Published in final edited form as:

Psychophysiology. 2017 December ; 54(12): 1929–1939. doi:10.1111/psyp.12970.

Age-related shifts in hemispheric dominance for syntactic processing

Michelle Leckey and Kara D. Federmeier

Psychology Department, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA

Abstract

Recent ERP data from young adults have revealed that simple syntactic anomalies elicit different patterns of lateralization in right-handed participants depending upon their familial sinistrality profile (whether or not they have left-handed biological relatives). Right-handed participants who do not have left-handed relatives showed a strongly lateralized response pattern, with P600 responses following left-hemisphere-biased presentations and N400 responses following right-hemisphere-biased presentations. Given that the literature on aging has documented a tendency to change across adulthood from asymmetry of function to a more bilateral pattern, we tested the stability of this asymmetric response to syntactic violations by recording ERPs as 24 older adults (age 60+) with no history of familial sinistrality made grammaticality judgments on simple two-word phrases. Results showed that the asymmetric pattern observed in right-handed adults without familial sinistrality indeed changes with age, such that P600 responses come to be elicited not only with left-hemisphere-biased but also with right-hemisphere-biased presentations in older adults. These findings suggest that, as with many other cognitive functions, syntactic processing becomes more bilateral with age.

Keywords

aging; ERPs; P600; syntactic processing

1 INTRODUCTION

Since Broca first reported asymmetric neural underpinnings for speech production, lateralization of cognitive functioning has been an important topic of research. Lesion and neuroimaging studies have established that there are hemispheric differences in a range of cognitive domains, including processing biases seen during motor and spatial tasks, memory retrieval, and language processing (see reviews by Cabeza, Locantore, & Anderson, 2003; Davidson & Hugdahl, 1995; Federmeier, Wlotko, & Meyer, 2008). Although this extensive research points to the prevalence of lateralization, important questions remain about the ways in which lateralization affects processing, how it might differ between individuals, and how it changes across the lifespan.

The best known asymmetry of cognitive functioning is arguably that of language, which has long been associated preferentially with the left hemisphere (LH). Much of the early research on language-related lateralization came from clinical populations, and views were thus shaped by the notable difficulty with language—especially language production—that was observed in patients with LH damage. However, over time, it became clear that there were also language impairments following right hemisphere (RH) damage, and we now know that the RH has more extensive language processing abilities than was previously appreciated (Baynes, Tramo, & Gazzaniga, 1992; Federmeier et al., 2008; Lindell, 2006). Moreover, the RH's role in specific aspects of language processing has become better delineated. For example, there is now evidence that the RH has the ability to extract meaning from both words and sentences and that it plays a role in the use of contextual information (Chiarello, Liu, Shears, Quan, & Kacinik, 2003; Coulson, Federmeier, Van Petten, & Kutas, 2005; Faust, Bar-Lev, & Chiarello, 2003; Kandhadai & Federmeier, 2007). Some studies have even found that RH processing is superior for some functions, such as the appreciation of event structure (Metusalem, Kutas, Urbach, & Elman, 2016) and the processing of joke-relevant information (Coulson & Wu, 2005). The field has thus begun moving away from the long-prevailing coarse-grained mapping between language and the LH and toward an appreciation of the need to characterize both hemispheres' specific contributions to language subprocesses.

One experimental method that has been used fruitfully to study hemispheric differences is that of ERPs, combined with the visual half-field (VF) paradigm. In the VF paradigm, stimuli are briefly presented in the periphery to either the right visual field or the left visual field. Because the initial processing of incoming visual sensory information is exclusive to the hemisphere contralateral to VF of presentation, this technique leads to processing biases that reveal hemispheric differences (Beaumont, 1983). The excellent temporal resolution of the ERP method allows these processing biases to be accurately measured as they unfold over time. Much of the literature using ERPs and the VF paradigm to study language has been focused on semantic processing, and, therefore, on the N400, a negative-going component that has been linked to the ease of accessing semantic information associated with meaningful stimuli (Kutas & Federmeier, 2011). VF studies measuring the N400 have revealed differences in how the two hemispheres make use of semantic context information (Federmeier & Kutas, 1999) and has shown that lateralization patterns are modulated both by individual differences and aging (Meyer & Federmeier, 2010). Whereas important progress has thus been made in characterizing the ability of each of the hemispheres to process word and message-level semantic information, surprisingly little work has been done looking at the hemispheres' abilities to make use of syntactic information.

The relative paucity of research on lateralization in syntactic processing generalizes beyond the ERP literature and has resulted in a lack of consensus about the RH's basic ability to appreciate language syntax. A number of behavioral studies with neurally intact participants have reported a lack of sensitivity in the RH to sentence level structure, suggesting a reduced ability to appreciate syntactic aspects of language (Arambel & Chiarello, 2006; Faust & Chiarello, 1998; Liu, Chiarello, & Quan, 1999). On the other hand, work with brain-damaged patients found that people with LH damage (intact RH) could better manipulate some kinds of syntactic information than those with damage in the RH (Schneiderman &

Saddy, 1988). Thus, the ability of the RH to process syntactic structure and the extent to which its syntactic processing is qualitatively similar to or distinct from that in the LH remains unclear.

In order to try to shed further light on the question of lateralization for syntax, Lee and Federmeier (2015) took advantage of the functional specificity of the ERP method to ask whether the RH is sensitive to syntactic violations and, if so, whether it is sensitive in the same way as the LH. In ERPs, syntactic processing is associated with modulations of a late positivity known as the P600, which has been linked to various different aspects of syntactic integration and reanalysis (Hahne & Friederici, 1999; Kuperberg, Caplan, Sitnikova, Eddy, & Holcomb, 2006; Osterhout & Holcomb, 1995). The component is usually seen between 500–700 ms (although this is variable) and, in young adults, the distribution is mainly posterior (Kaan, Harris, Gibson, & Holcomb, 2000).

