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It's all in the family: brain asymmetry and syntactic processing of word class

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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 RH's ability to appreciate syntactic aspects of language remains poorly understood. Here, using separable, functionally well-characterized electrophysiological indices of lexico-semantic and syntactic processes, we 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 is modulated by a genetically determined factor—familial sinistrality. The RH in right-handers without left-handed family members processes syntactic violations via the words' accompanying lexico-semantic unexpectedness. In contrast, the RH in right-handers with left-handed family members is able to process syntactic information in a qualitatively similar manner as the LH.

Keywords

hemispheric differences; language lateralization; right hemisphere syntactic processing; word class violation; N400; P600

1. Introduction

The often devastating consequences of left-sided brain injury for language functions have rendered an association between the left hemisphere (LH) and verbal processing one of the best known examples of functional hemispheric asymmetries and, more generally, of brain-area-to-function mappings. However, a growing literature derived from a wide range of

methods points to a more extensive and significant role for right hemisphere (RH) functioning in language comprehension than had typically been assumed, in processes including 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 RH are attested 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 -- i.e., 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, in addition to deriving meaning, the RH is able to use syntax. Data speaking to the RH's syntactic processing abilities are sparse and conclusions drawn from this limited literature range widely. Although some have argued that the RH 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., Arambel & Chiarello, 2006: word-class expectancy/violation; Liu, Chiarello, & Quan, 1999: number agreement). A few have suggested that the RH may actually be better than the LH 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, & Salvoli, 1996) of other words is required. Imaging studies show a similar lack of consistency: some report unilateral LH syntactic processing (Caplan, Alpert, Waters, & Olivieri, 2000: structural complexity such as subject-/object-relative sentences; Noguchi, Takeuchi, & Sakai, 2002: verb transitivity errors), whereas others find bilateral activations (Just, Carpenter, Keller, Eddy, & Thulborn, 1996: subject-/object-relative sentences; Moro et al., 2001: word-order or agreement errors; Service, Helenius, Maury, & Salmelin, 2007: case or word-class violations). Even when the RH appears to be sensitive to syntactic manipulations, it is often unclear whether it engages processes qualitatively similar to those used by the LH (as suggested by Schneiderman & Murasugi, 2003) or whether, instead, it is responding primarily to the accompanying word-level or semantic unexpectedness. The latter hypothesis is bolstered by findings showing that the isolated RH 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*") (Zaidel, 1983; Gazzaniga & Hillyard, 1971).

In light of this, the current study was designed to take a critical first step toward understanding the basic syntactic capabilities of the RH, particularly its ability to appreciate syntactic word-class information, as this lays the foundation for other syntactic processes such as inflection, agreement, word order, etc. To that end, we combined event-related potential (ERP) measures with visual half-field (VF) methods used to induce lateralized processing biases (Banich, 2002). When the corpus callosum is intact, information presented to one hemisphere can be transferred to the other. However, such transmission is delayed

and occurs with degraded information fidelity, as 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 VF manipulations predominantly reflect the processing biases of the contralateral hemisphere.

We use VF techniques in conjunction with ERPs, which provide functionally well-characterized indices of lexical-semantic and syntactic processes. We look for hemispheric processing biases in the form of different effect patterns as a function of VF on waveform characteristics linked to language processing. (Note that scalp topography of an ERP effect is not a reliable indicator of the location of its neural sources, as 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 with a broad, centrally-maximal distribution that peaks around 400ms (Kutas & Federmeier, 2011). VF-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 positivity (beginning after 500ms) over posterior scalp sites (reviewed by Kuperberg, 2007; see Federmeier et al., 2000, for P600 responses to word-class violations of the type used here).

