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Lateralization as a Symphony: Joint Influence of Interhemispheric Inhibition and
Transmission Delay on Brain Asymmetry and Syntactic Processing

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Abstract

The present study investigated the roles of cross-hemispheric communication in promoting left-lateralization of syntactic processing in the brain. Fifty-six young right-handers without familial sinistrality background underwent a divided visual field ERP grammaticality judgment experiment to assess syntactic responses from each hemisphere. Two behavioral tasks--bilateral flanker task and bilateral word-association task, were used to assess cross-hemispheric inhibition and transmission delays. The grand average ERP data showed a significant unilateral P600 grammaticality effect in the left hemisphere only. However, individual variations in the P600 responses were observed in both hemispheres. Results of correlational analyses showed that larger LH P600 effects were associated with slower inter-hemispheric transmission, and that smaller right hemisphere (RH) P600 effects were associated with more effective LH-on-RH inhibition. These results yielded support for both the callosal distance and inhibition hypotheses for language lateralization and demonstrated that different aspects of cross-hemispheric communication jointly influence the degree of syntactic lateralization.

Key words: syntactic lateralization, interhemispheric inhibition, interhemispheric transmission, Event-Related Potentials, P600, split-visual field paradigm, hemispheric differences

Introduction

Syntactic lateralization is among the most well-known examples of cerebral asymmetry. Classical discoveries of traumatic impact of the left hemisphere lesions on syntactic abilities (Manning & Thomas-Antérion, 2011) and imaging studies with healthy individuals (e.g., Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Hagoort, 2003) both indicate the dominant role of the LH in syntactic processing. Despite that the unilateral LH syntactic network is sometimes taken to implicate the absence of syntactic capability in the right hemisphere (RH), evidence indicates that the RH is capable of eliciting qualitatively similar syntactic responses as the LH does (Kemmer, Coulson, & Kutas, 2014; Lee & Federmeier, 2015). Hence, syntactic lateralization likely involves common basic mechanisms in both hemispheres that are activated to different degrees.

Two prominent theories have been put forward to try to explain how qualitatively similar language mechanisms are moderated across hemispheres. The inhibition hypothesis proposed that LH-equivalent language capabilities exist in the subordinate RH but are suppressed by transcallosal interhemispheric inhibition from the dominant LH (Chiarello & Maxfield, 1996; Cook, 2018). This hypothesis has gained support from increased RH activity in cases when the LH-on-RH moderations are weakened or eradicated due to brain damage (Moscovitch, 1976; Thiel et al., 2001) or transcranial-magnetic stimulation (TMS) (Thiel et al., 2006). However, evidence from undisrupted processing of healthy individuals is sparse. A recent study demonstrated a significant association between reduced RH P600 and more effective RH inhibition in young right-handers with familial sinistrality background (FS+) (Weng & Lee, 2020). However, as the FS trait has been associated with reduced LH dominance for language (Hécaen, Agostini, & Monzon-Montes, 1981), whether this association is specifically tied to the FS background or can be generalized to FS- right-handers is still unknown.

On the other hand, callosal distance hypothesis proposed that functional specialization in the dominant hemisphere is a consequence of avoiding the temporal delays and the cost of interhemispheric cross-talks in enlarged human brains to maintain the processing efficacy for tasks that demand high speed and temporal resolution (Aboitiz, López, & Montiel, 2003; Ringo, Dony, Demeter, & Simard, 1994). Leftward hemispheric dominance for language has been shown to associate with brain volume (Josse, Hervé, Crivello, Mazoyer, & Tzourio-Mazoyer, 2006) or head size (Tzourio-Mazoyer et al., 2010b). These studies focused on story listening and verb generation, which heavily depends on lexical processing. As pointed out in Josse et al. (2006),

lateralization of different language components could be differentially constrained by processing speed. As such, it is not clear whether these findings would hold for syntactic lateralization. Moreover, these studies provided anatomical evidence for the callosal distance hypothesis. However, direct evidence from inter-hemispheric transfer delay is still missing.

The above review highlights the scarcity of the understanding regarding the relation between syntactic lateralization and callosal communication in healthy young adults. Moreover, although the inhibition and distance theories focus on different callosal functions that are hypothesized to differentially affect the dominant and subordinate hemispheres and are thus not mutually exclusive (Bloom & Hynd, 2005), evidence for both theories from a same group of individuals is yet to be demonstrated. In light of these, the present study aimed to investigate whether and how asymmetry of instantaneous brain responses during syntactic processing can be accounted for by these two forms of interhemispheric communication. To that end, we assessed Event-Related Potential (ERP) responses from Taiwanese young right-handers with no left-handed blood relatives (FS-) while they read nouns and verbs projected to either the LH or the RH. These target words matched or mismatched the word class expectancy established by a preceding central function word, yielding grammatical or ungrammatical phrases. With this design, we aimed to measure the P600 grammaticality effect across hemispheres and examine how these effects are modulated by callosal communications.

