they have a more frontal or a more centro-posterior distribution. For simplicity, we will use the label "N400", but when discussing this pattern we clarify that effects in this time window may reflect different kinds of influences.

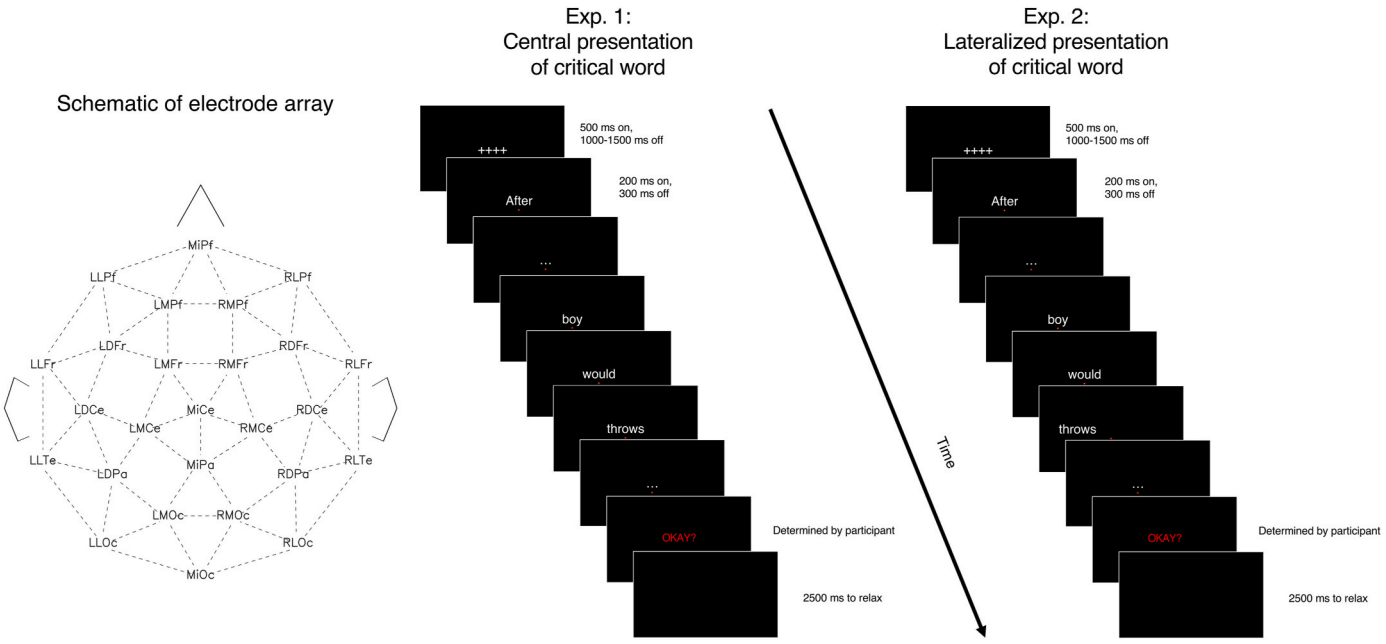

Fig. 1. (Left) Schematic of the array of the 26 electrodes used. (Right) Schematic of word-by-word presentation during the ERP experiment for Experiment 1, with central presentation of the critical word, and Experiment 2, with (left-)lateralized presentation of the critical word. The schematic demonstrates part of an example sentence from the morphosyntactic violation condition.

Type (control, pragmatic violation, morphosyntactic violation, thematic role violation) revealed a main effect of Sentence Type [$F_{(3, 138)} = 25.64$, $p < 0.001$] but no main effect of FS [$F_{(1, 46)} = 1.91$, $p = 0.17$] or interaction between FS and Sentence Type [$F_{(3, 138)} = 0.31$, $p = 0.73$].

3.2. ERP data

We examined responses to the morphosyntactic and thematic role animacy violations compared to controls in both an early (N400) and a later (P600) time window.[5] The original 2003 experiment by Kuperberg et al. found a P600 effect in response to the thematic role animacy violations (compared to controls). Using the same materials with the addition of morphosyntactic violations, Kuperberg et al. (2006) observed a biphasic N400/P600 response to the thematic role animacy violations and a P600 effect to the morphosyntactic violations.

Overall, in the N400 time window (300–500 ms), an ANOVA with 2 levels of FS (FS- and FS+) and 3 levels of Sentence Type (control, morphosyntactic violation, and thematic role violation) revealed a main effect of Sentence Type [$F_{(2, 92)} = 10.96$, $p < 0.001$]. There was no main effect of FS [$F_{(1, 46)} = 0.00$, $p = 0.97$] but there was an interaction of FS with Sentence Type [$F_{(2, 92)} = 7.43$, $p < 0.01$]. As detailed below, the interaction arose because the FS- group showed an N400-like effect (larger negativity to violations than control sentences) for both morphosyntactic and thematic role animacy violations, whereas the FS+ group showed this effect only for the thematic role animacy violations.

In the P600 time window (500–1200 ms), there was a main effect of Sentence Type [$F_{(2, 92)} = 120.93$, $p < 0.001$]. There was no main effect of FS [$F_{(1, 46)} = 0.33$, $p = 0.57$] and no interaction of FS with Sentence Type [$F_{(2, 92)} = 2.02$, $p = 0.14$]. As described next, both groups elicited a P600 to both violation types compared to controls.

3.2.1. Morphosyntactic violations vs. control sentences

N400 time window: In this time window, an ANOVA with 2 levels of FS (FS- and FS+) and 2 levels of Sentence Type (violation and control) showed no main effect of Sentence Type and no main effect of FS [F's < 2]. However, there was a significant interaction between the two variables [$F_{(1, 46)} = 12.99$, $p < 0.001$]. Pairwise comparisons indicate that this is driven by a significant main effect of Sentence Type in the FS- group [$F_{(1, 23)} = 9.54$, $p < 0.01$], in which the voltage in response to the violation is more negative (−0.2 μV) than that to the control (1.26 μV). This effect is numerically in the opposite direction (violations = 0.99 μV, control sentences = 0.34 μV) for the FS+ group [$F_{(1, 23)} = 3.53$, $p = 0.07$].

P600 time window: In the late time window, there was an effect of Sentence Type [$F_{(1, 46)} = 165.13$, $p < 0.001$], with the violation showing a more positive-going response (4.83 μV) than the control (0.27 μV). There was no effect of FS, nor was there an interaction between the variables [F's < 1], indicating that both groups responded similarly to this violation in this time window.

Summary: In the early window, the sentence type effect in the FS- group, with larger negativity to the violation, points to an N400-like effect for this violation type within this group. The same effect was not seen in the FS+ group, however. The large positivities seen for both groups in the late time window reflect a P600 response, which is in line with the Kuperberg et al. (2006) study. Thus, overall, the FS- group manifested a biphasic N400/P600 response to the morphosyntactic violations, whereas the FS+ group elicited only a P600 (Fig. 2).

3.2.2. Animacy violations vs. standard sentences

N400 time window: In the N400 time window, there was an effect of Sentence Type [$F_{(1, 46)} = 44.74$, $p < 0.001$], with a more negative-going voltage in response to the violation (−0.48 μV) compared to the control (0.8 μV). There was also a tendency for overall more negative voltages in the FS+ group (−0.13 μV) compared to the FS- group (0.45 μV) [$F_{(1, 46)} = 3.52$, $p = 0.07$]. In addition, there was a tendency toward an interaction between the two variables [$F_{(1, 46)} = 3.36$, $p = 0.07$] – although not for "correct" trials [$F_{(1, 46)} = 1.91$]. Follow-up comparisons on all trials showed effects of Sentence Type for both the FS- [$F_{(1, 23)} = 24.6$, p

[5] For a qualitative visualization of how each of these effects appears over time, topographical plots of each effect are provided in S1 for 100 ms time periods for central (Expt. 1) and lateralized (Expt. 2) presentations and for FS- and FS+ groups.

