

It's All in the Family: Brain Asymmetry and Syntactic Processing of Word Class



Psychological Science
2015, Vol. 26(7) 997–1005
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DOI: 10.1177/0956797615575743
pss.sagepub.com


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Abstract

Although left-hemisphere (LH) specialization for language is often viewed as a key example of functional lateralization, there is increasing evidence that the right hemisphere (RH) can also extract meaning from words and sentences. However, the right hemisphere's ability to appreciate syntactic aspects of language remains poorly understood. In the current study, we used separable, functionally well-characterized electrophysiological indices of lexico-semantic and syntactic processes to demonstrate RH sensitivity to syntactic violations among right-handers with a strong manual preference. Critically, however, the nature of this RH sensitivity to structural information was modulated by a genetically determined factor—familial sinistrality. The right hemisphere in right-handers without left-handed family members processed syntactic violations via the words' accompanying lexico-semantic unexpectedness. In contrast, the right hemisphere in right-handers with left-handed family members could process syntactic information in a manner qualitatively similar to that of the left hemisphere.

Keywords

hemispheric differences, language lateralization, right hemisphere syntactic processing, word class violation, N400, P600, open data, open materials

Received 8/20/14; Revision accepted 2/11/15

The often devastating consequences of left-sided brain injury for language functions reveal an important association between the left hemisphere (LH) and verbal processing. Indeed, this has become one of the best known examples of functional hemispheric asymmetries and, more generally, of brain-area-to-function mappings. However, a growing literature reporting on a wide range of methods points to a more extensive and significant role for right-hemisphere (RH) functioning in language comprehension than has typically been assumed. The processes linked to right hemisphere functioning include the apprehension of secondary word meanings (Atchley, Burgess, & Keeney, 1999), the flexible use of sentence context information (Coulson & Wu, 2005), and the appreciation of discourse-level meaning (Delis, Wapner, Gardner, & Moses, 1983). These functional contributions of the right hemisphere are confirmed by neuroimaging

studies showing bilateral neural activity associated with normal language comprehension (Bookheimer, 2002) and have been proposed as a mechanism for language recovery, especially for meaning processing, after aphasia-producing strokes (Cohen et al., 2004).

Language processing, however, also requires the ability to appreciate structured relationships among words—that is, language syntax, a property that critically differentiates human language from the communication systems used by other organisms (Hauser, Chomsky, & Fitch, 2002). It remains unclear whether the right hemisphere, in addition to deriving meaning, can use syntax.

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Evidence for the right hemisphere's syntactic processing abilities is sparse, and conclusions drawn from this limited literature vary widely. Although some researchers have argued that the right hemisphere is unable to appreciate even basic syntactic features (e.g., tense, case) and roles (e.g., subject, object; Gazzaniga & Hillyard, 1971), others have reported RH sensitivity to at least some syntactic cues (e.g., word-class expectancy/violation in Arambel & Chiarello, 2006; number agreement in Liu, Chiarello, & Quan, 1999). A few researchers have suggested that the right hemisphere may actually be better than the left at some types of syntactic revision, such as inserting a word into a well-formed expression to make another grammatically and semantically appropriate sentence, when reassignment of syntactic role (Schneiderman & Saddy, 1988) or word class (De Vreese, Neri, Rubichi, & Salvioli, 1996) of other words is required.

Imaging studies have a similar lack of consistency: Some show unilateral LH syntactic processing (of structural complexity manipulations, such as subject-relative and object-relative sentences in Caplan, Alpert, Waters, & Olivieri, 2000; verb transitivity errors in Noguchi, Takeuchi, & Sakai, 2002), whereas others find bilateral activations (for subject-relative and object-relative sentences in Just, Carpenter, Keller, Eddy, & Thulborn, 1996; word-order or agreement errors in Moro et al., 2001; case or word-class violations in Service, Helenius, Maury, & Salmelin, 2007). Even when the right hemisphere appears to be sensitive to syntactic manipulations, it is often unclear whether it engages processes that are qualitatively similar to those used by the left hemisphere (as suggested by Schneiderman & Murasugi, 2003) or, instead, is responding primarily to the accompanying word-level or semantic unexpectedness. The latter hypothesis is bolstered by findings showing that the isolated right hemisphere is better at making grammatical number distinctions that are lexically realized (e.g., *the fish is/are eating*) than those that are signaled through morphological markings (e.g., *the fish eats/eat*; Gazzaniga & Hillyard, 1971; Zaidel, 1983).