The P600 —sustained positive-going responses (beginning after 500 ms) over posterior scalp sites, has been observed to a wide range of syntactic violations across languages (e.g., Coulson, King, & Kutas, 1998; Hagoort & Brown, 2000; Osterhout & Holcomb, 1992). Even though there have been discussions on whether the P600 can be functionally linked to more domain-general processes (see Leckey & Federmeier, 2020 for a review), P600 is deemed a useful and reliable index for capturing online processing differences between ill-formed and grammatical syntactic structures (Tanner & Van Hell, 2014). A prior study using a similar design in English showed a unilateral P600 response to ungrammatical words presented to the right visual field (RVF) and LH in FS- young adults. A subset of participants elicited qualitatively similar P600 effects to syntactic violations in the RH as well; however, these effects were not significant at the group level (Lee & Federmeier, 2015). We expect to replicate these findings.

Going beyond the extant literature, we will then examine whether inter-individual variation of the P600 effects in the language dominant LH and the subordinate RH is

modulated by callosal communications. Two behavioral tasks were conducted to assess the two forms of inter-hemispheric communications in question. A bilateral flanker task was used to estimate the efficiency of RH inhibition (Eriksen & Eriksen, 1974; Spencer & Banich, 2005), and a word association task with unilateral and bilateral word presentations was used to estimate costs and delays due to inter-hemispheric transmission. According to the inhibition hypothesis, the functionally homologous P600 in the RH is subject to the moderation exerted from the dominant LH, leading to a response asymmetry. As such, we expect to see reduced magnitudes of the RH P600 to be associated with more efficient RH inhibition. In addition, based on the callosal distance hypothesis which suggested that LH specialization is promoted to deal with the temporal constraint from inter-hemispheric communication, we expect larger LH P600 to be associated with more costly inter-hemispheric transmission.

Methods

Participants

Fifty-six young adults participated (28 male; mean age = 22.8 years, range = 20-29 years). Data from 4 additional participants were excluded due to technical failures in the word association test. Participants were run in groups of four to maintain counterbalancing until 28 participants were obtained for each flanker experiment (described below). This number was estimated to give us 80% power to detect even relatively small P600 effects of about 1.5 μ V with an alpha level of 0.5 in a two-sided test (the sigma was estimated to be 2.8 μ V based on prior data from the lab). All participants were native speakers of Taiwan Mandarin with no exposure to other languages except for Taiwanese before age 5; none had histories of neurological, psychiatric disorders, or brain damage. All were right-handed as measured by the Mandarin translated version of Edinburgh inventory (Oldfield, 1970) (mean laterality quotient = 0.76; SD = 0.15, range = 0.25-1.00). No participants had known left-handed blood relatives, as assessed by a familial handedness questionnaire (Lee & Federmeier, 2015).

Behavioral paradigm

Bilateral Flanker Task

Effectiveness of interhemispheric inhibition was assessed by a bilateral version of the Eriksen flanker task (Eriksen & Eriksen, 1974; Spencer & Banich, 2005). Participants viewed an arrow on one side of the central fixation and, concurrently on

the other side, another arrow pointing toward the congruent or incongruent direction or a square with no apparent direction--the Congruent, Incongruent, and Neutral baseline conditions respectively. There were 212 trials, including 64 trials per condition and 20 trials for fixation check. In each trial, a plus sign appeared at the center of the screen for 500ms. Participants were instructed to fixate at the center at all times with their eye movements monitored via electrodes placed at the outer canthus of each eye in a bipolar montage. Following a random ISI of 500-1000ms, two flanker items were shown on screen for 150ms, each in one VF with the inner edge of the stimulus positioned 2 degrees to the center of the screen. Participants responded to the stimuli presented in a pre-specified VF with a button-pressing response, while ignoring the stimulus presented in the other VF, either upon presentation of a question mark on the screen with a 150 ms delay (as was in Weng & Lee, 2020; henceforth the delayed response group N=28) or as soon as they saw the flanker item (the speeded response group; N=28). Participants were told to withhold their responses for fixation check trials, which showed a central asterisk instead of a plus sign.

The experiment consisted of 4 blocks, and lasted for 15 minutes. Trials with horizontal eye-movements that may compromise the VF presentation manipulation and trials responded to with longer than 2.5 seconds were excluded from subsequent analysis. For all conditions, accuracy rates over 0.97 were observed. Reaction times (RT) for correct trials were measured from the onset of the flanker for the speeded response group, and from the onset of the question mark for the delayed response group. Consistent with the literature (Spencer & Banich, 2005; Weng & Lee, 2020), incongruent trials were responded to more slowly than neutral trials; the response differences (incongruent-neutral) were larger for the attend-LVF trials (speeded: 42.10 ms; delayed: 41.34 ms) than for the attend-RVF trials (speeded: 11.80 ms; delayed: 15.52 ms). These results indicate a relative LH advantage in inter-hemispheric competition and inhibition to direct attention to contralateral space.