In the Lee and Federmeier (2015) study, participants were asked to assess a series of two-word phrases, which were either grammatically congruent or incongruent. Grammatical phrases were either the word *the* paired with a noun (e.g., *the sofa*) or *to* paired with a verb (e.g., *to examine*), and ungrammatical phrases used the incorrect function word pairing (e.g., *the examine/to sofa*). The critical nouns and verbs were presented using the VF paradigm. As expected, an enhanced P600 was seen in the response to the grammatical violations with presentation biased to the LH (critical words presented in the right VF). Of greatest interest, then, was whether the RH was also capable of eliciting a P600 effect. Lee and Federmeier (2015) found that it was, but in a manner that was importantly influenced by familial sinistrality. Participants who had left-handed biological relatives (FS+) showed a P600 response with both RVF and LVF presentation. Thus, the RH does seem to be capable, in some cases, of producing a LH-like response. However, participants with no left-handed biological relatives (FS-) showed the P600 effect only with right visual field (RVF/LH) presentation. For these participants, left visual field (LVF/RH) presentation instead elicited an N400 effect, with a larger N400 seen in response to the violations. This suggests that, although the RH is sensitive to the fact that the word is unexpected in its context, it is not treating the anomaly as a violation of a syntactic category (cf. Tyler, Wright, Randall, Marslen-Wilson, & Stamatakis, 2010).

Lee and Federmeier (2015) suggested that the asymmetry seen in syntactic processing in their FS- subgroup may have arisen because RH syntactic processes were suppressed due to interhemispheric inhibition coming from the dominant LH. This idea finds support in the stroke literature, where it has been found that after a LH stroke there is often a rapid increase in activation in the RH homologues of language areas (Hamilton, Chrysikou, & Coslett, 2011). In this account, then, the RH of FS- individuals has the capacity for LH-like processing (i.e., the ability to elicit a P600 to syntactic violations), but this ability is normally suppressed. This hypothesis raises interesting and important questions about what might happen to such interhemispheric inhibition, and the functional lateralization that it supports, over the course of normal aging, given that aging has been associated with increases in bilateral processing in nonlanguage domains (Cabeza, 2002).

A growing number of studies have documented age-related shifts in lateralization patterns. In particular, functions that show strongly lateralized patterns in young adults are often found to elicit bilateral activity in older adults (see reviews by Cabeza, 2002; Park & Reuter-Lorenz, 2009). One account of this age-related decrease in neural asymmetry argues that the older brain recruits more neural processing resources, leading to more widespread brain activation during cognitive tasks, when compared to their younger counterparts. This increase in activation is thought to act in a compensatory way, reducing age-related decline in function, and, in line with this idea, in some cases better performance has been seen among those older adults who manifested the highest degree of neural recruitment (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, 2008; Reuter-Lorenz et al., 2000). The idea of compensatory bilateral activation has largely been documented in tasks that were not actively targeting linguistic processes; however, in the language domain there is some evidence of compensatory recruitment of the RH in patients, where greater language recovery has been seen in those patients who show bilateral activation of well-known language areas after brain damage (e.g., Cao, Vikingstad, George, Johnson, & Welch, 1999).

An alternative to the compensation account has been proposed, which suggests that bihemispheric patterns seen in older adults reflect dedifferentiation, wherein there is a loss of specificity in neural representations of cognitive processes resulting in less efficient processing (Li & Lindenberger, 1999). This account suggests that cognitive abilities that are distinct in young adults become more generalized with age, and evidence for this comes from increased correlations between cognitive abilities seen with advancing age (Baltes & Lindenberger, 1997). Despite the differences in these two accounts, they need not be mutually exclusive. For example, aging brains may have a tendency to experience dedifferentiation, with the resulting increased recruitment yielding benefits in some cases and costs in others.

Given that aging is associated with increases in bilateral processing, the stability of the asymmetry found during syntactic processing in the young FS- group (Lee & Federmeier, 2015) is an intriguing topic of investigation. Few studies have used ERPs to examine older adults' syntactic processing. However, one study has established that older adults elicit P600 responses to simple syntactic structures that are similar to those seen in younger adults in both size and timing, albeit with a topographic shift (more frontal in distribution relative to the P600 seen for young adults; Kemmer, Coulson, De Ochoa, & Kutas, 2004). To date, no study has used ERPs and VF methods to examine syntactic processing, and associated P600 responses, in older adults. Thus, the present study uses the paradigm of Lee and Federmeier (2015) with healthy right-handed older adults with no history of familial sinistrality—that is, the group that, for young adults, showed a strongly lateralized pattern. If that pattern seen in the young adult study remains, this will suggest that, at least in terms of this type of simple syntactic processing, lateralization of function is stable. However, if there is age-related change in lateralization—due to dedifferentiation or compensatory recruitment—then we would expect to see that in an older FS- group there will be a P600 for RH-biased, as well as LH-biased, presentation. This would support the idea that, with age, lateralization of language processing can change, such that the RH is able to process syntax in a LH-like fashion (e.g., when it is not being inhibited). In turn, such a finding would open up

opportunities to examine the functional consequences of lateralized versus more bilateral processing patterns in language.

2 METHOD

2.1 Participants

Electrophysiological data were recorded from 33 older adult participants, recruited from the local community around Champaign-Urbana and paid for their participation. All were right-handed, as assessed by self-report and the Edinburgh inventory (mean score 0.89; range 0.55–1; Oldfield, 1971), and were monolingual English speakers with no second language experience before the age of 5. Participants had normal or corrected-to-normal vision, were free of psychiatric or neurological disorders, and did not have prior history of skull fracture. As the literature provides support specifically for the idea that processing that is lateralized in young adults can become more bilateral with age, we targeted the group that, in the young adult study, showed the lateralized effect pattern. Therefore, all participants had an FS-profile. Familial handedness was assessed through completion of a questionnaire (Bishop, 1980), and FS- participants were defined as those who did not have any left-handed relatives.¹ Electrophysiological data from 9 of the participants were excluded from analysis due to excessive artifact contamination. Of the 24 remaining participants, 12 were female and 12 were male with a mean age of 67 (range 60–83). Of the 20 participants who provided educational information, all had completed high school, 16 had taken at least 2 years of college and, of these, 9 had completed a graduate degree. Before the ERP portion of the experiment, each participant completed the Montreal Cognitive Assessment (MoCA, Nasreddine et al., 2005) to screen for cognitive impairment. From a total of 30 points, all included participants scored 24 or higher when adjusted for education (mean 26, range 24–29), and thus were not displaying signs of notable cognitive impairment (Luis, Keegan, & Mullan, 2009; Rossetti, Lacritz, Cullum, & Weiner, 2011; Waldron-Perrine & Axelrod, 2012).