In light of this research, the current study was designed to take a critical first step toward understanding the basic syntactic capabilities of the right hemisphere, particularly its ability to appreciate syntactic word-class information, because this lays the foundation for other syntactic processes such as inflection, agreement, and word order. To that end, we combined event-related potential (ERP) measures with visual half-field methods used to induce lateralized processing biases (Banich, 2003). When the corpus callosum is intact, information presented to one hemisphere can be transferred to the other. However, such transmission is delayed, and the fidelity of the information is degraded, because there are fewer callosal than intrahemispheric connections (Hoptman & Davidson,

1994). Moreover, use of hemispheric resources is dynamically regulated, such that information is not always transferred even when it can be (Weissman & Banich, 2000). Thus, responses measured in the context of visual half-field manipulations predominantly reflect the processing biases of the contralateral hemisphere.

We used visual half-field techniques in conjunction with ERPs, which provide functionally well-characterized indices of lexico-semantic and syntactic processes. We looked for hemispheric processing biases in the form of different patterns of ERP effects linked to language processing as a function of visual half-field of presentation. (Note that the scalp topography of an ERP effect is not a reliable indicator of the location of its neural sources, because lateralized sources may elicit effects that are largest over the center of the head or even over the opposite hemisphere; thus, scalp topography should not be used to make inferences about lateralized processing.) Ease of semantic processing affects the amplitude of the N400, a negative-going component of the electroencephalographic (EEG) signal with a broad, centrally maximal distribution that peaks around 400 ms (Kutas & Federmeier, 2011). Visual half-field ERP studies focusing on the N400 have characterized the hemispheres' ability to access meaning from words and sentences (Federmeier, Wlotko, & Meyer, 2008). However, few have used this approach to examine syntactic processing, which is associated instead with P600 effects—sustained positive-going responses (beginning after 500 ms) over posterior scalp sites (reviewed by Kuperberg, 2007; for P600 responses to word-class violations of the type used here, see Federmeier, Segal, Lombrozo, & Kutas, 2000).

Individual differences in functional lateralization also may be contributing to the inconsistent findings regarding RH sensitivity to syntactic information. Language lateralization is linked with the other prominent human lateralization, hand preference (e.g., Knecht et al., 2000), although the biological basis for this association remains unclear. Even among right-handers (the typical focus of lateralization studies because their brain organization is considered more homogeneous than that of left-handers), the degree of functional asymmetry varies with strength of hand preference as well as familial sinistrality—that is, whether an individual has left-handed blood relatives (Chiarello, Vazquez, Felton, & Leonard, 2013; Tzourio-Mazoyer, Petit, et al., 2010). In particular, familial sinistrality has been shown to reduce the degree of leftward lateralization of language processing (Kee, Bathurst, & Hellige, 1983; Townsend, Carrithers, & Bever, 2001). LH lesions are more likely to cause language abnormalities in right-handers without familial sinistrality (FS–) than in those with left-handed relatives (FS+; Hécaen, De Agostini, & Monzon-Montes, 1981). When language deficits occur after LH strokes, FS+ right-handers recover

more quickly (Luria, 1970). However, FS+ individuals are more likely to suffer from language deficits after RH strokes (Brown & Hécaen, 1976; Subirana, 1958). Structural asymmetries of language-related brain areas (e.g., planum temporale; Tzourio-Mazoyer, Simon, et al., 2010) are also reduced in FS+ individuals.

These findings suggest that the right hemisphere may be able to engage syntactic processes that are qualitatively similar to those in the left hemisphere. The degree to which this is possible, however, may differ across individuals on the basis of genetically influenced factors that set up structural and functional asymmetries. Here, therefore, we also took participants' familial handedness into account to examine individual variability. Specifically, we tested whether the right hemispheres of FS- and FS+ individuals were sensitive to syntactic violations and, if so, what the nature of such sensitivity might be. If RH sensitivity to syntactic violations arises at the level of combinatorial processing, as does LH sensitivity to syntactic violations, we would expect to see a P600 effect when language stimuli mismatch syntactic expectancies. However, if the sensitivity of the right hemisphere is due to the lexico-semantic unexpectedness that accompanies syntactic unexpectedness, an N400 difference (i.e., more negative N400s for ungrammatical word pairs than for grammatical word pairs) would be expected. Furthermore, we investigated whether familial sinistrality affected the nature or degree of functional lateralization patterns in syntactic processing; specifically, we examined whether syntactic processing was qualitatively more similar across the hemispheres in FS+ individuals than in FS- individuals.