Word Association Task

Efficacy of inter-hemispheric transmission was assessed by a behavioral word association task. In this task, related or unrelated pairs of single-character words were presented with one word in one quadrant of the screen and the other in a vertically or horizontally opposite quadrant (with 2 degrees between the inner edge of the character and the center of the screen), yielding the Unilateral or Bilateral presentation conditions. Participants judged whether the presented words were associated with a button-press.

We focused on the related trials only as responses on the unrelated trials could be influenced by each participant's criterion for determining when to end the search of semantic memory (Chun & Wolfe, 1996), which may vary across participants. As for strongly related pairs (e.g., lexical associates: “*jiǎ/yǐ*”, *A /B*; synonym compounds: “*shān/qiū*”, *mountain/hill*; antonym compounds: “*gǔ/jīn*”, *ancient/modern*) used here, decisions could be unambiguously made, this task contrasts the intra-hemispheric and inter-hemispheric information relay in the Unilateral condition and the Bilateral condition respectively.

Stimuli were matched for number of strokes and familiarity. In total, 160 pairs were tested, with equal numbers of trials across presentation and association conditions. Four lists were generated to counterbalance the position for each word across participants. Each pair was presented on the screen for 450 ms, followed by a question mark after a 150 ms delay. Participants were instructed to fixate at the center at all times (again with their eye movements monitored via electrodes) and to respond by pressing buttons upon the question mark. Speed and accuracy of the responses were equally emphasized. Trials with horizontal eye-movements that may compromise the VF presentation manipulation, and trials responded to with longer than 2.5 seconds were excluded.

Comparable accuracy between the unilateral and bilateral trials were observed (mean accuracy rates: bilateral 0.817; unilateral 0.82). Group averaged RTs did not differ substantially between conditions (bilateral: 567.3 ms; unilateral: 577.9ms). However, a wide range of RT differences were observed (bilateral-unilateral: max: 187.1 ms, min: -399.3 ms; SD= 116.5 ms), indicating a wide range of relative advantage of intra- and inter-hemispheric transmissions across participants.

ERP paradigm

Materials. The materials were identical as those used in Weng and Lee (2020). A total of 216 two-word Taiwan Mandarin phrases were included as the critical stimuli. Each phrase contained a centrally presented syntactic cue (classifiers as cues for nouns; adverbs as cues for verbs) followed by an unambiguous noun or verb presented to either the left or right visual fields (LVF and RVF respectively). For each VF presentation, there were equal numbers of nouns and verbs, matching or mismatching the syntactic expectancy established by the syntactic cue—yielding the Grammatical condition (e.g. “*liǎng-dòng fang-zi*”/*two houses*, or “*jí-shí bang-máng*”/*immediately help*) and the Ungrammatical condition (e.g. “*jí-shí fang-zi*”/*immediately house*, or “*liǎng-dòng*

bang-máng/two houses of help). Syntactic cues and critical words were matched across conditions for syntactic category dominance, familiarity, and concreteness based on rating results. Additional 192 phrases of the same syntactic structure were added as fillers, among which 136 contained word-class ambiguous words in the head position. Four lists were generated, such that all critical words appeared in both the Grammatical and Ungrammatical condition in both VFs across lists and each participant saw each critical word only once. The stimuli were arranged pseudo-randomly so that no more than two trials were presented in the same visual field continuously. Each participant was randomly assigned to a list.

Procedure. Participants were seated 100 cm from the screen in a quiet testing room. The experiment began with a 15-trial practice to familiarize subjects with the task and the environment. To help participants fixate at the center and avoid orienting to the laterally presented words, a small red dot presented a few pixels below the center of the screen remained throughout the experiment. At the start of each trial, a plus sign appeared in the center of the screen for 500 ms. After an inter-stimulus interval ranging randomly between 500 and 1000 ms, the syntactic cue appeared centrally for 200 ms. After a 300 ms blank screen, the target was randomly presented to either VF for 200ms. 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 2 additional degrees of horizontal visual angle and 1 degree of vertical visual angle of vertical visual angle). Participants made a grammaticality judgment on the phrase upon the probe “Acceptable?” that was displayed 1000 ms after the offset of the target word and remained on the screen for 2500 ms or until participants responded. The next trial began after a delay of 1500 ms. Response hand for “yes” was counterbalanced across participants. The experiment included 6 blocks (68 trials each) and the total time of the experiment added up to 30 to 40 minutes.

Split visual field presentation. To assure validity of the lateralized presentation, target words were presented only briefly (200 ms), so that it was unlikely that participants could orient to the target word before it disappeared. To reduce the predictability of the presentation side, target words were randomly presented to either VF with no more than two consecutive presentations to the same side. We also monitored participants’ horizontal eye movements with the electrooculogram. Past findings showed considerable variations of ERPs for horizontal eye movements due to individual differences in eye-movement control as well as the online positioning of HEO channels, so we obtained individual thresholds for horizontal eye movements of

2-degree to reject trials involving horizontal eye movements for each participant (Bourne, 2006).