2.2 Materials

Materials were the same as those used by Lee and Federmeier (2015). They consisted of two-word phrases that were manipulated in terms of the visual field of presentation of the critical second word (RVF vs. LVF) as well as its grammaticality. Critical words consisted of 92 unambiguous nouns and 92 unambiguous verbs, while 184 noun/verb homographs (e.g., *drink*) were used as fillers. Unambiguous words were those for which the Oxford English Dictionary listed only in a noun or verb sense. As much as possible, words were matched for concreteness, frequency, and word length. All 368 words were used for each participant. For the unambiguous words, half were preceded by the correct determiner for the word class (*to* for the verbs and *the* for the nouns) and the other half were preceded by the incorrect determiner (*the* for verbs and *to* for nouns). Ambiguous homographs were used equally often in their noun and verb senses, making the proportion of ungrammatical trials in the experiment 25%. Across lists, critical items were used equally often in grammatical and

¹During periods encompassing the time that our participants and their relatives were growing up, it was a common practice in some places to force left-handed people to write with their right hand. Thus, our participants were questioned about this and, if the participant and/or his/her relatives were known to be subject to this practice, s/he was excluded from the study.

ungrammatical trials (and, for ambiguous items, as nouns and verbs). Visual field was also counterbalanced across lists, so that each word appeared equally often in the left and right visual field in each condition. Four lists were created, and participants were randomly assigned to one of the four.

2.3 Procedures

Participants were seated 100 cm from the screen in a quiet testing room and were instructed both in writing and verbally as to the nature of the task. Throughout the experiment, a small white square appeared just below the center of the screen to provide a fixation point, helping participants resist orienting to the laterally presented words. Each trial began with a series of four plus signs appearing in the center of the screen for 500 ms to alert the participant that a trial was about to begin. After a stimulus onset asynchrony ranging randomly between 1,000 and 1,500 ms (jittered to reduce the contribution of slow, anticipatory potentials to the average ERP signal), the determiner (*to/the*) was presented in the center of the screen for 200 ms. This was followed by a 300-ms interstimulus interval before the target word was presented to either the right or the left visual field for 200 ms. Presentation order for the phrases was randomized with the constraint that no more than two could appear consecutively in the same visual field. After an interval of 1,500 ms, the target word was followed by the word *OKAY?* At this point, the participant was required to make a judgment on the grammaticality of the two-word phrase, pressing a response button in one hand for “yes” (grammatical) and a button in the other hand for “no” (ungrammatical). The response hands were counterbalanced across participants. This probe remained on the screen until the participant made a response by pushing a button, and there was a further interval of 2,500 ms before the next trial began. Participants were instructed to maintain central fixation throughout the experiment and to try to minimize blinking. To prevent fatigue, the experiment was divided into seven equal blocks, each lasting around 6 min, with a short break in between each block.

2.4 EEG recording parameters

The EEG was recorded from 26 evenly spaced silver/silver-chloride electrodes attached to an elastic cap. The 26 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 (LDf and RDf), left and right lateral frontal (LLf and RLf), 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 scalp electrodes were referenced online to the left mastoid and rereferenced offline 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 electrooculogram (EOG), and another two electrodes were placed on the outer canthus of each eye to monitor the horizontal EOG. Electrode impedances were kept below 5 k Ω . The continuous EEG was amplified using Sensorium amplifiers through a band-pass filter of 0.02–100 Hz and recorded at a sampling rate of 250 Hz.

2.5 Data analysis

The EEG data for all trials were separated into epochs, which began 200 ms before the onset of the lateralized target word (noun/verb) and ended 1,500 ms after onset. A baseline acquired over the 200 ms prior to target onset was subtracted before averaging, and a digital band-pass filter of 0.1 to 20 Hz was applied to the data. Epochs tainted with lateral saccadic eye movements (17.5%), blocking (0.3%), or drift (1.7%) were rejected. Trials containing blinks were corrected for the 5 participants who had enough blink and nonblink trials to produce a reliable filter (see Dale, 1994, for the procedure); blink trials were removed for the remaining 19 participants (8.8%). To correct for sphericity, the Huynh-Feldt correction was applied where applicable, and the resulting corrected p values are reported. Interactions with electrode site are reported only when of theoretical significance.

Mean amplitude ERP responses were measured in three consecutive 300-ms time windows: 300–600 ms (N400), 600–900 ms (early P600), and 900–1,200 ms (late P600). The N400 window is the same as that used for young adults by Lee and Federmeier (2015). The P600 windows used here encompass much of the single (800–1,400 ms) time window used to measure the young adult P600, while allowing for a more detailed examination of the time course of the (less well-characterized) older adult P600 component. In all cases, we first analyzed ERP data of all trials, and then we conducted analyses on the data for correct trials only. This allowed us to ascertain whether aspects of the brain response were different for trials that afforded correct grammaticality judgments. Three participants were removed from this latter set of analyses due to high trial loss (resulting in fewer than 15 items for any critical bin) from a combination of artifacts and low accuracy (less than 50% in one or both visual fields); therefore, reports on correct trials are based on the remaining 21 participants. To afford inferences about age-related change, we also supplement the analyses done on the older adult group with direct statistical comparisons between that group and the young adult data from Lee and Federmeier (2015), which was collected in the same lab using the same procedures.