Method

Participants

Sixty-four University of Illinois undergraduate students (32 men, 32 women; mean age = 20 years, age range = 18–29 years) participated in the study for course credit or cash. All were monolingual speakers of English with no consistent exposure to other languages before age 5. Participants had no history of neurological or psychiatric disorders or brain damage. All were right-handed as assessed by the Edinburgh inventory (Oldfield, 1971). Participants were surveyed with a detailed questionnaire about the number and manual preferences of their blood relatives, including siblings, parents, aunts, uncles, and grandparents. Among the 64 participants, 29 of them had at least one left-handed blood relative, and 35 of them did not. Within the FS+ group, 3 participants reported two left-handed relatives and 26 reported only one (of these, 14 reported a left-handed parent, 9 a left-handed sibling or grandparent, and 3 a left-handed aunt or uncle;

the degree of relation did not affect the result pattern). The mean laterality quotient was 74.28 ($SD = 20.31$) for the whole group and did not differ reliably between people with and without left-handed blood relatives—FS+: $M = 77.59$, $SD = 15.23$; FS-: $M = 71.53$, $SD = 23.58$; $p = .2$. Participants were run in groups of 4 (to maintain counterbalancing) until data for at least 28 participants of each familial handedness condition were obtained, because we estimated that this number would give us 80% power to detect even relatively small P600 effects (i.e., of about 1.5 μV) with an alpha level of .05 in a two-sided test (on the basis of prior data from the lab, we estimated sigma to be 2.8 μV).

Materials

Syntactic contexts (*to* and *the*) were used to create expectancy for the word class of the following word. Participants read 184 critical word pairs constructed from words of unambiguous word class (92 nouns and 92 verbs). These words were arranged such that, within each visual half-field of presentation, half of the words were preceded by proper syntactic cues (i.e., *the* for nouns, *to* for verbs; grammatical condition). The other half of the words were preceded by cues more predictive of the other grammatical class (i.e., *the* for verbs, and *to* for nouns; ungrammatical condition). Across participants, all nouns and verbs were rotated through the grammatical and ungrammatical conditions within each visual half-field. A total of four lists was generated to allow for such counterbalancing. Each participant was randomly assigned to one list. We added to each list 184 filler trials (using words of ambiguous word class, such as *drink*) for 32 participants and 280 filler trials for the other 32 participants. Because results from the critical words did not differ as a function of the number of filler trials, data for all participants were combined in our report.

Procedure

Participants were seated 100 cm in front of a 21-in. computer monitor in a dim, quiet testing room. The experiment began with an 18-trial practice session to familiarize subjects with the task and the experimental environment. A small square (3×3 pixels), presented a few pixels below the center of the screen, remained visible throughout the experiment to help subjects fixate at the center and avoid orienting to the laterally presented words. At the start of each trial, a series of plus signs appeared in the center of the screen for 500 ms. After a random stimulus onset asynchrony of between 1,000 and 1,500 ms, the syntactic cue (*to* or *the*) was presented at the center of the screen for 200 ms. The offset of the cue was followed by a 300-ms interstimulus interval, and then the target

word was randomly presented to either the right visual field (RVF) or the left visual field (LVF) for 200 ms. Visual angle from the inner edge of the target word to the center of the screen was kept at 2° (from this point, words subtended between an additional 1.5° and 4.5° of horizontal visual angle and 0.5° of vertical visual angle). The probe "OKAY?" was displayed on the screen in red letters 1,500 ms after the offset of the target. Participants were instructed to judge the grammaticality of the phrase in the trial. The probe remained on the screen until the participant's response. The next trial began after a delay of 2,500 ms.

Split-visual-field presentation

To assure the validity of the lateralized presentation, we presented target words randomly to either visual field. Words appeared in the same visual field no more than twice in a row. The goal was to reduce the predictability of the location of the target word. The target words were also presented only briefly (200 ms), so that it was unlikely that participants would be able to orient to the target word before it disappeared. In addition, we also monitored participants' horizontal eye movement with the electrooculogram (described in the next section) and excluded from data analyses any trials involving horizontal eye movements.