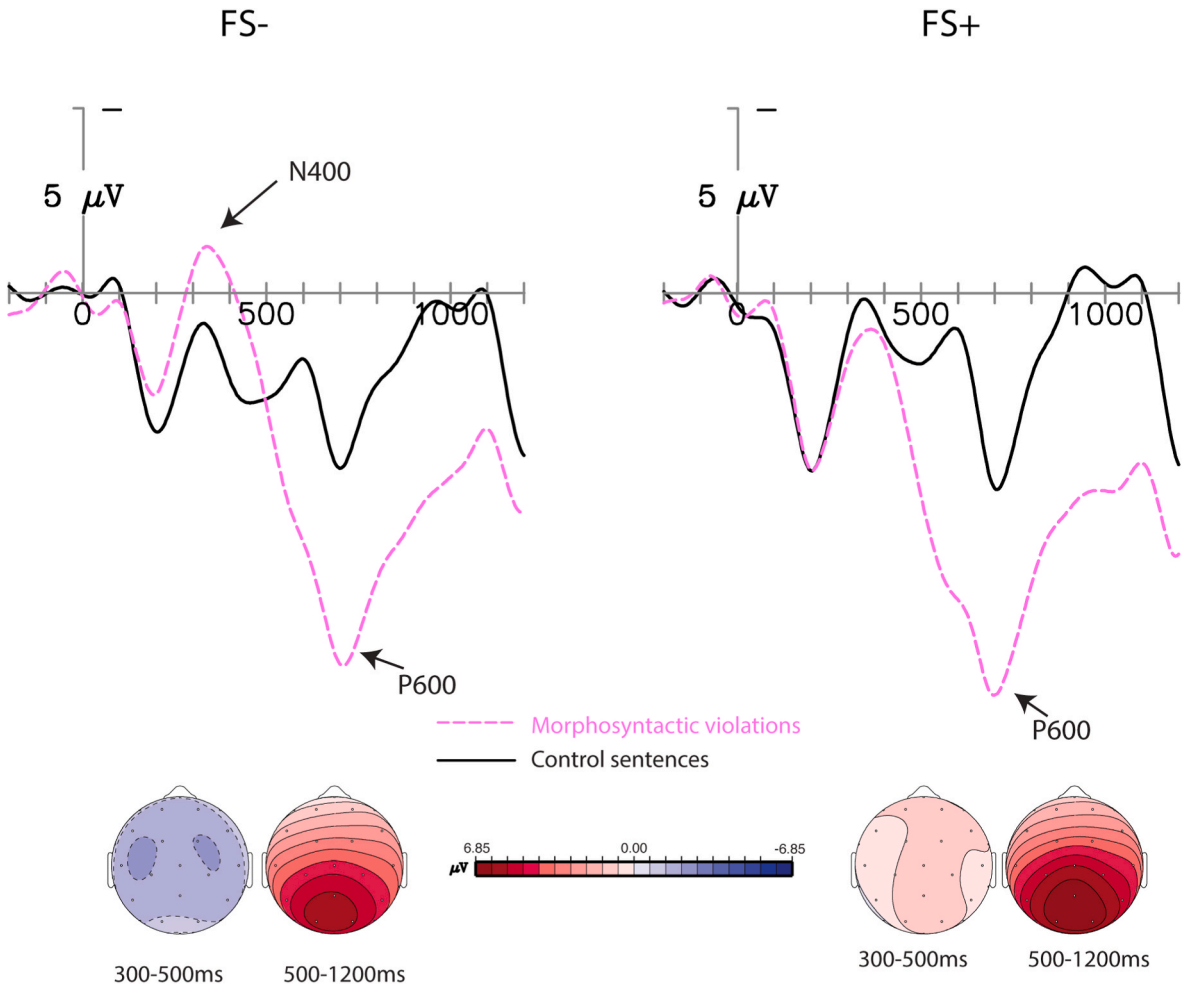

Fig. 2. Grand-averaged ERPs for each familial sinistrality group to all critical words in control sentences and those with morphosyntactic violations. FS- is shown to the left of the panel and FS+ is shown to the right. Waveforms plot ERPs recorded at a representative midline central electrode. Significant effects are indicated on the waveforms with an arrow. At bottom of the figure, head diagrams (seen from above, nose at top) show effect topography in the N400 (300–500 ms) and P600 (500–1200 ms) measurement windows.

< 0.001] and the FS+ group [$F_{(1,\ 23)} = 22.5$, $p < 0.001$], albeit a larger effect for the FS- participants (violation = −0.37 μV, control sentence = 1.26 μV) in comparison to the FS+ participants (violation = −0.59 μV, control sentence = 0.34 μV).

P600 time window: In the later time window, there was an effect of Sentence Type [$F_{(1,\ 46)} = 122.72$, $p < 0.001$], with a more positive voltage seen to the violations (2.68 μV) compared to the controls (0.27 μV). There was no effect of FS nor an interaction between the variables in this window for all trials [F's < 2.5], although, for "correct" trials there was a tendency for more positive voltages overall in the FS+ group [$F_{(1,\ 46)} = 4$, $p = 0.051$].

Summary: The more negative going response to the violation in the early time window is indicative of an N400-like effect to this violation type, and the marginal FS by sentence type interaction is suggestive that there might be a larger effect in the FS- group when compared with the FS+ group – a pattern similar to that seen for the morphosyntactic violations. The positive-going response in the late time window represents a P600 response from both groups to this violation (Fig. 3), and this again fits with the results of both original Kuperberg et al. papers (2003; 2006), which found a P600 effect for these thematic role animacy violations.

4. Interim discussion

Overall, ERP responses in Experiment 1 largely replicated the findings of Kuperberg et al. (2006). Thematic role animacy violations elicited differing patterns in the original Kuperberg et al. (2003), study (P600 only) and the 2006 follow up (N400/P600). Here, for both FS groups, we found biphasic responses consistent with those seen in the Kuperberg et al. (2006) study, the experiment for which the present study is a direct replication. This biphasic pattern has also been seen in other studies using this type of violation (e.g., Kuperberg et al., 2010). One possible explanation for the difference between the patterns across the two Kuperberg et al. studies is the inclusion of the morphosyntactic violations in both the Kuperberg et al. (2006) study and the present study. Because number agreement is marked with a single letter, participants may learn that they need to read more attentively to try to catch these errors (cf. effects of divided attention on N400 effects; Hubbard and Federmeier, 2021), and/or more generally the inclusion of this other error type may have changed comprehenders' approach to the task, which, at least in the case of agreement processing, has been shown to modulate the tendency to elicit biphasic responses versus only N400-like or P600-like patterns (reviewed in Molinaro et al., 2011).