An additional factor that may be contributing to the inconsistent findings regarding RH sensitivity to syntactic information is individual differences in functional lateralization. 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 homogenous), degree of functional asymmetry varies with strength of hand preference as well as familial sinistrality— i.e., whether or not 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), and, when language deficits occur following LH strokes, FS+ right-handers recover more quickly (Luria, 1970). However, FS+ individuals are more likely to suffer from language deficits subsequent to 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 results suggest that the RH may be able to engage syntactic processes qualitatively similar to those in the LH, but to a degree that differs across individuals based on 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 test whether the RH of FS– and FS+ individuals is sensitive to syntactic

violations and, if so, what the nature of such sensitivity is. If the RH sensitivity arises at the level of combinatorial processing as in the LH, we would expect to see a P600 effect to the condition mismatching the syntactic expectancy. However, if the sensitivity is due to the accompanying lexico-semantic unexpectedness, a N400 difference, with more negative N400s in the mismatching than in the matching condition would be expected. Furthermore, we investigate whether familial sinistrality affects the degree of functional lateralization patterns in syntactic processing; specifically, whether syntactic processing is qualitatively more similar across the hemispheres in the FS+ than the FS– group.

2. Method

2.1 Participants

Sixty-four University of Illinois undergraduate students (32 males; mean age 20 years, 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/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, parents' siblings, and grandparents. Among the 64 participants, 29 of them had at least one left-handed blood relative (FS+), and 35 of them did not (FS–). Within the FS+ group, 3 participants reported two left-handed relatives and 26 reported only one (14 reported a left-handed parent, 9 a sibling or grandparent, and 3 an aunt or uncle; degree of relation did not affect the result pattern). The mean and SD for the laterality quotient was 74.28 ($\pm$ 20.31) for the whole group, and did not differ reliably between people with (FS+) and without (FS–) left handed blood relatives (FS+: 77.59 $\pm$ 15.23; FS–: 71.53 $\pm$ 23.58; $p=0.2$). Participants were run in groups of four (to maintain counterbalancing) until at least 28 participants of each familial handedness condition were obtained, as 28 participants was estimated to give us the target 80% power to detect even relatively small P600 effects of about 1.5 μ V at alpha equal to 0.05 for a two-sided test (sigma was estimated to be 2.8 μ V based on prior data from the lab).

2.2 Materials

Syntactic contexts ('to'/'the') were used to create expectancy for the word class (verb/noun) of the following word. Each participant read 184 critical trials, constructed from word class unambiguous words (92 nouns and 92 verbs). These words were arranged such that, within each VF of presentation, half of the words were preceded by proper syntactic cues ('the' for nouns, and 'to' for verbs)—the 'matched' condition, while the other half were preceded by cues more predictive of the other grammatical class ('the' for verbs, and 'to' for nouns)—the 'mismatched' condition. Across participants, all nouns and verbs were rotated through the matched and mismatched conditions within each VF. Four lists in total were generated to allow for such counterbalancing. Each participant was randomly assigned to each list. To each of these lists, 184 filler trials (using word class ambiguous words, such as 'drink') were added for 32 participants and 280 filler trials for the other 32 participants. As results from the critical words did not differ as a function of the number of filler trials, these were combined in our report.

2.3 Procedure

Participants were seated 100 cm in front of a 21" 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 by 3 pixels) presented a few pixels below the center of the screen remained 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 500ms. After a stimulus onset asynchrony (SOA) ranging randomly between 1000 and 1500ms, the syntactic cue ('to'/'the') was presented at the center for 200ms. The offset of the cue was followed by a 300ms inter-stimulus interval (ISI) and then the target word was randomly presented to either visual field for 200 ms. Visual angle from the inner edge of the target word to the center of the screen was kept at 2 degrees (from this point, words subtended between 1.5 and 4.5 additional degrees of horizontal visual angle and 0.5 degrees of vertical visual angle). Participants were instructed to make a grammaticality judgment on the phrase after the probe 'OKAY?' which was displayed on the screen in red color 1500ms after the offset of the target and remained on the screen until the participant's response. The next trial then began after a delay of 2500 ms.

2.4 Split visual field presentation

To assure the validity of the lateralized presentation, target words were randomly presented to either visual field with no more than two consecutive presentations to the same visual field, in order to reduce the predictability of the location of the target word. The target words were also briefly presented (200ms), so that participants would be unlikely to 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 session) and excluded trials involving horizontal eye movements from data analyses.