EEG recording parameters and data analysis

EEGs were recorded from 26 geodesically arranged Ag/AgCl electrodes attached to an elastic cap. All scalp electrodes were referenced on-line to the left mastoid and rereferenced off-line to the average of the right and the left mastoids. In addition, to detect vertical and horizontal eye movements, the electrooculogram was measured from 1 electrode placed on the left infraorbital ridge and 1 electrode on each lateral canthus. Electrode impedances were kept below 3 k Ω . The continuous EEG was amplified through a bandpass filter of 0.02 to 100 Hz and recorded at a sampling rate of 250 Hz.

Epochs of EEG data began 100 ms before stimulus onset and ended 1,500 ms after stimulus onset. Epochs containing artifacts from amplifier blocking, signal drift, excessive eye movements, or muscle activity were rejected off-line before averaging. Trials contaminated by eye blinks were corrected for participants who had enough blinks to obtain a stable filter (for the procedure, see Dale, 1994); for all other participants, trials with blink artifacts were excluded from analysis. Trial loss averaged 15.54%. Artifact-free ERPs were averaged by stimuli type after subtraction of the 100-ms prestimulus baseline. Before

measurement, ERPs were digitally filtered with a bandpass of 0.2 to 20 Hz. Only ERP data for trials with correct responses were included in the statistical analysis.

ERP responses were quantified using omnibus analyses of variance (ANOVAs) with the following within-subjects factors: 2 levels of visual-field presentation (LVF vs. RVF), 2 levels of grammaticality (grammatical vs. ungrammatical), and 22 levels of electrode site (frontal electrode sites: midline prefrontal, left lateral prefrontal, right lateral prefrontal, left medial prefrontal, right medial prefrontal, left lateral frontal, right lateral frontal, left dorsal frontal, right dorsal frontal, left medial frontal, and right medial frontal; central/posterior electrode sites: midline central, left medial central, right medial central, left dorsal central, right dorsal central, midline parietal, left dorsal parietal, right dorsal parietal, left medial occipital, right medial occipital, and midline occipital). Analyses were conducted on mean amplitudes of data measured between 300 and 600 ms after stimulus onset for the N400 effects and between 800 and 1,400 ms after stimulus onset for the P600 effects. To correct for violations of sphericity associated with repeated measures, we applied the Huynh-Feldt adjustment to the degrees of freedom for all F tests with more than one degree of freedom in the numerator; the corrected p values are reported. For all analyses, main effects of electrode and interactions with electrode sites are not reported unless they are of theoretical significance. We performed analyses first for all participants and then with familial sinistrality as an additional between-subjects factor (FS+ vs. FS-).

Results

Behavioral data

For all participants as a group, accuracy was higher for RVF than for LVF words, although better-than-chance accuracy was seen in both visual fields (RVF: 81%; LVF: 75%). The same pattern held regardless of familial sinistrality: for FS- participants, RVF accuracy was 80% and LVF accuracy was 73%; for FS+ participants, RVF accuracy was 82% and LVF accuracy was 77%. Results of the ANOVA with factors of familial sinistrality, visual field, and grammaticality showed main effects of visual field, $F(1, 62) = 37.39$, $p < .001$, and grammaticality, $F(1, 62) = 18.51$, $p < .001$, but no effect of familial sinistrality ($p = .3$). There was also no Visual Field \times Grammaticality interaction ($p = .8$) or familial sinistrality interactions ($ps > .3$).

ERP data

ERP data from all participants showed the classic N400 and P600 word-class-violation effects (Fig. 1). The