3 RESULTS

3.1 Behavioral results

Participants correctly judged the grammaticality of the phrase 76% of the time on average. Accuracy ranged from 44% to 89% in individual participants; note that rapidly presented lateralized words can be difficult for participants to accurately consciously perceive, and participants were instructed to prioritize maintaining eye control over behavioral accuracy. There was no significant difference between accuracy for ungrammatical and grammatical trials, $t(23) = -0.831$; $p > .05$, indicating that participants were not biased toward a particular response. Accuracy was higher for RVF presentation (79%) than for LVF presentation (72%), $t(23) = 4.61$; $p < .001$. This performance was only slightly poorer than that reported for young subjects by Lee and Federmeier (2015), who found 81% accuracy for RVF and 75% for the LVF. To directly compare the groups, we conducted a repeated measures analysis of variance (ANOVA) with two levels of VF (LVF and RVF) and the between-subjects factor of group (older adults and young adults). This analysis revealed no effect of group, $F(1, 57) = 0.152$; $p > .05$, but did show an effect of VF, $F(1, 57) = 53.992$; $p < .001$,

highlighting the greater accuracy in both groups to trials in which the critical word was presented to the RVF/LH.

3.2 ERP results: Older adults

3.2.1 N400 time window—For young FS- adults, Lee and Federmeier (2015) found that N400 amplitudes were equivalent across grammatical and ungrammatical trials for RVF/LH presentation, but differed in the LVF/RH, with ungrammatical trials eliciting larger amplitude (more negative) N400s than grammatical ones. To test for this pattern in the older adult sample, mean amplitudes between 300 and 600 ms were subjected to a repeated measures ANOVA with two levels of VF (RVF, LVF), two levels of grammaticality (grammatical, ungrammatical), and 26 levels of electrode (all scalp channels). There was a main effect of VF, $F(1, 23) = 5.69$; $p < .05$, with larger N400 responses overall in the RVF/LH. This main effect interacted with electrode, $F(25, 575) = 10.07$; $p < .001$, reflecting the typical mediocentral distribution of the N400. There was no main effect of grammaticality, $F(1, 23) = 4.04$, $p > .05$, and, different from the pattern in the young, no interaction between VF and grammaticality, $F(1, 23) = 0.85$, $p > .05$.

For analyses limited to correct trials, in addition to the main effect of VF, $F(1, 20) = 4.97$; $p < .05$, there was also a main effect of grammaticality, $F(1, 20) = 6.23$, $p < .05$, with larger N400 responses seen to the violations in comparison to the grammatically correct phrases. This may indicate that some level of semantic processing is boosting the analysis of the phrases that are being judged correctly. Critically, however, there was again no significant interaction between VF and grammaticality, $F(1, 20) = 1.29$, $p > .05$. Thus, different from FS- young adults, FS- older adults did not elicit a lateralized N400 grammaticality response, regardless of whether all trials or only correct trials are considered.

3.2.2 P600 time windows—Of critical interest in this study is the P600 effect of grammaticality. Given findings that the topography of the P600 shifts with age (Kemmer et al., 2004), we first assessed the distribution of the basic P600 grammaticality effect using a repeated measures ANOVA with two levels of grammaticality (grammatical, ungrammatical), and the 16 electrode sites that could be averaged across two levels of hemisphere (left, right), two levels of laterality (central, lateral) and four levels of anteriority (prefrontal [including LLPf, LMPf, RMPf, RLPf], frontal [including LLFr, LMFr, RMFr, RLFr], central [LLTe, LMCE, RMCE, RLTe], occipital [including LLOc, LMOc, RMOc, RLOc]). The distribution in both the early and late time windows was similar. Grammaticality interacted with laterality in both time windows (early: $F(1, 23) = 12.62$, $p < .01$, and late: $F(1, 23) = 4.36$, $p < .05$), indicating larger P600 effects over central than lateral sites, as has typically been observed. Also in both time windows, this effect was moderated by a three-way interaction among grammaticality, laterality, and anteriority (early: $F(3, 69) = 10.32$, $p < .001$, and late: $F(3, 69) = 4.36$, $p < .05$), as the tendency for larger P600 effects over central versus lateral sites was less pronounced over both the prefrontal and occipital locations. All other interactions in both time windows were not significant ($F_s < 2.3$; $p_s > .14$). Thus, different from the strongly posterior distribution attested in young adults, older adults' P600 distribution was broader and also encompassed anterior electrode sites. Accordingly, we analyzed P600 responses in both time windows using a repeated measures

ANOVA with two levels of VF (RVF, LVF), two levels of grammaticality (grammatical, ungrammatical), and all 26 levels of electrode (rather than only posterior sites, as in Lee & Federmeier, 2015).

3.2.3 Early P600 time window (600–900 ms)—In this early time window, there was no main effect of VF, $F(1, 23) = 3.05$, $p > .05$, indicating that the P600 effect was comparable with presentation biased to either hemisphere. The main effect of grammaticality was significant, $F(1, 23) = 11.22$, $p < .01$, reflecting a larger P600 in response to syntactic violations when compared to syntactically correct phrases (RVF ungrammatical 4.25 μV , RVF grammatical 3.59 μV , LVF ungrammatical 3.87 μV , LVF grammatical 3.32 μV). Critically, however, grammaticality did not interact with VF, $F(1, 23) = 0.12$, $p > .05$. Thus, different from FS- young adults, FS- older adults did not show a lateralized P600 response. This pattern was identical when only correct trials were analyzed (no main effect of VF, $F(1, 20) = 2.81$, $p > .05$; main effect of grammaticality, $F(1, 20) = 10.15$, $p < .005$; no Grammaticality $\times$ VF interaction, $F(1, 20) = 0.03$, $p > .05$).