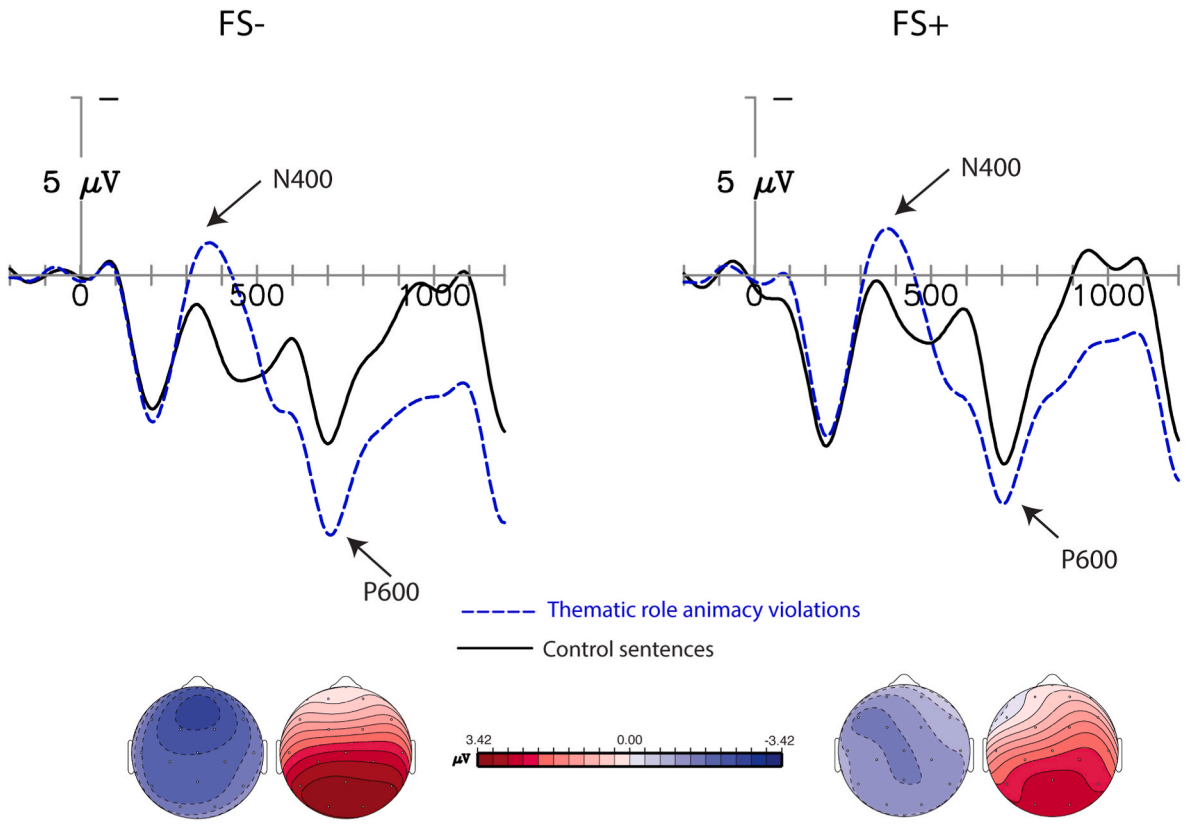

Fig. 3. Grand-averaged ERPs for each familial sinistrality group to all critical words from control sentences and those with thematic role animacy violations. FS- is shown to the left of the panel and FS+ is shown to the right. Waveforms plot ERPs recorded at a representative midline central electrode. Significant effects are indicated on the waveforms with an arrow. At bottom of the figure, head diagrams (seen from above, nose at top) show effect topography in the N400 (300–500 ms) and P600 (500–1200 ms) measurement windows.

For the morphosyntactic violations, Kuperberg et al. (2006) found just a P600 effect. That result was replicated in the current study, but only in the FS+ group. In the FS- group, we instead saw a biphasic N400/P600 effect to the violations, a pattern that is also attested in the larger literature (Molinaro et al., 2011). As described in the introduction, we expected that we might see this pattern of FS-based differences, extrapolating from the work looking at lateralization effects for phrase structure violations (Lee and Federmeier, 2015). In that study, FS+ individuals showed a P600 response pattern for stimuli biased to both the LH and the RH, predicting the possibility that their response to centrally-presented violations would also be just a P600. In contrast, the FS- group elicited a P600 effect only for LH-biased presentation. Responses with RH-biased stimulation showed just an N400-like effect. It is striking, then, that in the present study this group elicits a biphasic pattern, which includes both of these response types. Thus, it is possible that with central presentation we are observing the sum of different effect patterns elicited by the two hemispheres.

To further assess this possibility, Experiment 2 will again examine responses to morphosyntactic and thematic role animacy violations, but this time combining ERPs and VF presentation to preferentially stimulate each cerebral hemisphere, in order to allow for a direct look at lateralization patterns as a function of FS status. As reviewed earlier, prior work using ERPs to examine lateralized contributions to syntactic processing has focused on phrase structure. These studies (Lee and Federmeier, 2015; Weng and Lee, 2020; Yeh et al., 2022) found that FS- participants elicit different response patterns across the hemispheres, such that the P600 was elicited only for LH-biased processing. In contrast, consistent with more general patterns in the literature suggesting an increased prevalence of bilateral processing for FS+ individuals, bilateral P600 effects have been found for FS+ individuals in these studies. We would thus predict a similar pattern for the morphosyntactic violations in the present study (i.e., suggesting that the pattern attested in Kemmer et al. (2014) holds primarily for FS- individuals).

No prior study has examined lateralization patterns for thematic role violations. As discussed in the introduction, the semantic and syntactic P600s have, up to this point, been assumed to be the same component. This lateralized experiment thus provides an important first test of that assumption. If the components are the same, then there should be similar patterns as a function of VF and FS for both. If, however, the fact that, for example, the RH is especially sensitive to events means that it contributes differentially to processing the thematic structure of a sentence, then we might find some initial evidence that the two variants of the P600 are not identical in their eliciting conditions.

5. Methods, lateralized presentation

5.1. Participants

EEG data were collected from 66 young adult participants recruited from the student population of the University of Illinois at Urbana-Champaign, who were provided with class credit for their participation. All participants gave written, informed consent before beginning study procedures. Participants had normal or corrected-to-normal vision, were free of psychiatric or neurological disorders, and did not

have prior history of head injury or prolonged concussion. All were monolingual English speakers with no second language experience before the age of 5. Participants were all right-handed, as assessed by self-report and the Edinburgh inventory (overall mean score 0.8; range 0.44–1; Oldfield, 1971), and they were separated into familial sinistrality groups based on the criteria outlined for Experiment 1, as assessed by a familial sinistrality inventory (Bishop, 1980). ERP data for 2 of the participants were excluded from analysis due to excessive artifact contamination. The final FS- group consisted of 32 participants (24 females and 8 males) with a mean age of 19 years (range 18–22) and a mean handedness score of 0.84 (range = 0.5–1). The FS+ group was also made up of 32 participants (16 females and 16 males), with a mean age of 19 years (range 18–22); the mean handedness score for this group was 0.76 (range = 0.44–1).

5.2. Materials

Materials again consisted of sentences from Kuperberg et al. (2006), with half of each of the four sentence types assigned to each VF condition, counterbalanced across lists. Participants were randomly assigned to one of the eight lists. Within each of the lists, no sentence frame appeared more than once and, across lists, each critical verb was seen in each condition and each visual field an equal number of times.

5.3. Procedures

The procedure was the same as that in Experiment 1, except that the critical word in each sentence was presented at two degrees of horizontal visual angle to either the LVF or the RVF. The order of presentation for the sentences was randomized with the constraint that no more than two of a particular sentence type would be presented consecutively and no more than two sentences in a row had their target word lateralized to the same visual field.

5.4. EEG recording parameters

Recording parameters were the same as those described in Experiment 1.

5.5. Data analysis

The EEG data were screened for artifacts, including lateral saccadic eye movements, blinks, blocking and drift. Trials containing an artifact were excluded from further analysis (average rejection rate 18.2%; range 15.3%–21.7%); an ANOVA with 2 levels of FS (FS- and FS+) 2 levels of VF (RVF and LVF) and 4 levels of Sentence Type (control, pragmatic violation, morphosyntactic violation, thematic role violation) revealed no difference in artifact rejection rates as a function of group, VF, or sentence type. Epoch and baseline information are as in Experiment 1.