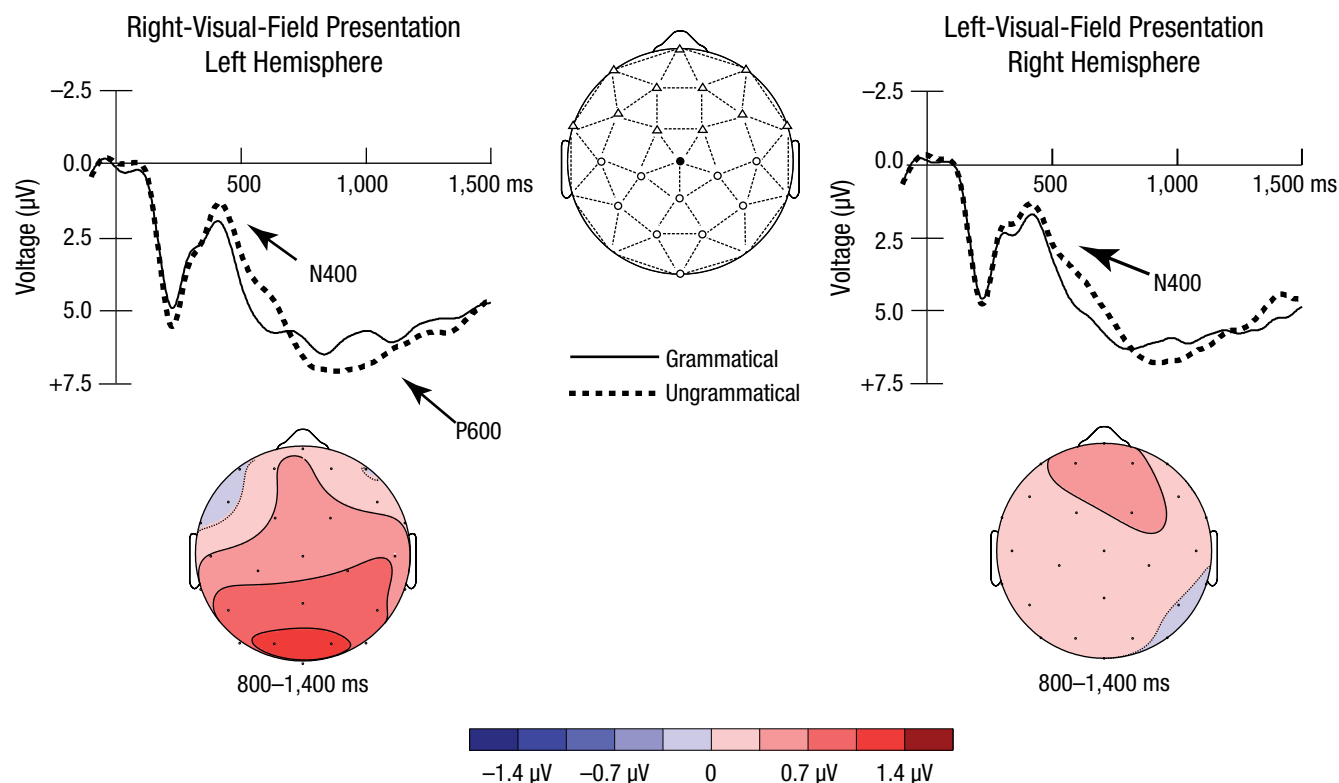


Fig. 1. Grand-average event-related potentials (ERPs) for all participants and scalp topography of the P600 difference between grammatical and ungrammatical word pairs. Results for the right visual field are presented on the left, and results for the left visual field are presented on the right. The graphs (top) present the ERPs recorded at a representative electrode site over the center of the head (black dot). Negative voltage is plotted upward. The waveforms elicited by grammatical and ungrammatical word pairs are shown separately. N400 and P600 components are indicated. The scalp-topography illustrations (bottom) depict the distribution of ERP differences (ungrammatical word pairs minus grammatical word pairs) in the P600 (800- to 1,400-ms) time window.

grammaticality effect in the N400 time window (300–600 ms; greater negative responses to ungrammatical word pairs than to grammatical word pairs), $F(1, 63) = 8.6$, $p = .005$, was not modulated by visual field ($p > .6$). In contrast, the grammaticality effect in the P600 time window (800–1,400 ms; greater positive responses to ungrammatical word pairs than to grammatical word pairs) was modulated by visual field and electrode site, $F(21, 1323) = 4.39$, $p < .005$. With RVF-LH presentation, there was a reliable grammaticality effect with a typical central-posterior P600 distribution, $F(1, 63) = 5.61$, $p < .05$. However, there was no P600 effect with LVF-RH presentation ($p = .2$).