EEG recording. The electroencephalogram (EEG) was recorded using 32 sintered Ag/AgCL electrodes from the 10-20 system (QuickCap, Neuromedical Supplies, Sterling, TX, USA). All scalp electrodes were referenced to a common vertex reference located between CZ and CPZ online, and re-referenced to the average of the right and left mastoids offline. Vertical eye movements were recorded via a pair of electrodes placed on the supraorbital and infraorbital ridge of the left eye; horizontal eye movements were recorded via electrodes placed at the outer canthus of each eye in a bipolar montage. Impedances were kept below 5 k Ω for all electrodes. The continuous EEG was amplified by the SYNAMPS2 amplifiers (Neuroscan, Inc., EL Paso, Texas, USA) with a bandpass of 0.05-100Hz and was digitized online with a sampling rate of 1000Hz .

EEG data analysis. The EEG data were segmented offline into 1400 ms epochs, spanning 200 ms pre-stimulus to 1200 ms post-stimulus. Trials contaminated by artifacts from amplifier blocking, signal drifting, muscle activity, eye blinks and movements were rejected before averaging. On average, 27.03% of the trials were rejected; a substantial amount of which were due to horizontal eye-movements. Artifact-free ERPs were averaged by stimuli type after subtraction of the 200 ms pre-stimulus baseline. For all participants, there were at least 15 trials in each condition. Prior to measurement, ERPs were digitally filtered with a bandpass of 0.1–30 Hz. Only ERP data for trials that were responded to correctly were included in the statistical analysis.

ERP component measurement. ERPs were analyzed with omnibus repeated-measures ANOVAs for the P600 effect and, for comparisons with prior findings, the N400 effect. Both effects were measured from all thirty scalp electrodes (FP1, FP2, F7, F3, FZ, F4, F8, FT7, FC3, FCZ, FC4, FT8, T7, C3, CZ, C4, T8, TP7, CP3, CPZ, CP4, TP8, P7, P3, PZ, P4, P8, O1, OZ, O2). The N400 response was quantified as the mean amplitudes of data measured between a typical N400 time window—300 to 600 ms (Kutas & Federmeier, 2011). As the temporal and spatial overlap from the N400 response inevitably affect the mean amplitudes of the subsequent positive P600 responses, we quantified the P600 responses by measuring the amount of positive-going deviation from the N400 response. This approach has been thought to better capture the data pattern on the P600 by correcting for the overlap with the preceding N400 effect that is known to vary across studies (Brouwer, Crocker, Venhuizen, &

Hoeks, 2017) or even participants (Tanner & Van Hell, 2014) (see Lee, 2018; Steinhauer, Alter, & Friederici, 1999, for a similar approach). As such, the P600 response was measured as the peak-to-peak amplitude difference between peaks of the N400s (local minimums—most negative voltage values preceded and followed by more positive values between 300-600 ms) and peaks of the P600s (local maximums between 600-1200 ms) from all scalp channels. As peak-based measures are sensitive to high-frequency noise, to avoid spurious peaks from high frequency noise (Luck, 2014), for this analysis the waveforms were additionally filtered with a 5 Hz low pass filter. To correct for violations of sphericity associated with repeated measures, the Greenhouse-Geisser adjustment to the degrees of freedom was applied for each analysis of variance (ANOVA). Consequently, for all F tests with more than one degree of freedom in the numerator, the corrected p value is reported. In addition, significance levels of all correlational analyses were adjusted for multiple comparisons using the false discovery rate (FDR) method, and Benjamini-Hochberg adjusted P values were reported.

Results

Behavioral grammaticality judgment data

In line with previous findings, better-than-chance accuracy was seen in both VFs, but the accuracy was higher for the RVF-LH presentation than the LVF-RH presentation (RVF-LH: 92.88%, LVF-RH: 90.5%) [$t(55) = -3.06, p < .005, d = -0.36, 95\% \text{ CI} = -0.6, -0.12$].

ERP data

ERP data showed the classic N400 and P600 word-class-violation effects (Fig. 1). Results of the omnibus ANOVAs showed a significant N400 grammaticality effect (larger negativity to ungrammatical than to grammatical words) [$F(1,55) = 43.11, p < .001, \eta^2 = 0.04, \text{ CI} = 0.24, 0.58$] that was not modulated by VF presentation ($p = .56$). In contrast, the P600 grammaticality effect (larger positivity to ungrammatical than to grammatical words) [$F(1,55) = 14.16, p < .001; \eta^2 = 0.03, \text{ CI} = 0.05, 0.37$] was modulated by VF presentation [$F(1,55) = 4.14, p < .05, \eta^2 = 0.01, \text{ CI} = 0.01, 0.22$]. Subsequent comparisons showed that the group-level P600 grammaticality effect was significant with the RVF-LH presentation [$F(1,55) = 18.71, p < .001, \eta^2 = 0.06, \text{ CI} = 0.08, 0.42$], but not with the LVF-RH presentation ($p = 0.13$).