As in Experiment 1, the primary focus was on analyses using all trials, but we also conducted analyses limited to sentences for which participants' classifications aligned with the experimental condition designations (i.e., control sentences with a "yes" judgment and violation sentences with a "no" judgment). For those analyses, two participants were removed from each FS group due to having less than 10 artifact-free trials for one or more condition. We report analyses on correct trials only if they yielded different statistical outcomes from those conducted using all trials. The time windows and electrodes used in the analysis were the same as those for Experiment 1. For each time window, we used a mixed ANOVA with two levels of FS (FS+ and FS-), two levels of VF (RVF and LVF), 2 levels of sentence type (violation and control) and the appropriate number of electrodes for the time window (26 for the 300–500 ms window and 15 for the 500–1200 ms window, treated as a single region of interest).

6. Results, lateralized presentation

6.1. Behavioral data

As in Experiment 1, we used a judgment task to encourage participants' attention to the stimuli. We expected these judgments to be more difficult for participants in this experiment because the critical manipulations occur on a rapidly presented lateralized word. In particular, overt appreciation of the morphosyntactic violations might be especially difficult, as these violations are based on a single letter difference in the critical verb. However, as before, the behavioral responses are not of particular theoretical interest in this series of studies and are presented here to serve as an attention check.

Participants were again fairly unlikely to say that they detected anything wrong with the control sentences, saying "no" to the "OKAY?" prompt 17.3% of the time. In contrast, participants were more likely to report an error in all of the sentence types with violations: 72.6% for non-thematic role pragmatic violations, 77.6% for thematic role animacy violations and 48.6% for morphosyntactic violations. Thus, the pattern of discrimination performance attests that participants were attending to the stimuli.

To compare discrimination performance across FS status and VF, we used a mixed ANOVA with two levels of FS (FS+ and FS-), two levels of visual field (VF: RVF and LVF) and four levels of sentence type (control sentence, non-thematic role pragmatic violation, morphosyntactic violation, and thematic role animacy violation). In addition to the main effect of sentence type [$F_{(3,\ 186)} = 70$, $p < 0.0001$], there was also a main effect of VF [$F_{(1,\ 62)} = 33.99$, $p < 0.01$], as, consistent with past work (Coulson et al., 2005; Huang et al., 2010; Lee and Federmeier, 2015), explicit judgments were more likely to align with sentence condition following RVF (72.5%) compared to LVF (67.5%) presentation. This effect of VF interacted with sentence type [$F_{(3,\ 186)} = 5.6$, $p = 0.001$]. Follow-up analysis showed that participants were less likely to say that a control sentence had an error when the critical word was presented to the RVF (14%) as compared with the LVF (20.8%) [$F_{(1,\ 63)} = 23.18$, $p < 0.001$]. For morphosyntactic violations, participants were more likely to report the error when it appeared in the RVF (53%) than in the LVF (43.5%) ([$F_{(1,\ 63)} = 19.63$, $p < 0.0001$]. Judgment patterns were not reliably different across VF for either the non-thematic role pragmatic violations (RVF 73.2%, LVF 72%) or the thematic role animacy violations (RVF 79%, LVF 76.2%) [p's > 0.05]. As in Experiment 1, there were no differences in classification patterns between the FS groups (p's > 0.05).

6.2. ERP data

We again examined effects for the morphosyntactic and thematic role animacy violations compared to controls. As can be seen in Fig. 4, which shows the response from all participants (both FS groups combined) to the sentence types in order to provide a global picture of the effect of lateralization, both morphosyntactic and thematic role violations elicited a negativity in the 300–500 ms window compared to control sentences. However, responses in the P600 time window differed across these violation types. Morphosyntactic violations elicited a left-lateralized P600 effect in the overall data. Based on previous studies looking at the syntactic P600 with lateralized phrase structure violations (Lee and Federmeier, 2015; Weng and Lee, 2020; Yeh et al., 2022), we expect that this pattern may interact with FS, with FS- individuals

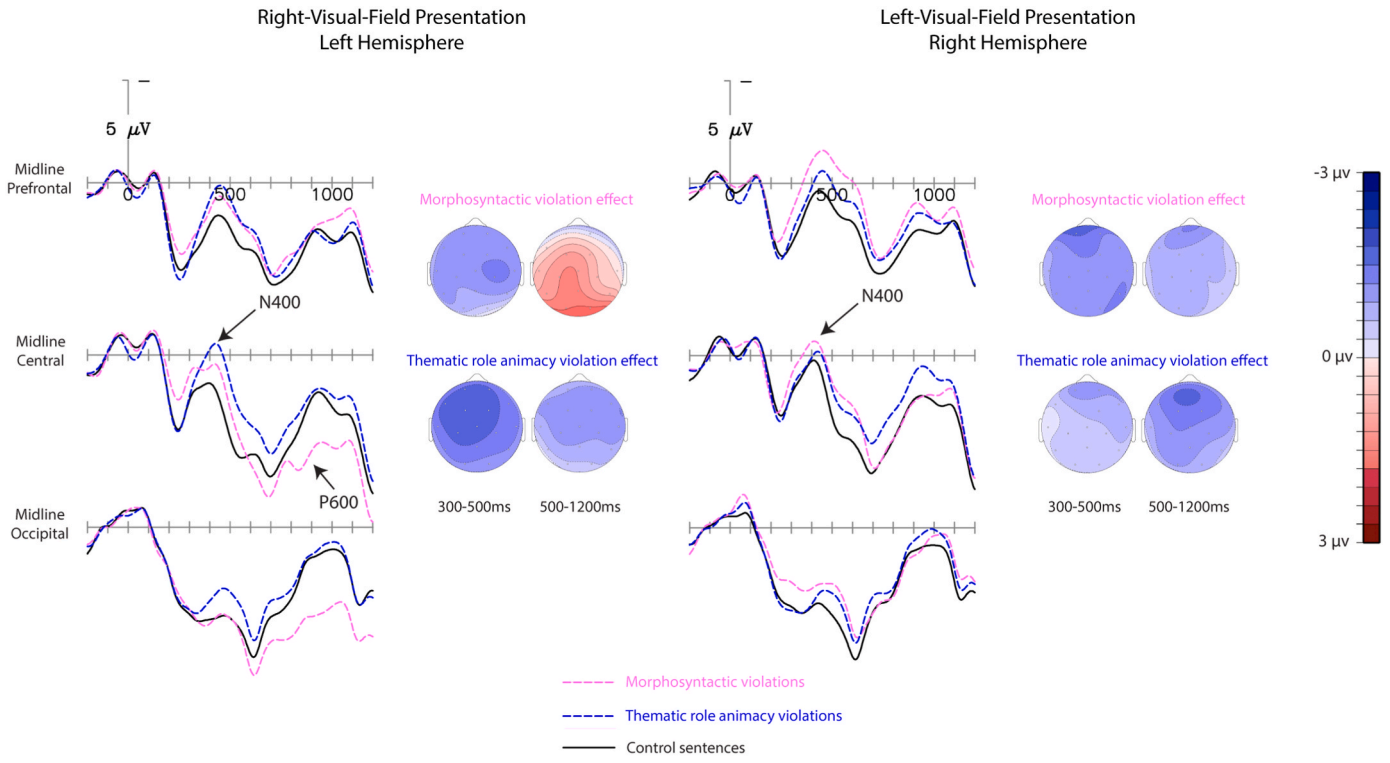

Fig. 4. Grand-averaged ERPs across all 64 participants to critical words from trials that were explicitly classified as being control sentences or violations (see Figs. 5 and 6 for ERPs plotted over all trials). Critical words from control sentences are overlayed with those that were morphosyntactic violations and animacy violations at three electrodes along the midline (prefrontal, central, occipital). Significant effects are indicated on the waveforms (at the midline central electrode) with an arrow. Next to the waveforms, head diagrams (seen from above, nose at top) show effect topography in the N400 (300–500 ms) and P600 (500–1200 ms) measurement windows for each type of violation.

showing a more lateralized response pattern. No prior study has examined the processing of thematic role animacy violations with lateralized presentation. The pattern in Fig. 4 suggests that the semantic P600 is not observed with either RVF or LVF presentation – and, thus, that it differs from the syntactic P600. Next, we present analyses taking both VF and FS into consideration for each violation type in the two time windows of interest.