Analyses with familial sinistrality included as a between-subjects factor revealed striking differences in the RH response (Fig. 2). The grammaticality effect in both the N400 and P600 time windows interacted with familial sinistrality and visual field—N400: $F(1, 62) = 5.79$, $p < .05$; P600: $F(1, 62) = 8.25$, $p < .01$. The FS– participants showed the group-level pattern, with a significant N400 grammaticality effect, $F(1, 34) = 18.32$, $p < .001$, unaffected by visual field ($p = .2$), but a P600 Grammaticality \times

Visual Field interaction, $F(1, 34) = 8.86$, $p = .005$. This interaction was driven by an effect with RVF-LH presentation, $F(1, 34) = 5.4$, $p < .05$, but not with LVF-RH presentation ($p = .1$). Thus, FS– participants elicited a biphasic N400/P600 response to grammatical anomalies in the left hemisphere but only an N400 effect in the right hemisphere. In contrast, for FS+ participants, there was no reliable N400 effect of grammaticality ($p = .7$). There was also no reliable Grammaticality \times Visual Field interaction ($p = .06$), although there was a trend for larger N400 effects with RVF presentation. However, in the P600 time window, there was a significant main effect of grammaticality, $F(1, 28) = 8$, $p < .01$, not modulated by visual field ($p = .2$). For FS+ participants, grammatical anomalies thus elicited a broadly distributed P600 effect in both hemispheres.

Figure 3 plots the degree of hemispheric bias of the grammaticality effect (ungrammatical minus grammatical) in the P600 time window for individual subjects as a function of familial sinistrality. There is a striking asymmetry for the FS– participants, most of whom elicited notably larger P600s with RVF presentation than with LVF presentation.