Fig. 1. Grand-average event-related potentials (ERPs) and scalp topographies of the N400 and P600 grammaticality effects. The graphs present the ERPs recorded at representative midline electrode sites (FZ, CZ, and PZ, black dot). Negative voltage is plotted upward. The waveforms elicited by grammatical (solid line) and ungrammatical (dashed line) word pairs are overlaid. Plotted ERPs were additionally filtered with a 10 Hz lowpass filter for clarity of visualization.

Consistent with previous observations, our data demonstrated a wide range of inter-individual variations. The majority of the participants elicited the LH P600 effect; among them some additionally elicited the RH- P600 effect. For the rest of the participants, some showed just the RH P600 effect and some no P600 effects at all. Fig. 2a shows the magnitudes of LH and RH P600 effects for each individual. To further illustrate that these were meaningful differences on the P600 component, Fig. 2B plots the averaged waveforms for participants with relatively more dominant LH P600 effects (LH lateralized) and those with relatively more dominant RH P600 effects (RH lateralized), divided by the diagonal dashed line in Fig. 2a.

Fig. 2. (a) The magnitude of each participant's RVF-LH P600 grammaticality effect is plotted on the X axis against their LVF-RH P600 grammaticality effect on the Y axis. The dashed lines represent equal RVF-LH and LVF-RH P600 effect magnitudes. Individuals below/to the right of the dashed line showed primarily an RVF-LH P600 effect (LH lateralized), while individuals above/to the left of the dashed line showed primarily a LVF-RH P600 effect (RH lateralized). (b) Grand average ERPs to grammatical (solid line) and ungrammatical (dotted line) targets presented to each VF are plotted at a representative electrode site (C4) for participants with LH lateralized P600 effect on top and RH lateralized P600 effect at the bottom.

Individual differences analyses: Correlating RH inhibition with the LVF-RH P600 effect

RH inhibition is indexed by the RT flanker effect (incongruent-neutral) in the attend-RVF condition, in which targets were perceived through the RVF and preferentially processed by the LH while distractors to be suppressed were perceived through the LVF and preferentially processed by the RH. A smaller value indicates less cost for suppressing the RH distraction, and thus more effective inter-hemispheric inhibition. Previous research showed an association between more effective RH inhibition and smaller RH P600 grammaticality effect in FS+ young adults (Weng & Lee, 2020). Below, we examined whether such association can be generalized to FS-young adults.

The results showed a significant correlation for the speeded response condition ($r = 0.39$; $p < 0.05$), with more effective RH inhibition associated with smaller RH P600 effects (Fig. 3a). This correlation remains significant after excluding an outlier whose flanker effect was two-SDs larger than the mean flanker effect of the group ($r = 0.41$; $p < 0.05$). No significant correlation was observed for the delayed response condition ($r = -0.26$; $p = 0.91$). Fig.3b illustrates this correlation by plotting the LVF-RH ERP responses from participants in the first and last quartiles of the flanker effect, demonstrating that the correlation was indeed driven by differences on the P600 component.

Fig. 3. (a) The magnitude of each participant's flanker effect is plotted on the X axis against their LVF-RH P600 grammaticality effect on the Y axis. The trend line plots the correlation between the two effects for the whole group. (b) Grand average ERPs to grammatical (solid line) and ungrammatical (dashed line) target words with LVF-RH presentation are plotted at C3 for participants with less effective RH inhibition (larger flanker congruency effect) on top and more effective RH inhibition (smaller flanker congruency effect) at the bottom.

Individual differences analyses: Correlating inter-hemispheric transmission delay with the RVF-LH P600 effect

Next, we investigated the role of inter-hemispheric transmission delays (computed from the RT differences for related trials between the Bilateral and Unilateral conditions in the word association task) in centralizing P600 processing in the LH. The results showed a significant correlation ($r = 0.37$, $p < 0.005$), with larger LH P600 effects associated with greater inter-hemispheric transmission delays. Fig.4b illustrates this by plotting the RVF-LH ERP responses from participants in the first and last quartiles of the transmission delay values, confirming that the correlation was driven by ERP differences on the P600 component.

Fig. 4. (a) The magnitudes of each participant's reaction time differences in the word association task are plotted on the X axis against their RVF-LH P600 grammaticality effects on the Y axis. The trend line plots the correlation between the two effects for the whole group. (b) Grand average ERPs to grammatical (solid line) and ungrammatical (dashed line) target words with the RVF-LH presentation are plotted at the CPZ channel for participants with less effective inter-hemispheric transmission (greater transmission delay) on top and more effective inter-hemispheric transmission (smaller transmission delay) at the bottom.