2.5 EEG recording parameters and data analysis

The electroencephalogram (EEG) was recorded from twenty-six geodesically-arranged silver/silver-chloride electrodes attached to an elastic cap. All 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. In addition, one electrode was placed on the left infraorbital ridge to monitor the vertical EOG, and another two electrodes were placed on the outer canthus of each eye to monitor the horizontal EOG. Electrode impedances were kept below 3k Ω . The continuous EEG was amplified through a bandpass filter of 0.02–100Hz and recorded at a sampling rate of 250Hz.

Epochs of EEG data were taken from 100 ms before stimulus onset to 1500 ms after. Those 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 (see Dale, 1994 for the procedure); 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 pre-stimulus baseline. Prior to measurement, ERPs were

digitally filtered with a bandpass of 0.2–20 Hz. Only ERP data for trials that were responded to correctly were included in the statistical analysis.

ERP responses were quantified using omnibus ANOVAs with the following within-subjects factors: 2 levels of VF of Presentation (LVF vs. RVF), 2 levels of Grammaticality (matched vs. mismatched), and 22 levels of Electrode Site (front: MiPf, LLPf, RLPf, LMPf, RMPf, LLFr, RLFr, LDFr, RDFr, LMFr, RMFs; central/posterior electrode sites: MiCe, LMce, RMce, LDce, RDce, MiPa, LDPa, RDPa, LMOc, RMOc, and MiOc). Analyses were conducted on mean amplitudes of data measured between 300–600ms for the N400 effects and between 800–1400ms for the P600 effects. To correct for violations of sphericity associated with repeated measures, the Huynh–Feldt adjustment to the degrees of freedom was applied for all *F* tests with more than 1 degree of freedom in the numerator; the corrected *p* value is reported. For all analyses, main effects of electrode and interactions with electrode sites are not reported unless they are of theoretical significance. Analyses were first done for all participants, and then with FS– and FS+ as an additional between-subjects factor FS (FS+ vs. FS–).

3. Results

3.1 Behavioral data

For all participants as a group, accuracy was higher for right visual field than left visual field words, although better than chance accuracy was seen in both VFs (RVF; 81%; LVF; 75%). The same pattern held across FS background [FS–: RVF=80%, LVF=73%; FS+: RVF=82%, LVF=77%]. Results of the ANOVA with factors of FS, VF, and Grammaticality showed main effects of VF [$F(1,62)=37.39$, $p<0.001$] and Grammaticality [$F(1,62)=18.51$, $p<0.001$], but no effect of FS [$p=0.3$]. There was also no VF by Grammaticality interaction [$p=0.8$] or FS level interactions [$ps > 0.3$].

3.2 ERP data

ERP data from all participants showed the classic N400 and P600 word class violation effects (Figure 1). The grammaticality effect in the N400 (300–600 ms) time window (more negative responses to ungrammatical than grammatical words) [$F(1,63)=8.6$, $p=.005$] was not modulated by VF [$p > 0.6$]. In contrast, the grammaticality effect in the P600 (800–1400 ms) time window (increased positivity to ungrammatical words) was modulated by VF and electrode site [$F(21,1323)=4.39$, $p<0.005$]. With RVF/LH presentation, there was a reliable grammaticality effect with a typical central-posterior P600 distribution [$F(1,63)=5.61$, $p<0.05$]. However, there was no P600 effect with LVF/RH presentation [$p = 0.2$].