6.2.1. *Morphosyntactic violations vs. control sentences*

N400 time window: There was a significant main effect of sentence type [$F_{(1,\ 62)} = 16.02$, $p < 0.001$] for this contrast, with more negative responses (larger N400) to the morphosyntactic violations (0.79 μV) than the control sentences (1.55 μV). There was no main effect of FS [$F < 1.5$] but there was a main effect of VF [$F_{(1,\ 62)} = 9.19$, $p < 0.01$] with overall more positive responses for RVF presentation (1.5 μV) compared to LVF presentation (0.8 μV). There were no significant interactions [F's < 2.2] between any of the three variables of interest (FS, VF, and sentence type) in the analysis for all trials, but the analysis for "correct" trials only showed a three way interaction [$F_{(1,\ 58)} = 4.55$, $p = 0.037$]. This pattern was driven by the fact that N400 effects were larger for RVF than for LVF presentation in the FS+ group but were larger for LVF than for RVF presentation in the FS- group (possibly because of overlap with the P600 effect, described next). However, both groups individually showed a reliable effect of sentence type (FS-: [$F_{(1,\ 29)} = 4.22$, $p = 0.049$]; FS+: [$F_{(1,\ 29)} = 6.35$, $p = 0.017$]).

P600 time window: In this time window, there was no main effect of sentence type or FS or interaction between them (F's < 1.8), but there continued to be a significant main effect of VF [$F_{(1,\ 62)} = 9.06$, $p < 0.01$], with overall more positive voltages for RVF presentation (2.68 μV) than for LVF presentation (2.09 μV). There was also a tendency for a sentence type x VF × FS interaction [$F_{(1,\ 62)} = 2.84$, $p = 0.09$]. To see if this reflected the same effect pattern seen in Lee and Federmeier (2015), we looked at sentence type and VF effects within each FS group.

For the FS+ group, a sentence type (morphosyntactic violation vs. control) x VF (RVF vs. LVF) x channel (15 posterior sites) repeated measures ANOVA yielded no main effects of sentence type or VF [F's < 2.2] and no interaction between the two [$F_{(1,\ 31)} = 0.07$]. As can be seen in Figure 5, in the FS+ group, responses to the violations did not differ notably from those to the control sentences, and, importantly, were very similar across VF. In contrast, when we performed the same ANOVA for the FS- group, a different pattern emerged. There was again no main effect of sentence type [$F_{(1,\ 31)} = 2.67$] but there was a main effect of VF [$F_{(1,\ 31)} = 7.77$, $p < 0.01$], with more positive voltages for RVF presentation (3.03 μV) than for LVF presentation (2.26 μV). Critically, there was also an interaction between VF and sentence type [$F_{(1,\ 31)} = 4.25$, $p = 0.048$]. A significant P600 response is seen to morphosyntactic violations compared to control sentences with presentation to the RVF ([$F_{(1,\ 31)} = 5.0$, $p = 0.033$]; violations = 3.57 μV, control sentences = 2.48 μV). However, this effect is not observed with presentation to the LVF ([$F_{(1,\ 31)} = 0.02$]; violations = 2.23 μV, control sentences = 2.28 μV). Thus, we replicate the pattern seen for the FS- group in both Lee and Federmeier (2015) and Yeh et al. (2022), with a syntactic P600 response limited to RVF presentation. Whereas Lee and Federmeier (2015) and Weng and Lee (2020) observed a bilateral P600 response for phrase structure violations in the FS+ group, we observed a bilateral N400-like effect (and no P600) for morphosyntactic violations in this group.

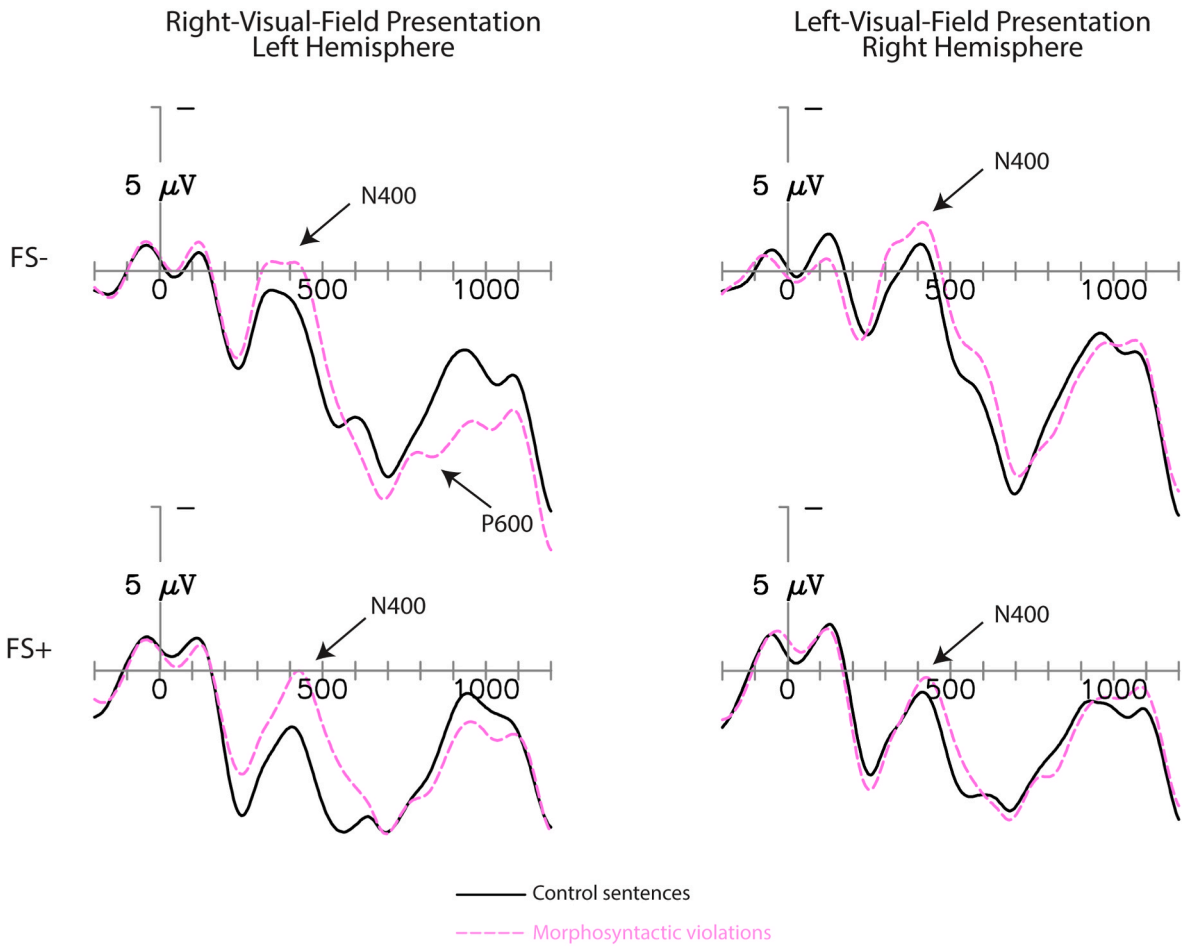

Fig. 5. Grand-averaged ERPs for each familial sinistrality group to all critical words from control sentences and those with morphosyntactic violations. FS- is shown at the top of the panel and FS+ is shown at the bottom. Waveforms plot ERPs recorded at a representative midline central electrode. Significant effects are indicated on the waveforms with an arrow.