Discussion

This study examined the inhibition hypothesis and callosal distance hypothesis for syntactic lateralization in neurotypical young right-handers with no familial sinistrality background (FS-)—the most typical population tested in the psycholinguistic literature. Data from fifty-six individuals showed a group pattern of a unilateral LH P600 grammaticality effect and a bilateral N400 grammaticality effect. With data from a language with almost zero morpho-syntactic marking, these results provide cross-linguistic validation for left-lateralized syntax-related combinatorial processes and bilateral lexical semantic processes in young adults (e.g., Bozic, Tyler, Ives, Randall, & Marslen-Wilson, 2010; Chen et al., 2018; Tyler, Wright, Randall, Marslen-Wilson, & Stamatakis, 2010b). Underneath the group-level pattern, the ERP data showed high inter-individual variations, indicating higher heterogeneity of syntactic lateralization in young right-handers than typically assumed. Across individuals, increased LH P600 magnitudes were reliably associated with less efficient inter-hemisphere transmission, yielding support for the callosal distance hypotheses. On the other hand, a substantial

number of individuals elicited a RH P600 effect to some extent, with smaller RH P600 effects associated with more effective RH inhibition, providing support for the inhibition hypothesis. Together, these findings demonstrate that leftward asymmetry of syntactic processing, at least in the case of syntactic category comprehension, involves qualitatively similar responses in both hemispheres that are differentially shaped by different aspects of callosal communications. Below we discuss these points in turn.

Individual variation in language lateralization has been noted to be primarily driven by differences in the RH activation (Seghier, Kherif, Josse, & Price, 2011). Nevertheless, our results demonstrated that individuals do vary in the magnitudes of their LH syntactic responses, and the differences could be accounted for by the efficiency of their inter-hemispheric information transmission. Inter-hemispheric coordination is known to be accompanied by processing cost. For example, performance for delayed-recognition tasks or probe-target matching tasks is generally poorer when the information required by the task is initially presented to different hemispheres rather than to a same hemisphere (Banich & Belger, 1990; Hellige, Jonsson, & Michimata, 1988). The consequences from delayed information relays could be particularly deleterious for processes that require rapid resolution. As such, the callosal distance hypothesis holds that some processes may be specialized to one hemisphere due to such constraints on inter-hemispheric communications (Aboitiz et al., 2003; Ringo et al., 1994). Along this vein, our data showed that the influence of time constraint on hemispheric specialization can also be seen among individuals. With individuals who were slower for cross-hemispheric transmission eliciting a more enhanced LH P600 effect, our data support the view that syntactic processing is promoted to the LH to minimize delay and cost from reciprocal transcallosal communication

Our data also demonstrated that even in FS- young right-handers--the population typically considered most left lateralized for syntactic processing (Hécaen et al., 1981; Kee, Bathurst, & Hellige, 1983), the RH is capable of engaging qualitatively similar processes as the LH does (indexed by the P600 response) and these RH responses are modulated by interhemispheric inhibition. This finding extends prior research by showing that although FS- and FS+ young right-handers elicit different group-level lateralization patterns--unilateral LH and bilateral P600 grammaticality effects respectively (Weng & Lee, 2020; Lee & Federmeier, 2015), their RH P600s are similarly modulated by RH inhibition at the individual level. These results suggest that interhemispheric inhibition and familial sinistrality may provide non-overlapping, and

possibly additive, modulations on RH syntactic processing (Lee, 2018). Based on the properties of FS and interhemispheric inhibition, our findings also raise the possibility that some aspects of RH modulation in syntactic processing may be more malleable than others. While FS has a genetic basis and has been linked to reduced structural asymmetry in the grey matter (Tzourio-Mazoyer et al., 2010a), part of the interhemispheric inhibition is hypothesized to be proportional to the activity strength in the dominant hemisphere (Netz, Ziemann, & Hömberg, 1995; Wey, Cook, Landis, Regard, & Graves, 1993). If the activity strength in the dominant hemisphere could be increased as language experience or knowledge accumulate or weakened due to lesions or deterioration, the amount of interhemispheric inhibition on the specific type of information could also change accordingly (Hutner & Liederman, 1991).

These results thus highlight the dynamic relation between the homologous P600 responses across the hemispheres, and suggest a potential compensatory role of the RH in syntactic processing. RH P600 has been seen in cases when syntactic processing is more challenging, such as in low proficiency L2 learners (Chen et al., 2018) or healthy older adults (Leckey & Federmeier, 2017). However, it is still unclear to what extent could the RH take up the syntactic function as the LH does. Extant findings in the literature also present a mixed picture. Some studies showed that initial recruitment of the RH is predictive of successful learning of grammar in healthy young adults, endorsing the RH capacity of syntactic processing (see Qi & Legault, 2020 for a review). However, it has also been shown that increased RH activation in homologous regions of the compromised LH in patients or healthy older adults did not correlate with their syntactic performance, suggesting that the RH activation may not perform the same linguistic computations as the LH activation does (Raja Beharelle et al., 2010). In the light of these findings, further characterization of the antecedents and corollaries of the RH P600 effect could help delineate the circumstances under which RH syntactic capacity can be optimally recruited when the LH is in compromised or challenging scenarios.