3.2.4 Late P600 time window (900–1,200 ms)—In the later time window, there was no main effect of VF, $F(1, 23) = 0.46$, $p > .05$, indicating that in this time window the response was again comparable for presentation in either VF. The significant main effect of grammaticality continued into this time window, suggesting that the early and late analyses are tapping into the same response, $F(1, 23) = 4.55$, $p < .05$ (RVF ungrammatical 2.52 μV , RVF grammatical 1.69 μV , LVF ungrammatical 2.56 μV , LVF grammatical 2.02 μV). The critical interaction of Grammaticality $\times$ VF was again not significant in this time window, $F(1, 23) = 0.82$, $p > .05$. When only correct trials were analyzed, there were no significant effects in this time window, although the numerical pattern of the grammaticality effect was the same (RVF ungrammatical 2.41 μV , RVF grammatical 1.76 μV , LVF ungrammatical 2.64 μV , LVF grammatical 2.03 μV); this outcome may have been influenced by the reduction in power for this analysis, given that it was done with fewer subjects. Again, critically, there was no interaction between grammaticality and VF, $F(1, 20) = 0.01$, $p > .05$.

3.3 ERP results: Direct comparison of young adults and older adults

Figure 1 shows the asymmetric pattern in the young adults from Lee and Federmeier (2015) alongside the bilateral P600 of the older adult group from the current study, highlighting the different patterns that have been demonstrated in the within-subject statistics of the two groups. Note that changes in both the timing and the distribution of the P600 (which shifts from a largely posterior distribution in young adults to a more widespread distribution in older adults, encompassing frontal electrode sites; cf. Kemmer et al., 2004) creates difficulties for direct statistical comparisons between the groups' waveforms. Here, in the interest of comparing the VF-based grammaticality effect pattern in the two groups, we used the time window (800–1,400 ms) and channel distribution (15 posterior channels) from the young adult analysis, since this also captures the more widespread effect in the older adults. Note that, although this choice may underrepresent the amplitude of the older adults' responses, the question of primary interest is not about the effect size but rather whether the groups differ in the pattern of their grammaticality effect as a function of the VF manipulation.

Thus, to directly compare the critical effect pattern in the two groups, we computed a grammaticality effect laterality index for the P600, in which the RH grammaticality effect is subtracted from the LH grammaticality effect. Figure 2 shows this effect for all individuals in both the young (see also Lee & Federmeier, 2015, figure 3) and older adult (present study) groups. This figure clearly shows that the pattern for the young group is highly skewed, with most subjects showing larger P600 effects in the LH. In contrast, the older adult group does not manifest this bias (similar to the young FS+ group in Lee & Federmeier, 2015, figure 3). Using this index (and again retaining the time window and channel distribution originally used for the younger adults, since their effects were more distributionally restricted), we compared the groups using a two-way mixed ANOVA with 2 levels of group (old vs. young) and 15 levels of electrode, revealing a significant effect of group, $F(1, 57) = 5.526$; $p < .05$. Thus, with age, there is a shift from a strongly lateralized pattern to a bilateral one.

4 DISCUSSION

The present experiment aimed to determine whether the left-lateralized pattern of syntactic processing observed in FS-young adults (Lee & Federmeier, 2015) remained stable with age. In the young sample, the two hemispheres were found to qualitatively differ in their response to syntactic violations. Responses elicited to LH-biased presentation showed the P600 response pattern that is normatively associated with the appreciation of syntactic violations in monolingual speakers. However, with initial presentation to the RH, ERPs instead revealed sensitivity to the violations in the form of a larger N400 response to ungrammatical phrases compared to grammatical phrases. N400 amplitude modulations have been associated with ease of semantic access; therefore, Lee and Federmeier (2015) suggested that the RH of FS- young adults responded only to the lexicosemantic unexpectedness of the words, as opposed to their syntactic properties. The aging literature proposes an alternative outcome in an older adult sample. There is often an increase in bilateral processing with age, which leads to the prediction that the asymmetric response seen in the young adults may disappear, such that the pattern in older adults will more closely resemble that of FS+ young adults, who showed a P600 response in both the LH and the RH.

Behavioral results indicated that the older participants had a similar level of accuracy in identifying syntactic violations as the young adult sample. This is consistent with prior results showing that, although comprehension is often slowed in older adults, accuracy is comparable to that of a younger sample (Wingfield, Peelle, & Grossman, 2003). ERP results, however, reveal that this comparable accuracy is not arising from the same pattern of neural processing in the young and older adults. For presentation biased to the LH, older adults show a response that is qualitatively similar to that seen for the young adult group. In particular, there is an increased positivity (P600) to the ungrammatical words, beginning around 600 ms and continuing to around 1,200 ms. Only one prior study has investigated syntactic processing in older adults using ERPs (Kemmer et al., 2004), and they found that older adults elicited a P600 effect of similar size as and with similar timing to that of young adults, but with a shifted distribution, such that the P600 response was larger over posterior sites in young adults but larger over frontal sites in older adults. Here, too, we found a robust P600 response over a similar time window (if anything, the older adult response seemed to

start and end earlier than that seen in the young adult study), but with a broader topography that included anterior electrode sites. This pattern is similar to that seen for the P300, which is often linked with the P600 (e.g., Coulson, King, & Kutas, 1998) and which also manifests a frontal shift in distribution with advancing age (Fabiani, Friedman, & Cheng, 1998; Iragui, Kutas, Mitchiner, & Hillyard, 1993). The source of the age-related distributional shift is unclear; importantly, however, both groups elicit a morphologically, functionally, and temporally similar response to grammaticality violations. Of primary interest for this study, then, is whether this response changes its pattern of lateralization with age, as assessed using the VF paradigm.²

In the young sample, FS- adults failed to show a similar P600 with RH-biased presentation, instead showing an N400 modulation (Lee & Federmeier, 2015). In the present study, however, older adults from this same FS- group instead elicited a P600 response that was similar in timing and distribution to that seen in the LH/RVF. The P600 was numerically smaller than that in the LH; however, this size difference did not prove to be statistically significant. Interestingly, when accounting for correctness, a similar N400 response was seen in the older adult sample, suggesting that these correct judgments were receiving a semantic boost; however, as with the P600 response in this group, this effect was also seen bilaterally.