Summary: Morphosyntactic violations elicited larger negativities in the 300–500 ms time window compared to control sentences in both VFs of both FS groups. In addition, these violations elicited a P600, but in a manner that was qualified by both FS group and VF of presentation (see Fig. 5). Like the pattern seen for phrase structure violations (Lee and Federmeier, 2015; Yeh et al., 2022), FS- participants elicited a biphasic response – including both an N400 and P600 effect – to the violations with RVF presentation, but only an N400 effect with LVF presentation. Thus, FS- individuals seem to respond similarly to morphosyntactic violations in the present study as to prior observations for phrase structure violations. FS+ participants, in contrast, showed a bilateral N400 response, and no P600 effect to this violation type. In all cases (Lee and Federmeier, 2015; Weng and Lee, 2020) FS+ participants show bilateral response patterns, but these seem differ for phrase structure violations (bilateral P600) and morphosyntactic (number agreement) violations (bilateral N400-like effects).

For the FS- group, the pattern of results here aligns with that seen in the centralized version in Experiment 1 and suggests that the biphasic N400/P600 response seen with central presentation could be the result of contributions from both hemispheres. However, the FS+ group shows divergent patterns across centralized and lateralized presentations. Whereas in the centralized version this group elicited a P600, when the stimuli were lateralized, the result was a bilateral N400. As will be discussed in more detail, this may suggest that, for this participant group, the two hemispheres must work in tandem to produce a P600 response to morphologically marked syntactic violations.

6.2.2. Animacy violations vs. standard sentences

N400 time window: There was an N400 effect for animacy violations compared to control sentences [$F_{(1, 62)} = 10.38$, $p < 0.001$], with more negative responses to the violations (0.91 μV) compared to the control sentences (1.55 μV). There was no main effect of FS [$F_{(1, 62)} = 2.24$] but there was a main effect of VF [$F_{(1, 62)} = 7.49$, $p < 0.01$], with overall more positive responses for RVF presentation (1.5 μV) compared to LVF presentation (0.95 μV). There were no interactions between any of the three main variables [F's < 1.2], although there was a tendency for larger effects in the RVF (control: 2.0 μV; violation: 1.0 μV) than in the LVF (control: 1.1 μV; violation: 0.8 μV) [$F_{(1, 62)} = 2.95$, $p = 0.09$]. Analyses on "correct" trials yielded the same pattern, but with no main effect of VF [$F_{(1, 58)} = 2.67$] or trend toward a VF by sentence type interaction [$F_{(1, 58)} = 1.75$].

P600 time window: There was a tendency for the effect pattern present in the N400 time window (more positive voltages to control sentences than to violations) to continue into this window [$F_{(1, 62)} = 3.53$, $p < 0.065$]. Otherwise, there were no main effects or interactions for the variables of interest [F's < 2.2].

Summary: There was a bilateral negativity in the 300–500 ms time window for both FS groups (as can be seen in Fig. 6). However, there was

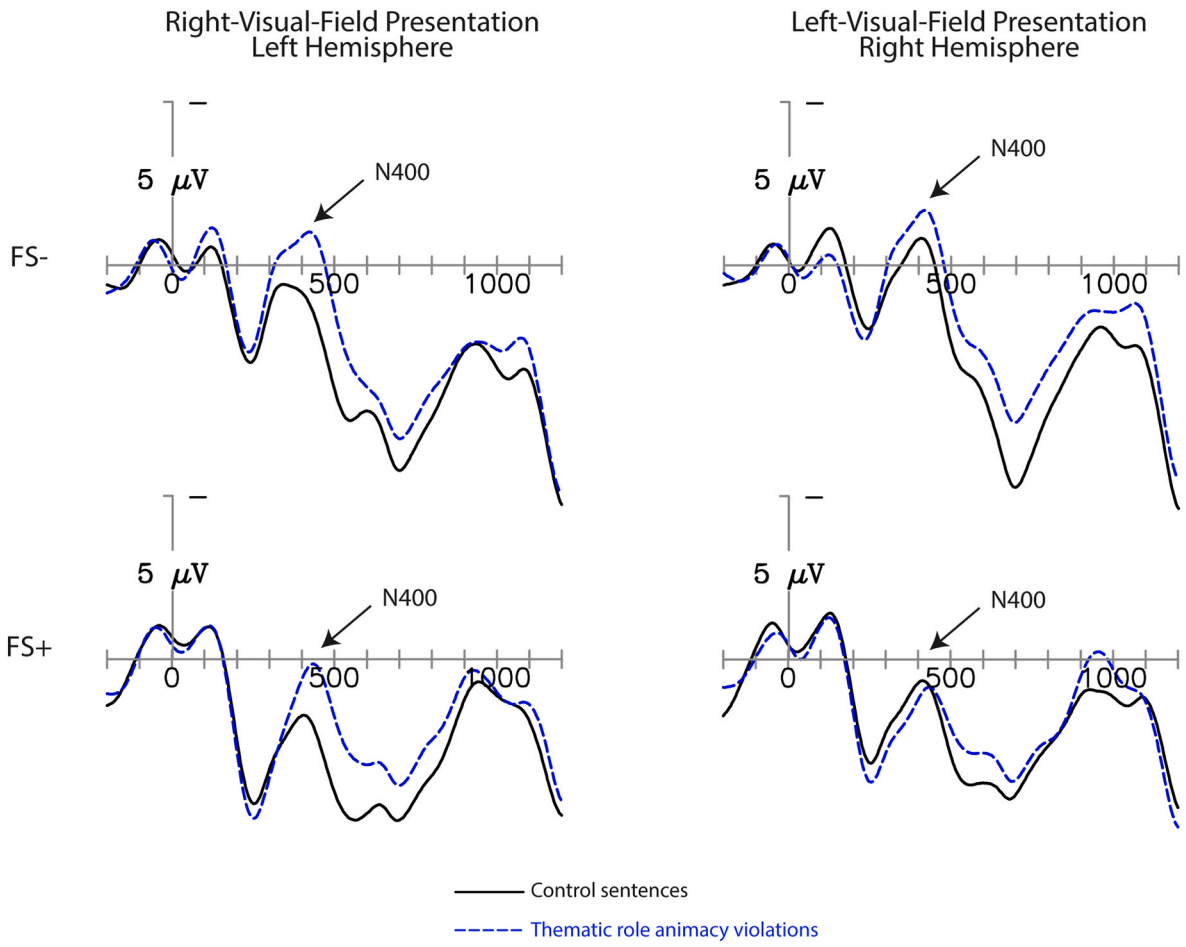

Fig. 6. Grand-averaged ERPs for each familial sinistrality group to critical words from all sentences with thematic animacy violations and all control sentences. FS- is shown at the top of the panel and FS+ is shown at the bottom. Waveforms show ERPs recorded at a representative midline central electrode.

no indication of a P600 response in either hemisphere of either group. This notably contrasts with the pattern that has consistently been seen to these violations with centralized presentation, including the pattern we observed in Experiment 1. Critically, it also contrasts with the pattern seen for the morphosyntactic violations, showing a dissociation between the syntactic and semantic P600s.