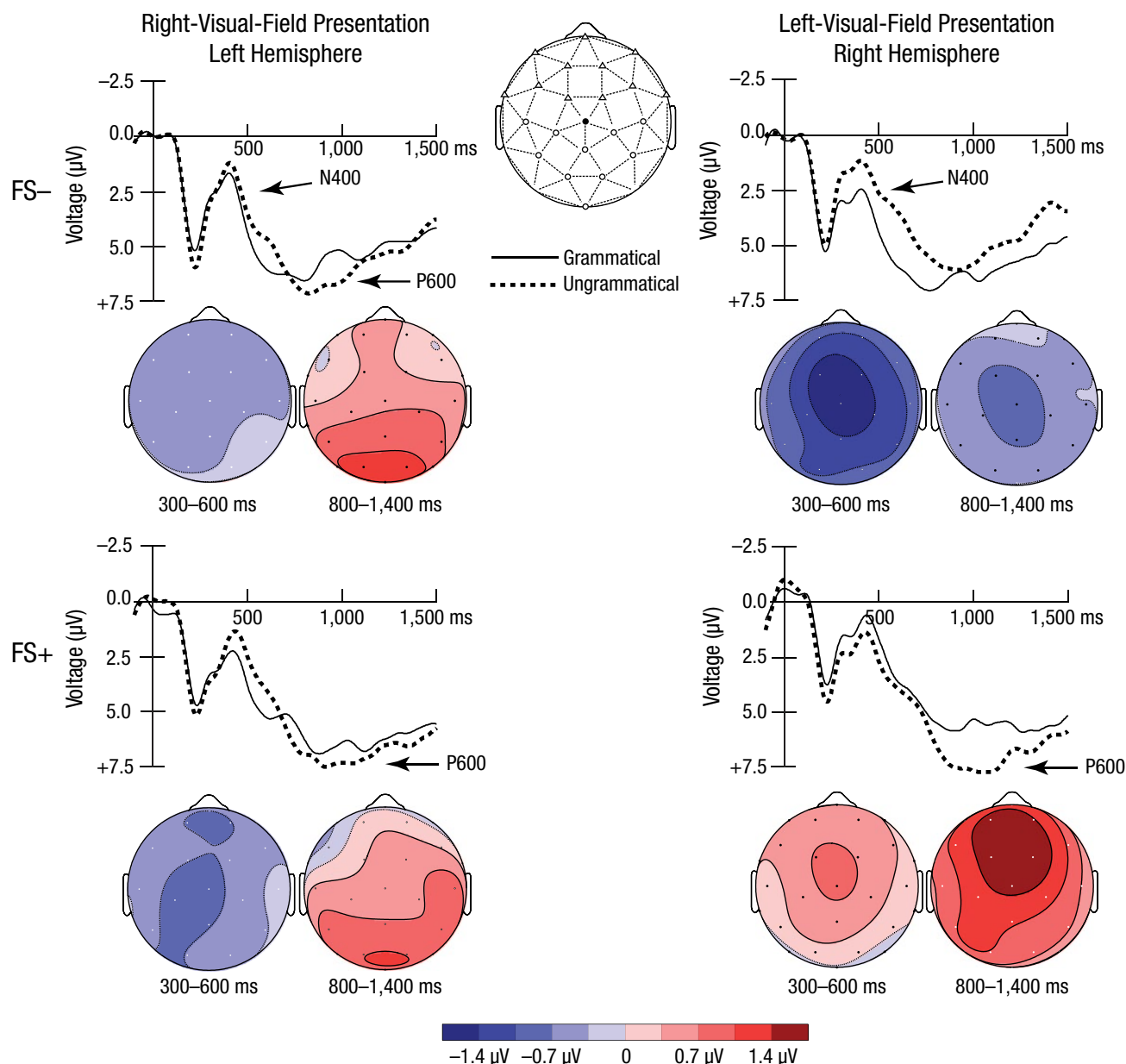


Fig. 2. Grand-average event-related potentials (ERPs) and scalp topography of the N400 and P600 differences between grammatical and ungrammatical word pairs for participants without familial sinistrality (FS-; top panels) and with familial sinistrality (FS+; bottom panels). Results for the right visual field are presented in the left panels, and results for the left visual field are presented in the right panels. The graphs present the ERPs recorded at a representative electrode site over the center of the head (black dot). Negative voltage is plotted upward. The waveforms elicited by grammatical and ungrammatical word pairs are shown separately. N400 and P600 components are indicated. The scalp-topography illustrations depict the distributions of ERP differences (ungrammatical word pairs minus grammatical word pairs) for the N400 (300- to 600-ms) time window and the P600 (800- to 1,400-ms) time window.

In contrast, the distribution for FS+ participants is centered around zero, with fewer RVF-biased responses and more LVF-biased responses across individuals.

Discussion

Our results demonstrate that RH sensitivity to syntactic information is qualitatively moderated by familial sinistrality.

For FS- participants, syntactic processing, as indexed by the P600 grammaticality effect, was unilaterally manifested in the LH. Although the right hemispheres of FS- participants responded differently in the grammatical condition than in the ungrammatical condition, this effect, seen on the N400, was qualitatively different and more likely to be lexical in nature. N400 effects have also been seen in response to syntactic violations in early stages of second language

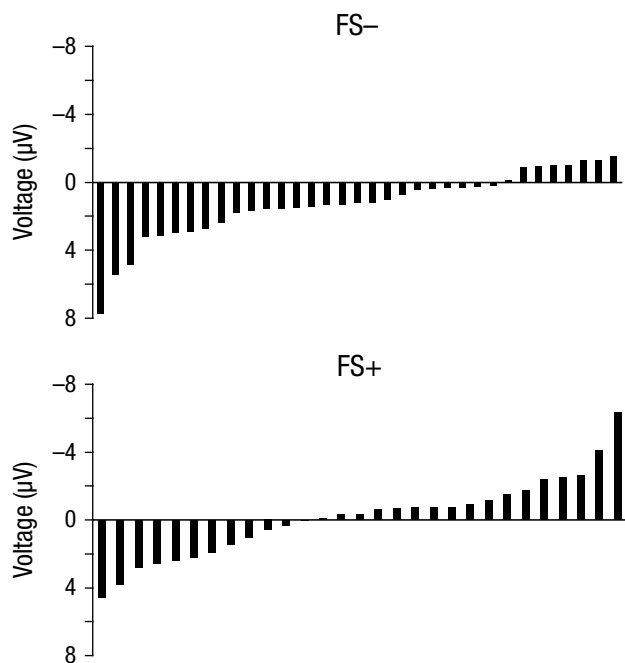


Fig. 3. Laterality of the P600 effect (size of effect for left-hemisphere presentation minus size of effect for right-hemisphere presentation) for individual participants without familial sinistrality (FS-) and with familial sinistrality (FS+). The P600 effect was measured between 800 and 1,400 ms.

learning, before learners fully develop knowledge of the morphosyntactic regularities in that language; with increased experience and fluency, these learners come to elicit a P600 response to the violations (e.g., Osterhout et al., 2008). Thus, as has been previously proposed in the literature on RH syntactic processing (e.g., Zaidel, 1983), in FS- individuals, RH language-processing mechanisms may be ineffective for combinatorial analysis and thus respond to syntax via patterns of lexical association.