The results of this study are interesting, as they provide the first evidence that the P600 can be elicited by the RH in a homogenous FS- sample, a group that is particularly associated with left-lateralized language processing. When taken with the young study by Lee and Federmeier (2015), the results also show a shift from a highly lateralized pattern of syntactic processing to a much more bilateral one over the course of normal aging—a pattern similar to that documented for many other cognitive processes (e.g., Reuter-Lorenz et al., 2000; Stebbins et al., 2002). Despite the fact that these age-related shifts to bilateral processing have been widely attested, prior to the present experiment this had not been investigated in the area of syntactic processing, and the shift toward a more bilateral pattern in older adults is particularly striking in this domain, given that language in general and syntax in particular (Tyler et al., 2010) is one of the functions that is most associated with asymmetry in the brain.

An advantage of ERPs is that they provide information not only about whether there is lateralized or bilateral activity but, more specifically, about the type(s) of processes being engaged. Thus, the use of ERPs in the present study allows us to see that the RH of older adults is not only responding to the syntactic violations but is responding in a way that suggests that there appears to be a functional ability to appreciate syntactic category. A similar pattern is seen in young adults with familial sinistrality. The age-related shift seen for FS- individuals is similar to the pattern that is seen in the literature looking at second language acquisition, wherein learners show N400 effects to syntactic violations when they

²Determining the nature and source of the distributional shift is difficult because of the inverse problem—here, specifically the fact that many different types of changes to the underlying neural generators could produce the same change in distribution at the scalp. The distributional shift may reflect nothing more than a shift in orientation of the same generator due to, for example, age-related structural changes in the brain. Alternatively, this shift may reflect additions to or changes in the brain areas that are responsible for the effect pattern. Because we do not have information that can allow us to determine the cause of this shift, we do not try to interpret it here. Importantly, note that the inferences we draw about the lateralization of the P600 are different in source, as they are not based on scalp topographic patterns but, instead, on sensitivity to the VF manipulation.

are in the early stages of learning a language and, over time, come to elicit the more typical P600 (Osterhout et al., 2008). In this line of research, investigators have proposed that the change from N400 to P600 reflects the “grammaticalization” of features associated with the newly acquired language. Thus, it is possible that with age (and concomitant increases in language experience), the RH of FS- individuals shifts to begin to grammaticalize particular features of the native language.

Lee and Federmeier (2015) hypothesized that the lateralized pattern seen in the young FS-group might arise due to interhemispheric inhibition. Inhibition between the hemispheres is thought to be reduced in the FS+ population, allowing increased access to RH processing (Prichard, Propper, & Christman, 2013). What is not clear from the extant data in young adults is whether such inhibition suppresses what would be a functional response in the RH, or, instead, whether inhibition or other factors prevent the RH of FS-individuals from acquiring that functional response. Although the present data cannot provide a definitive answer to that question, they do seem to indicate an ability of the RH to process grammatical violations in a manner qualitatively similar to that of the LH, even in FS- individuals, once those individuals are older. This is thus consistent with the hypothesis that age-related changes reduce interhemispheric inhibition (which could be seen as a form of age-related dedifferentiation) and thus reveal a functional RH response in this group. It is unclear from this data alone whether RH syntactic processing abilities can serve a compensatory role for FS- older adults. More generally, ERP studies of hemispheric change with age have suggested that some types of bilateral processing patterns are associated with higher functioning in older adults, whereas other types of bilateral activation patterns are associated with lower functioning; thus, hemispheric recruitment in older adults is more complicated than predicted by either a dedifferentiation or a compensatory account alone (Meyer & Federmeier, 2010). Importantly, in the present study, the nature of the response observed with RH-biased processing at least suggests the possibility that the RH could make useful contributions to the processing of syntactic information for older adults. This, in turn, has important implications for recovery from brain damage in this group.

Acknowledgments

Funding information

James S. McDonnell Foundation, National Institutes of Health (grant AG026308) (to K. D. F.)

References

- Arambel SR, Chiarello C. Priming nouns and verbs: Differential influences of semantic and grammatical cues in the two cerebral hemispheres. *Brain and Language*. 2006; 97(1):12–24. <https://doi.org/10.1016/j.bandl.2005.07.003>. [PubMed: 16099493]
- Baltes PB, Lindenberger U. Emergence of a powerful connection between sensory and cognitive functions across the adult life span: A new window to the study of cognitive aging? *Psychology and Aging*. 1997; 12(1):12–21. <https://doi.org/10.1037/0882-7974.12.1.12>. [PubMed: 9100264]
- Baynes K, Tramo MJ, Gazzaniga MS. Reading with a limited lexicon in the right hemisphere of a callosotomy patient. *Neuropsychologia*. 1992; 30(2):187–200. [https://doi.org/10.1016/0028-3932\(92\)90027-J](https://doi.org/10.1016/0028-3932(92)90027-J). [PubMed: 1560896]
- Beaumont, JG. Methods for studying cerebral hemispheric function. In: Young, AW., editor. *Functions of the right cerebral hemisphere*. London, UK: Academic Press; 1983. p. 114–146.