Conclusion

Overall, our findings underscored the role of transcallosal communications in driving language lateralization (Hinkley et al., 2016), and indicated that multiple independent biases play a role in driving functional cerebral asymmetries of syntactic processing in the human brain (Badzakova-Trajkov, Corballis, & Häberling, 2016). Our results raise the possibility that, beyond the genetically determined predisposition

(Annett, 1985; McManus & Bryden, 1992) and brain maturation (Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013), the degree of language lateralization may be altered in adulthood not only during long-term aging trajectories (e.g., Nunez et al., 2011; Tyler et al., 2010a), but also during short time periods as a result of language experience or training. These investigations can bring implications for offsetting reduced hemispheric specialization resulting from biological aging and facilitating redistribution of the syntactic processing in foreign language learning.

Author Contributions

All authors developed the study concept and contributed to the study design. M.-H. Chen constructed the stimuli and set up the experiment. Yeh, M.-H. Chen, and P.-H. Chen collected data, performed the data analysis and interpretation under the supervision of Lee. Yeh drafted the manuscript, M.-H. Chen and P.-H. Chen provided feedback, and Lee provided critical revisions. All authors approved the final version of the manuscript for submission.

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Reference

- Aboitiz, F., López, J., & Montiel, J. (2003). Long distance communication in the human brain: timing constraints for inter-hemispheric synchrony and the origin of brain lateralization. *Biol Res*, 36, 89-99.
doi:<https://doi.org/10.4067/S0716-97602003000100007>
- Annett, M. (1985). *Left, right, hand and brain: The right shift theory*: Psychology Press (UK).
- Badzakova-Trajkov, G., Corballis, M. C., & Häberling, I. S. (2016). Complementarity or independence of hemispheric specializations? A brief review. *Neuropsychologia*, 93, 386-393.
doi:<https://doi.org/10.1016/j.neuropsychologia.2015.12.018>
- Banich, M. T., & Belger, A. (1990). Interhemispheric interaction: how do the hemispheres divide and conquer a task? *Cortex*, 26, 77-94.
doi:[https://doi.org/10.1016/S0010-9452\(13\)80076-7](https://doi.org/10.1016/S0010-9452(13)80076-7)
- Bloom, J. S., & Hynd, G. W. (2005). The role of the corpus callosum in interhemispheric transfer of information: excitation or inhibition? *Neuropsychology Review*, 15(2), 59-71. doi:<https://doi.org/10.1007/s11065-005-6252-y>
- Bourne, V. J. (2006). The divided visual field paradigm: Methodological considerations. *LATERALITY*, 11(4), 373-393.
doi:<https://doi.org/10.1080/13576500600633982>
- Bozic, M., Tyler, L. K., Ives, D. T., Randall, B., & Marslen-Wilson, W. D. (2010). Bihemispheric foundations for human speech comprehension. *Proceedings of the National Academy of Sciences*, 107(40), 17439-17444.
doi:<https://doi.org/10.1073/pnas.1000531107>
- Brouwer, H., Crocker, M. W., Venhuizen, N. J., & Hoeks, J. C. J. (2017). A neurocomputational model of the N400 and the P600 in language processing. *Cognitive Science*, 41(6), 1318-1352. doi:<https://doi.org/10.1111/cogs.12461>
- Chen, P.-H., Yeh, C., Lu, C.-R., Hsieh, S.-K., Chou, T.-L., Su, L. I.-W., & Lee, C.-L. (2018). Multiple scaffolding mechanisms for L2 syntactic processing: An Event-Related Potential study. *Journal of Chinese Language Teaching*, 15(2), 63-93.

- Chiarello, C., & Maxfield, L. (1996). Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. *Brain and cognition*, 30(1), 81-108.
doi:<https://doi.org/10.1006/brcg.1996.0006>
- Chun, M. M., & Wolfe, J. M. (1996). Just say no: How are visual searches terminated when there is no target present? *Cognitive psychology*, 30(1), 39-78.
doi:<https://doi.org/10.1006/cogp.1996.0002>
- Cook, N. D. (2018). *The brain code: Mechanisms of information transfer and the role of the corpus callosum* (Vol. 2): Routledge.
- Coulson, S., King, J. W., & Kutas, M. (1998). Expect the unexpected: Event-related brain response to morphosyntactic violations. *Language and Cognitive Processes*, 13(1), 21-58. doi:<https://doi.org/10.1080/016909698386582>
- Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, 16(1), 143-149. doi:<https://doi.org/10.3758/BF03203267>
- Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral Cortex*, 13, 170-177.
doi:<https://doi.org/10.1093/cercor/13.2.170>
- Hagoort, P. (2003). How the brain solves the binding problem for language: a neurocomputational model of syntactic processing. *NeuroImage*, 20, S18-S29.
doi:<https://doi.org/10.1016/j.neuroimage.2003.09.013>
- Hagoort, P., & Brown, C. (2000). ERP effects of listening to speech compared to reading: the P600/SPS to syntactic violations in spoken sentences and rapid serial visual presentation. *Neuropsychologia*, 38(11), 1531-1549.
doi:[https://doi.org/10.1016/S0028-3932\(00\)00053-1](https://doi.org/10.1016/S0028-3932(00)00053-1)
- Hécaen, H., Agostini, M. D., & Monzon-Montes, A. (1981). Cerebral organization in left-handers. *Brain and Language*, 12(2), 261-284.
doi:[https://doi.org/10.1016/0093-934X\(81\)90018-3](https://doi.org/10.1016/0093-934X(81)90018-3)
- Hellige, J. B., Jonsson, J. E., & Michimata, C. (1988). Processing from LVF, RVF and BILATERAL presentations: Examinations of metacontrol and interhemispheric interaction. *Brain and cognition*, 7(1), 39-53.
doi:[https://doi.org/10.1016/0278-2626\(88\)90020-6](https://doi.org/10.1016/0278-2626(88)90020-6)
- Hervé, P.-Y., Zago, L., Petit, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2013). Revisiting human hemispheric specialization with neuroimaging. *Trends in cognitive sciences*, 17(2), 69-80. doi:<https://doi.org/10.1016/j.tics.2012.12.004>