7. General discussion

Across two experiments, we sought to assess the contributions of left and right hemisphere networks to various aspects of language processing. We measured ERP responses to morphologically marked number agreement violations, which typically elicit a syntactic P600 effect, and to thematic role animacy violations, which typically elicit a semantic P600 effect. Violations were presented both in central vision (in Experiment 1) and with visual half-field presentation (in Experiment 2), and in both experiments we recruited participants with differing familial sinistrality profiles. There is a relatively established literature using ERPs, especially the N400, to examine the contributions of the two hemispheres to the processing of lexico-semantic information. However, few prior studies have examined the lateralization of syntactic processing, as indexed by the syntactic P600; our work using morphosyntax builds on research that highlighted differences in laterality based on FS profile for the processing of phrase structure (Lee and Federmeier, 2015; Weng and Lee, 2020; Yeh et al., 2022). No prior work has examined the processing of thematic role information in the context of FS or hemispheric differences. In doing so, the current study not only extends our understanding of each hemisphere's language processing capabilities but also offers a critical test of the assumption that the syntactic and semantic P600 are the same component – as, if true, they should show similar patterns of sensitivity to VF and FS.

For the morphosyntactic (number agreement) violations, in the centralized Experiment 1, responses differed based on FS profile, with both groups eliciting a P600 but only the FS- group showing an N400 effect as well. When the critical word was lateralized in Experiment 2, the results also differed according to FS group. The overall pattern replicated the findings of Kemmer et al. (2014), such that a P600 effect was seen only with initial presentation to the left hemisphere. However, our study further showed that elicitation of that LH P600 varies with FS. The FS- group replicated the pattern seen previously in FS- individuals for phrase structure violations, in both English (Lee and Federmeier, 2015) and Mandarin (Yeh et al., 2022). In particular, a P600 effect was seen for RVF/LH presentation (following an N400 effect), whereas with LVF/RH presentation there was an N400 effect but no P600. This pattern accords well with the observations for the FS- group in Experiment 1, in showing a combination of an N400 and a P600 effect. The FS+ group instead elicited a bilateral N400 effect pattern (and no P600, in either hemisphere). Thus, as in prior studies, the FS+ group showed a symmetrical, as opposed to a lateralized, response pattern for syntactic violations. However, different from the response of FS+ individuals to lateralized phrase structure violations in Lee and Federmeier (2015) and Weng and Lee (2020) and the response to centrally-presented morphosyntactic violations in Experiment 1, the effect was an N400-like one, rather than a P600.

The question of why morphosyntactic violations, which canonically have been linked to P600 responses, sometimes also – or instead – elicit

an earlier, negative-going (N400 or perhaps LAN – e.g., Friederici, 1995; Osterhout and Holcomb, 1992) effect pattern does not have a clear answer, although there have been a number of studies documenting this and attempting to uncover the conditions under which each type of response occurs. Variation in ERP effect patterns to agreement violations across languages has been proposed to reflect the potentially differing engagement of lexico-semantic processing in appreciating these relationships (Molinaro et al., 2011; cf. similar proposals about the source of language variation in ERP responses to thematic role violations, Bornkessel-Schlesewsky et al., 2011). Within a language, however, there also seems to be individual variation in the tendency to elicit these differing response patterns. For example, Tanner and van Hell (2014) showed that group-level biphasic responses to morphosyntactic violations reflected multiple, different patterns observed within individual participants, who elicit either just an N400-like effect, just a P600, or a biphasic pattern of both. These individual differences have been linked, as in the present study, to FS (Tanner and Van Hell, 2014), as well as to personality factors (Jimenez-Ortega et al., 2022) and language proficiency. For example, in a series of experiments following native English speakers learning French (McLaughlin et al., 2010; Osterhout et al., 2008; Osterhout et al., 2006), it was found that, in response to French syntactic violations, new learners tended to elicit an N400-like effect. One interpretation is that new learners had enough knowledge to appreciate that the word they were getting was somehow unexpected but did not yet have enough knowledge and/or experience to treat this as a categorical or "rule-based" violation. However, as they became more proficient in the new language, learners began to show a P600 response to these violations, rendering their responses more like those seen in (many) native French speakers. Other work has shown that whereas language proficiency modulates the P600 but not the N400 (Pakulak and Neville, 2010), the N400-like effect is modulated by working memory but not proficiency (Tanner et al., 2016).

The lack of P600 in the FS+ group's responses to lateralized morphosyntactic violations could be seen as coherent with prior proposals about global differences in the language processing strategies used by FS+ versus FS- individuals. Bever and colleagues have argued that people with an FS+ profile access lexical information more easily than their FS- counterparts, whereas FS- individuals may attend more to syntactic information (e.g., Bever et al., 1987; Hancock and Bever, 2013); . Ullman (2004, 2016) has put forward an alternate theory, with an emphasis on mapping linguistic processing onto memory systems. Specifically, whereas lexical knowledge relies on the declarative memory system (which is bilateral), syntactic processing has been linked with the procedural memory system, which is argued to be LH dominant (Babcock et al., 2012). Ullman and colleagues propose that being FS+, and therefore processing more bilaterally, confers an advantage for declarative memory-based processing. On the other hand, because FS- individuals are more left lateralized, they should be better than FS+ individuals at using procedural memory systems. The theory therefore links FS- to better procedural memory and superior syntactic processing and FS+ to superior use of declarative memory systems to support lexical processing – thus sharing similarities with Bever and colleagues' view. On these kind of accounts, one might posit that FS+ individuals would be more likely to elicit N400-like responses to violations (if the N400 is assumed to reflect lexico-semantic processing) whereas FS- individuals would be more likely to elicit P600-like responses (if the P600 is assumed to index syntax processing). However, first, such mappings of component to "type" of language process are likely too simplistic: N400 responses are sensitive to not only lexico-semantic factors but also to global event structure and aspects of sequential, predictive processing (reviewed in Federmeier, 2022), and the P600 has been observed to violations that are not syntactic in nature, including more 'lexical' like manipulations (e.g., Van de Meerendonk, Indefrey, Chwilla and Kolk, 2011; Vissers et al., 2006). Second, and more importantly, these accounts do not predict the larger pattern of FS-based effects. In Experiment 1, with central presentation, FS+ individuals showed *only* a P600 response; it was the FS- group, instead, that also showed an N400-like effect. Moreover, both in English and in Mandarin, FS+ individuals have been shown to elicit bilateral P600 responses to lateralized phrase structure violations (Lee and Federmeier, 2015; Weng and Lee, 2020). Thus, there does not seem to be a generalized tendency for FS+ individuals to be more likely to elicit negativities rather than P600s to manipulations of syntax.

The more consistent, and striking, aspect of the pattern observed across studies is that FS- individuals show divergent responses for processing biased to each hemisphere, whereas FS+ individuals consistently show bilaterally symmetric patterns. Table 1 shows these effect patterns across types of syntactic manipulations and across languages. FS+ individuals show different types of ERP effects across violation type and language, from only negativities to only P600s to biphasic patterns. In all cases, however, the patterns are symmetric across hemisphere. In contrast, FS- individuals consistently show a P600 effect that is lateralized to the left hemisphere for all syntactic manipulations (although, as discussed below, critically *not* for thematic role animacy violations).

Thus, the pattern across FS groups adds to a growing literature supporting the hypothesis that language processing by FS- individuals tends to be more differentiated across the hemispheres, whereas processing in the LH and RH tends to be similar for FS+ individuals. Lee and Federmeier (2015) proposed that the lateralized P600 pattern seen in the FS- group reflects interhemispheric inhibition from the dominant LH onto the RH, suppressing a P600 response in that hemisphere. This view has received support from findings that the degree of hemispheric lateralization observed in young adults is correlated with measures of interhemispheric inhibition (Weng and Lee, 2020; Yeh et al., 2022) as well as by findings that, with age, response patterns in FS- adults become more bilateral, consistent with the idea that age-related changes, which may include reduced interhemispheric inhibition, allowed this response to emerge in the population that showed a lateralized response when they were young (Leckey and Federmeier, 2017). Lee and Federmeier (2015) suggested that this interhemispheric inhibition is reduced in

Table 1
Effect patterns for FS- (left half of table) and FS+ (right half of table) individuals to violations lateralized to bias processing toward the left or right hemisphere. A checkmark indicates the (statistically-significant) presence of that effect pattern, whereas an X symbol indicates the lack of that effect. Rows show results from studies that vary in language and type of violation: English phrase structure results taken from Lee and Federmeier (2015); Mandarin phrase structure results taken from Weng and Lee (2020) and Yeh et al. (2022); number agreement violation results taken from present study. Note that thematic role animacy violation results (also taken from present study) are the only condition not to show a left hemisphere P600 in FS- individuals (and, thus, the only condition not to show a lateralized effect pattern in this group).