Whereas data from FS- participants supported traditional views of the functional lateralization of syntactic processing, results from the FS+ participants provided compelling evidence that the right hemisphere is capable of engaging syntactic processes that are qualitatively similar to those found in the left hemisphere. Our findings thus extend prior work showing that familial sinistrality reduces structural brain asymmetry (Tzourio-Mazoyer, Simon, et al., 2010) by establishing that functional asymmetry, at least for the processing of the syntactic word-class information tested here, is reduced as well. Because prior studies showing reduced asymmetry have typically measured laterality by subtracting data for one hemisphere from data for the other, it has been unclear whether the findings reflected reduced LH contribution or increased RH contribution. Our results demonstrate that the reduced functional asymmetry in the FS+ group arises because of LH-like syntactic processing in the right hemisphere, rather than altered processing capabilities in

the left hemisphere (Seghier, Kherif, Josse, & Price, 2011). This result is consistent with findings showing that decreased leftward asymmetry in gray matter volume in FS+ individuals reflects reduced synaptic pruning in the right hemisphere (Tzourio-Mazoyer, Simon, et al., 2010).

It has been proposed that LH-equivalent language capabilities exist in the right hemisphere but are usually masked by transcallosal interhemispheric inhibition from the dominant left hemisphere (Karbe et al., 1998). This hypothesis has been supported by research showing increased activation in the RH homologues of LH language areas after LH strokes, which presumably release the left hemisphere's inhibitory effect (Hamilton, Chrysikou, & Coslett, 2011). Given this view, the bilateral syntactic processing we found in the FS+ group could be a consequence of reduced interhemispheric inhibition. Interhemispheric interaction has been shown to be beneficial for tasks that are complex and require more attentional capacity (e.g., Scalf, Banich, Kramer, Narechania, & Simon, 2007) but inefficient for tasks that are simple or require independent control of homologous areas (e.g., Belger & Banich, 1998). Accordingly, familial sinistrality has been associated not with overall better or worse performance on language tasks but with different patterns of strengths and weaknesses. For example, FS+ right-handers are better than FS- right-handers at understanding sentences presented under difficult reading/listening conditions but seem less sensitive to clausal structure and word position (Hancock & Bever, 2013). FS+ right-handers also have better explicit memory but poorer implicit memory for words or letter strings (Christman & Propper, 2001; Townsend et al., 2001).

Conclusions

Overall, our findings demonstrate that even in right-handers with a strong manual preference, the right hemisphere is capable of LH-like language syntax processing. However, the tendency to show LH-like syntactic processing in the right hemisphere, as indexed by P600 effects, is notably modulated by participants' familial handedness background. This variability in language lateralization has important implications not only for understanding the (sometimes inconsistent) patterns of hemispheric differences in language processing reported in the basic science literature, but also for neurosurgical interventions and the potential for recovery after unilateral brain damage. It may also inform debates about the mechanisms and implications of shifts from lateralized to more bilateral processing with healthy aging (Cabeza, Anderson, Locantore, & McIntosh, 2002; Park & Reuter-Lorenz, 2009). Finally, our findings also support the hypothesis that the functional asymmetry of language—in particular, appreciation of language syntax—is at least partially genetically determined (Annett, 1998; Corballis, 2009; Francks et al., 2007).

Author Contributions

K. D. Federmeier and C. Lee developed the study concept and contributed to the study design. C. Lee performed the data collection, data analysis, and interpretation under the supervision of K. D. Federmeier. C. Lee drafted the manuscript, and K. D. Federmeier provided critical revisions. Both authors approved the final version of the manuscript for submission.

Acknowledgments

We thank Cynthia Fisher, Susan Garnsey, Duane Watson, and Sarah Brown-Schmidt for insightful comments.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was supported by a James S. McDonnell Foundation Scholar Award (to K. D. Federmeier), by National Institute on Aging Grant R01-AG026308 (to K. D. Federmeier), and by Taiwan Ministry of Science and Technology Grants NSC102-2410-H-002-055 and MOST103-2410-H-002-215-MY2 (to C. Lee).

Open Practices



All data and materials have been made publicly available via Open Science Framework and can be accessed at <http://osf.io/djzh3>. The complete Open Practices Disclosure for this article can be found at <http://pss.sagepub.com/content/by/supplemental-data>. This article has received badges for Open Data and Open Materials. More information about the Open Practices badges can be found at <https://osf.io/tvyxz/wiki/view/> and <http://pss.sagepub.com/content/25/1/3.full>.

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