- Bishop DVM. Measuring familial sinistrality. *Cortex*. 1980; 16(2):311–313. [https://doi.org/10.1016/S0010-9452\(80\)80067-0](https://doi.org/10.1016/S0010-9452(80)80067-0). [PubMed: 7471771]
- Cabeza R. Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging*. 2002; 17(1):85–100. <https://doi.org/10.1037/0882-7974.17.1.85>. [PubMed: 11931290]
- Cabeza R, Anderson ND, Locantore JK, McIntosh AR. Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage*. 2002; 17:1394–1402. <https://doi.org/10.1006/nimg.2002.1280>. [PubMed: 12414279]
- Cabeza R, Locantore JK, Anderson ND. Lateralization of prefrontal activity during episodic memory retrieval: Evidence for the production-monitoring hypothesis. *Journal of Cognitive Neuroscience*. 2003; 15(2):249–259. <https://doi.org/10.1162/089892903321208187>. [PubMed: 12676062]
- Cao Y, Vikingstad EM, George KP, Johnson AF, Welch KMA. Cortical language activation in stroke patients recovering from aphasia with functional MRI. *Stroke*. 1999; 30(11):2331–2340. <https://doi.org/10.1161/01.STR.30.11.2331>. [PubMed: 10548667]
- Chiarello C, Liu S, Shears C, Quan N, Kacinik N. Priming of strong semantic relations in the left and right visual fields: A time-course investigation. *Neuropsychologia*. 2003; 41(6):721–732. [https://doi.org/10.1016/S0028-3932\(02\)00220-8](https://doi.org/10.1016/S0028-3932(02)00220-8). [PubMed: 12591029]
- Coulson S, Federmeier KD, Van Petten C, Kutas M. Right hemisphere sensitivity to word- and sentence-level context: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2005; 31(1):129–147. <https://doi.org/10.1037/0278-7393.31.1.129>.
- Coulson S, King JW, Kutas M. Expect the unexpected: Event-related brain response to morphosyntactic violations. *Language and Cognitive Processes*. 1998; 13:21–58. <https://doi.org/10.1080/016909698386582>.
- Coulson S, Wu YC. Right hemisphere activation of joke-related information: An event-related brain potential study. *Journal of Cognitive Neuroscience*. 2005; 17(3):494–506. <https://doi.org/10.1162/0898929053279568>. [PubMed: 15814008]
- Dale, AM. Source localization and spatial discriminant analysis of event-related potentials: Linear approaches. University of California; San Diego, La Jolla, CA: 1994.
- Davidson, RJ., Hugdahl, K. Brain asymmetry. Cambridge, MA: MIT Press; 1995.
- Fabiani M, Friedman D, Cheng JC. Individual differences in P3 scalp distribution in older adults, and their relationship to frontal lobe function. *Psychophysiology*. 1998; 35(6):698–708. <https://doi.org/10.1111/1469-8986.3560698>. [PubMed: 9844431]
- Faust M, Bar-Lev A, Chiarello C. Sentence priming effects in the two cerebral hemispheres: Influences of lexical relatedness, word order, and sentence anomaly. *Neuropsychologia*. 2003; 41(4):480–492. [https://doi.org/10.1016/S0028-3932\(02\)00138-0](https://doi.org/10.1016/S0028-3932(02)00138-0). [PubMed: 12559164]
- Faust M, Chiarello C. Constraints on sentence priming in the cerebral hemispheres: Effects of intervening words in sentences and lists. *Brain and Language*. 1998; 63(2):219–236. <https://doi.org/10.1006/brln.1997.1941>. [PubMed: 9654432]
- Federmeier KD, Kutas M. Right words and left words: Electrophysiological evidence for hemispheric differences in meaning processing. *Cognitive Brain Research*. 1999; 8(3):373–392. [https://doi.org/10.1016/S0926-6410\(99\)00036-1](https://doi.org/10.1016/S0926-6410(99)00036-1). [PubMed: 10556614]
- Federmeier KD, Wlotko EW, Meyer AM. What's 'right' in language comprehension: Event-related potentials reveal right hemisphere language capabilities. *Language and Linguistics Compass*. 2008; 2(1):1–17. <https://doi.org/10.1111/j.1749-818X.2007.00042.x>. [PubMed: 19777128]
- Grady CL. Cognitive neuroscience of aging. *Annals of the New York Academy of Sciences*. 2008; 1124:127–144. <https://doi.org/10.1196/annals.1440.009>. [PubMed: 18400928]
- Hahne A, Friederici AD. Electrophysiological evidence for two steps in syntactic analysis: Early automatic and late controlled processes. *Journal of Cognitive Neuroscience*. 1999; 11(2):194–205. <https://doi.org/10.1162/089892999563328>. [PubMed: 10198134]
- Hamilton RH, Chrysikou EG, Coslett B. Mechanisms of aphasia recovery after stroke and the role of noninvasive brain stimulation. *Brain and Language*. 2011; 118:40–50. <https://doi.org/10.1016/j.bandl.2011.02.005>. [PubMed: 21459427]