	FS-				FS+			
	Left Hemisphere		Right Hemisphere		Left Hemisphere		Right Hemisphere	
	N400 effect	P600 effect	N400 effect	P600 effect	N400 effect	P600 effect	N400 effect	P600 effect
Phrase structure violations (English)	✓	✓	✓	✖	✖	✓	✖	✓
Phrase structure violations (Mandarin)	✓	✓	✓	✖	✓	✓	✓	✓
Number agreement violations (English)	✓	✓	✓	✖	✓	✖	✓	✖
Thematic role animacy violations (English)	✓	✖	✓	✖	✓	✖	✓	✖

young FS+ individuals. That we here again observe a bilateral response in the FS+ group (as did Weng and Lee, 2020) fits with this hypothesis, and, more generally, with observations of reduced asymmetry of anatomy and physiology in FS+ compared to FS- individuals (Annett, 1994; Brown and Hécaen, 1976; Hecaen and Sauget, 1971; Hund-Georgiadis et al., 2002; Tzourio-Mazoyer et al., 2010).

It is noteworthy that the FS+ group elicited N400 responses when morphosyntactic violations were preferentially presented to each cerebral hemisphere but elicited a P600 response (and no accompanying N400) when the same stimuli were presented in central vision. This pattern points to a role for joint ("central") attentional resources in eliciting syntactic P600 effects under some circumstances. In general, there are data suggesting that N400-like effects to grammatical violations reflect processing that is more automatic and implicit, whereas the P600 depends on attentional resources and reflects explicit processing, decision-making, and judgments (e.g., Gunter et al., 2007; Jimenez-Ortega et al., 2014; Jimenez-Ortega et al., 2021; cf. discussion in Leckey and Federmeier, 2020 about similar properties of the P3b). Bilateral coordination of attention may be difficult for lateralized stimuli, and, in the case of the syntactic P600, the pattern in the FS+ group for morphosyntactic violations seen here compared to that seen for phrase structure violations suggests that such coordination may be important for the processing of some types of syntactic manipulations. The phrase structure violations used in Lee and Federmeier (2015) and Yeh et al. (2022) may not have required this coordination either because the information was available at the whole word level or because the violations were presented as two word phrases, making it easy to determine when the violation might occur. In contrast, fully appreciating a morphologically marked violation in a sentence seems to be something that, for FS+ but not FS- individuals, requires central attention, at least to elicit the kind of processing reflected in the P600.

Strikingly, for thematic role violations, different patterns were observed for central versus lateralized presentation in *both* FS groups. For thematic role violations, both groups showed a biphasic N400/P600 response for central presentation of these violations, but both groups then elicited only an N400-like effect in both hemispheres when these items were lateralized. Indeed, as can be seen in Table 1, this is the only case wherein FS- individuals did not elicit a P600 for a (centrally P600-eliciting) violation when stimuli were lateralized to the RVF/LH. Other studies have also documented cases wherein a component that was observed in centralized vision is not found with lateralized presentation. In a 2007 study, Federmeier and colleagues presented participants with sentences that differed in constraint and in the expectedness of the final word (e.g., strongly constraining: "He bought her a pearl necklace for her … birthday (expected)/collection (unexpected)"; weakly constraining: "He looked worried because he might have broken his … arm (expected)/collection (unexpected)"), with all words in the sentence being presented centrally. In response to the unexpected endings in strongly constraining sentences, they found a post-N400 positivity with an anterior distribution. This positivity has subsequently been replicated in a number of studies and has been shown to be a reliable response (in young adults) to words that are plausible but unexpected because they violate a strong prediction for a different word (see, e.g., review by Van Petten and Luka, 2012). However, when Wlotko and Federmeier (2007) used this same design with lateralized presentation, the frontal positivity did not manifest in either visual field. Payne et al. (2016) further showed that the frontal positivity is absent for words in parafoveal preview. This effect thus seems to require joint processing by the two hemispheres and/or central attentional resources. Thus, the semantic P600 may share commonalities with the anterior positivity in requiring integrated processing across the hemispheres, irrespective of FS status. In other domains, hemispheric integration has been shown to be critical for error correction (Hochman et al., 2011). It is interesting to speculate, therefore, that these kind of language effects that obtain only for foveated words may be similarly related to corrective processes involved in dealing with competing activations from mispredicting (in the case of the anterior positivity) or in addressing the conflict created when there are mismatches between nouns and their (typical) thematic roles (in the case of the semantic P600).

More generally, the dissociation of the patterns across the morphosyntactic and thematic role animacy violations in the FS- group is theoretically important. As already discussed, if the syntactic and semantic P600s are actually the "same" component, they should pattern together. Here, they clearly do not, for at least some individuals. This is, to our knowledge, the first demonstration of a difference in the eliciting conditions for these components and, therefore, a first indication that they may not, in fact, reflect the same underlying process. The current results thus call into question proposals that unify these responses and link them to the same underlying neural and/or cognitive mechanisms (e.g., Bornkessel-Schlesewsky and Schlesewsky, 2008; Kuperberg, 2007; Van Herten, Kolk and Chwilla, 2005; Van Herten, Chwilla and Kolk, 2006).

In summary, our pair of studies provides additional evidence that familial sinistrality importantly modulates how the two cerebral hemispheres process syntactic information and coordinate their contributions. FS- individuals exhibit more functional lateralization when probed with VF presentation, and these disparate response patterns are apparent during normal (central) processing, suggesting that, in this group, although both hemispheres contribute to syntactic processing, they do so differently and perhaps independently. In contrast, FS+ individuals consistently show bilateral response patterns to syntactic violations and, in some cases (such as for morphosyntactic violations), divergence between the patterns seen with processing biased to a single hemisphere versus central presentation. Thus, in this group, central processing patterns may reflect interactions between the hemispheres that yield emergent responses.

In addition, the current findings argue against the prevalent assumption that the late, posterior postivities observed in conjunction with syntactic manipulations and with various thematic-role violations reflect identical underlying processing. Instead, we show here that the "syntactic P600" and "semantic P600" have different patterns of sensitivity to FS and lateralization. As discussed in Leckey and Federmeier (2020), the field has shown a preference to use domain as a core organizing principle when thinking about components with similar surface characteristics, thus grouping together (even without direct empirical tests) late positivities that occur in language but showing more resistance to grouping those with the domain general P3b, a component that shares both morphological characteristics and similarities in its eliciting conditions. Whereas a number of studies have provided evidence suggesting that the syntactic P600 may be a variant of the domain general P3b (Leckey and Federmeier, 2020), the present results suggest that the semantic P600 may require more cross-hemispheric coordination than the syntactic P600, at least for FS- individuals, and, more generally, that the field may need to re-examine theories that have assumed that the two P600 responses reflect the same underlying processing.

Author credit statement

Michelle Leckey: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. Melissa Troyer: Writing – original draft, Writing – review & editing, Visualization. Kara Federmeier: Conceptualization, Methodology, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2022.108441.

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