Analyses with the FS subgroups included as a between subject factor revealed striking differences in the RH response (Figure 2). The grammaticality effect in both the N400 and P600 time windows interacted with FS and VF [N400: $F(1,62)=5.79$, $p<0.05$; P600: $F(1,62)=8.25$, $p<0.01$]. The FS– participants showed the group-level pattern, with a significant N400 grammaticality effect [$F(1,34)=18.32$, $p<.001$] unaffected by VF [$p=0.2$], but a P600 grammaticality by VF interaction [$F(1,34)=8.86$, $p=0.005$], driven by an effect with RVF/LH presentation [$F(1,34)=5.4$, $p<0.05$], but not with LVF/RH presentation

[$p=0.1$]. Thus, FS– participants elicit a biphasic N400/P600 response to grammatical anomalies in the LH, but only an N400 effect in the RH. In contrast, for FS+ participants, there was no reliable N400 effect of grammaticality [$p=0.7$]. There was also no reliable grammaticality by VF 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 [$F(1,28)=8$, $p<0.01$], not modulated by VF [$p=0.2$]. 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 than with LVF presentation. In contrast, the distribution for FS+ participants is centered around zero, with smaller RVF-biased responses and larger LVF-biased responses across individuals.

4. Discussion

Our results demonstrate RH sensitivity to syntactic information that is qualitatively moderated by familial sinistrality. For FS– participants, syntactic processing, as indexed by the P600 grammaticality effect, is unilaterally manifested in the LH. Although the RH of FS– participants responds differentially in grammatical versus ungrammatical conditions, this effect, seen on the N400, is qualitatively different and more likely to be lexically based. N400 effects have also been seen to syntactic violations in early stages of second language learning, before learners fully develop knowledge of the morpho-syntactic 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 supports traditional views of the functional lateralization of syntactic processing, results from the FS+ participants provide compelling evidence that the RH is capable of engaging syntactic processes that are qualitatively similar to those found in the LH. Our findings thus importantly 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 syntactic word class information tested here, is reduced as well. Because prior studies showing reduced asymmetry have typically used laterality indices subtracting measures between the two hemispheres, it has been unclear whether the findings reflect 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 RH, rather than altered LH processing capabilities (Seghier, Kherif, Josse, & Price, 2011). This is consistent with findings showing that decreased leftward asymmetry in gray matter volume in FS+ individuals reflects reduced synaptic pruning in the RH (Tzourio-Mazoyer, Simon, et al., 2010).

It has been proposed that LH-equivalent language capabilities exist in the RH but are usually masked by transcallosal interhemispheric inhibition from the dominant LH (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 LH's inhibition (Hamilton, Chrysikou, & Coslett, 2011). On 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., Scaff, Banich, Kramer, Narechania, & Simon, 2007), while inefficient for tasks that are simple and/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+ (compared to FS-) right-handers are better at understanding sentences presented under difficult reading/listening conditions but seem less sensitive to clausal structure and word position (Hancock & Bever, 2013), and they have better explicit memory but poorer implicit memory for words/letter strings (Christman & Propper, 2001; Townsend et al., 2001).

5. Conclusions

Overall, our findings demonstrate that even in right-handers with a strong manual preference, the RH is capable of processing language syntax in a manner similar to the LH. However, the tendency to show LH-like syntactic processing in the RH, as indexed by P600 effects, is importantly 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 observed in the basic science literature on language processing, but also for neurosurgical interventions and the potential for recovery after unilateral brain damage. It may also speak to 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; Francks et al., 2007; Corballis, 2009).

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Figure 1.

Grand average ERPs from all participants, shown (at top) at a representative electrode site over the center of the head. With presentation to the LH (RVF), syntactic violations elicit larger N400 and P600 responses (labeled). Presentation to the RH (LVF) yields a significant effect only in the N400 time window. The scalp topography of the P600 effect (ungrammatical minus grammatical) is shown at bottom.

Figure 2.

Grand average ERPs and scalp topography of the N400 and P600 effects (ungrammatical minus grammatical), shown for presentation to the LH (RVF) and RH (LVF) for participants without (FS-; at top) and with (FS+; at bottom) familial sinistrality. P600 effects were observed with LH presentation in both groups, but with RH presentation only in the FS+ group.

Figure 3.

Laterality of the P600 effect (size of effect for LH presentation minus size of effect for RH presentation) for individual participants in each familial sinistrality group. Nearly all FS- participants show a bias, with larger P600 responses with presentation to the LH than to the RH. In contrast, FS+ participants show an unbiased distribution.