- Iragui VJ, Kutas M, Mitchiner MR, Hillyard SA. Effects of aging on event-related brain potentials and reaction times in an auditory oddball task. *Psychophysiology*. 1993; 30(1):10–22. <https://doi.org/10.1111/j.1469-8986.1993.tb03200.x>. [PubMed: 8416055]
- Kaan E, Harris A, Gibson E, Holcomb P. The P600 as an index of syntactic integration difficulty. *Language and Cognitive Processes*. 2000; 15(2):159–201. <https://doi.org/10.1080/016909600386084>.
- Kandhadai P, Federmeier KD. Multiple priming of lexically ambiguous and unambiguous targets in the cerebral hemispheres: The coarse coding hypothesis revisited. *Brain Research*. 2007; 1153:144–157. <https://doi.org/10.1016/j.brainres.2007.03.046>. [PubMed: 17459344]
- Kemmer L, Coulson S, De Ochoa E, Kutas M. Syntactic processing with aging: An event-related potential study. *Psychophysiology*. 2004; 41:372–384. <https://doi.org/10.1111/1469-8986.2004.00180.x>. [PubMed: 15102122]
- Kuperberg GR, Caplan D, Sitnikova T, Eddy M, Holcomb PJ. Neural correlates of processing syntactic, semantic, and thematic relationships in sentences. *Language and Cognitive Processes*. 2006; 21(5):489–530. <https://doi.org/10.1080/01690960500094279>.
- Kutas M, Federmeier KD. Thirty years and counting: Finding meaning in the N400 component of the event related brain potential (ERP). *Annual Review of Psychology*. 2011; 62:621–647. <https://doi.org/10.1146/annurev.psych.093008.131123>.
- Lee C, Federmeier KD. It's all in the family: Brain asymmetry and syntactic processing of word class. *Psychological Science*. 2015; 26(7):997–1005. <https://doi.org/10.1177/0956797615575743>. [PubMed: 25963616]
- Li, S-C., Lindenberger, U. Cross-level unification: A computational exploration of the link between deterioration of neurotransmitter systems dedifferentiation of cognitive abilities in old age. In: Nilsson, L-G., Markowitsch, HJ., editors. *Cognitive Neuroscience of Memory*. Seattle, WA: Hogrefe & Huber; 1999. p. 103-146.
- Lindell AK. In your right mind: The hemisphere contributions to language processing and production. *Neuropsychology Review*. 2006; 16:131–148. <https://doi.org/10.1007/s11065-006-9011-9>. [PubMed: 17109238]
- Liu SR, Chiarello C, Quan N. Hemispheric sensitivity to grammatical cues: Evidence for bilateral processing of number agreement in noun phrases. *Brain and Language*. 1999; 70(3):483–503. <https://doi.org/10.1006/brln.1999.2185>. [PubMed: 10600230]
- Luis CA, Keegan AP, Mullan M. Cross validation of the Montreal Cognitive Assessment in community dwelling older adults residing in the Southeastern US. *International Journal of Geriatric Psychiatry*. 2009; 24(2):197–201. <https://doi.org/10.1002/gps.2101>. [PubMed: 18850670]
- Metusalem R, Kutas M, Urbach TP, Elman JL. Hemispheric asymmetry in event knowledge activation during incremental language comprehension: A visual half-field ERP study. *Neuropsychologia*. 2016; 84:252–271. <https://doi.org/10.1016/j.neuropsychologia.2016.02.004>. [PubMed: 26878980]
- Meyer AM, Federmeier KD. Event-related potentials reveal the effects of aging on meaning selection and revision. *Psychophysiology*. 2010; 47(4):673–686. <https://doi.org/10.1111/j.1469-8986.2010.00983.x>. [PubMed: 20210876]
- Nasreddine ZS, Phillips NA, Bédirian V, Charbonneau S, Whitehead V, Collin I, ... Chertkow H. The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society*. 2005; 53(4):695–699. <https://doi.org/10.1111/j.1532-5415.2005.53221.x>. [PubMed: 15817019]
- Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*. 1971; 9(1):97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4). [PubMed: 5146491]
- Osterhout, L., Holcomb, PJ. Event-related potentials and language comprehension. In: Rugg, MD., Coles, MGH., editors. *Electrophysiology of mind: Event-related brain potentials and cognition*. Oxford. UK: Oxford University Press; 1995. p. 171-215.
- Osterhout L, Poliakov A, Inoue K, McLaughlin J, Valentine G, Pitkanen I, ... Hirschensohn J. Second-language learning and changes in the brain. *Journal of Neurolinguistics*. 2008; 21(6):509–521. <https://doi.org/10.1016/j.jneuroling.2008.01.001>. [PubMed: 19079740]
- Park DC, Reuter-Lorenz P. The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*. 2009; 60:173–196. <https://doi.org/10.1146/annurev.psych.59.103006.093656>.

- Prichard E, Propper RE, Christman SD. Degree of handedness, but not direction, is a systematic predictor of cognitive performance. *Frontiers in Psychology*. 2013; 4(9):98–103. <https://doi.org/10.3389/fpsyg.2013.00009>. [PubMed: 23459598]
- Reuter-Lorenz PA, Jonides J, Smith EE, Hartley A, Miller A, Marshuetz C, Koeppel A. Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience*. 2000; 12(1):174–187. <https://doi.org/10.1162/089892900561814>. [PubMed: 10769314]
- Rossetti HC, Lacritz LH, Cullum CM, Weiner MF. Normative data for the Montreal Cognitive Assessment (MoCA) in a population-based sample. *Neurology*. 2011; 77(3):1272–1275. <https://doi.org/10.1212/WNL.0b013e318230208a>. [PubMed: 21917776]
- Schneiderman EI, Saddy JD. A linguistic deficit resulting from right-hemisphere damage. *Brain and Language*. 1988; 34(1):38–53. [https://doi.org/10.1016/0093-934X\(88\)90123-X](https://doi.org/10.1016/0093-934X(88)90123-X). [PubMed: 3382932]
- Stebbins GT, Carrillo MC, Dorfman J, Dirksen C, Desmond JE, Turner DA, ... Gabrieli JDE. Aging effects on memory encoding in the frontal lobes. *Psychology and Aging*. 2002; 17(1):44–55. <https://doi.org/10.1037/0882-7974.17.1.44>. [PubMed: 11933895]
- Tyler LK, Wright P, Randall B, Marslen-Wilson WD, Stamatakis EA. Reorganization of syntactic processing following left-hemisphere brain damage: Does right-hemisphere activity preserve function? *Brain*. 2010; 133:3396–3408. <https://doi.org/10.1093/brain/awq262>. [PubMed: 20870779]
- Waldron-Perrine B, Axelrod BN. Determining an appropriate cutting score for indication of impairment on the Montreal Cognitive Assessment. *International Journal of Geriatric Psychiatry*. 2012; 27(11):1189–1194. <https://doi.org/10.1002/gps.3768>. [PubMed: 22228412]
- Wingfield A, Peelle JE, Grossman M. Speech rate and syntactic complexity as multiplicative factors in speech comprehension by young and older adults. *Aging, Neuropsychology and Cognition*. 2003; 10(4):310–322. <https://doi.org/10.1076/anec.10.4.310.28974>.

FIGURE 1.

Grand-averaged ERPs and scalp topography for both the young and the older group. Topography plots show the difference between grammatical and ungrammatical trials and are shown for each of the time windows analyzed for that particular age group. Young adult data are shown in the top panel with older adult data below. Results for the left hemisphere are shown on the left and results for the right hemisphere are shown on the right. The waveforms represent ERPs recorded at an electrode that was representative for both groups (indicated by the black dot)

FIGURE 2.

Laterality effect of the P600 in the young and older adult groups. The laterality effect is the size of the effect for LH presentation minus the size of the effect for RH presentation. The majority of the young adult group show a larger P600 response with LH presentation, whereas the older adult group do not show any such bias