- Hinkley, L. B. N., Marco, E. J., Brown, E. G., Bukshpun, P., Gold, J., Hill, S., Findlay, A. M., Jeremy, R. J., Wakahiro, M. L., Barkovich, A. J., et al. (2016). The contribution of the corpus callosum to language lateralization. *The Journal of Neuroscience*, 36(16), 4522–4533.
doi:<https://doi.org/10.1523/JNEUROSCI.3850-14.2016>
- Hutner, N., & Liederman, J. (1991). Right hemisphere participation in reading. *Brain and Language*, 41(4), 475 - 495. doi:[https://doi.org/10.1016/0093-934X\(91\)90169-2](https://doi.org/10.1016/0093-934X(91)90169-2)
- Josse, G., Hervé, P.-Y., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2006). Hemispheric specialization for language: brain volume matters. *Brain Research*, 1068(1), 184-193.
doi:<https://doi.org/10.1016/j.brainres.2005.11.037>
- Kee, D. W., Bathurst, K., & Hellige, J. B. (1983). Lateralized interference of repetitive finger tapping: Influence of familial handedness, cognitive load and verbal production. *Neuropsychologia*, 21(6), 617-624.
doi:[https://doi.org/10.1016/0028-3932\(83\)90059-3](https://doi.org/10.1016/0028-3932(83)90059-3)
- Kemmer, L., Coulson, S., & Kutas, M. (2014). Grammatical number agreement processing using the visual half-field paradigm: An event-related brain potential study. *International Journal of Psychophysiology*, 91(2), 88-103.
doi:<https://doi.org/10.1016/j.ijpsycho.2013.12.002>
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual review of psychology*, 62, 621-647.
doi:<https://doi.org/10.1146/annurev.psych.093008.131123>
- Leckey, M., & Federmeier, K. D. (2017). Age-related shifts in hemispheric dominance for syntactic processing. *Psychophysiology*, 54(12), 1929-1939.
doi:<https://doi.org/10.1111/psyp.12970>
- Leckey, M., & Federmeier, K. D. (2020). The P3b and P600 (s): Positive contributions to language comprehension. *Psychophysiology*, 57(7), e13351.
doi:<https://doi.org/10.1111/psyp.13351>
- Lee, C.-L. (2018). *Familial Sinistrality and Language Processing*.: Academic Press.
- Lee, C.-L., & Federmeier, K. D. (2015). It's all in the family: brain asymmetry and syntactic processing of word class. *Psychological Science*, 26(7), 997-1005.
doi:<https://doi.org/10.1177/0956797615575743>

- Luck, S. J. (2014). *An introduction to the event-related potential technique*: MIT press.
- Manning, L., & Thomas-Antérion, C. (2011). Marc Dax and the discovery of the lateralisation of language in the left cerebral hemisphere. *Revue neurologique*, 167(12), 868-872. doi:<https://doi.org/10.1016/j.neurol.2010.10.017>
- McManus, I. C., & Bryden, M. P. (1992). The genetics of handedness, cerebral dominance, and lateralization. In I. Rapin & S. J. Segalowitz (Eds.), *Handbook of neuropsychology* (pp. 115-115). Amsterdam, The Netherlands: Elsevier.
- Moscovitch, M. (1976). On the representation of language in the right hemisphere of right-handed people. *Brain and Language*, 3(1), 47-71. doi:[https://doi.org/10.1016/0093-934X\(76\)90006-7](https://doi.org/10.1016/0093-934X(76)90006-7)
- Netz, J., Ziemann, U., & Hömberg, V. (1995). Hemispheric asymmetry of transcallosal inhibition in man. *Experimental Brain Research*, 104(3), 527-533.
- Nunez, S. C., Dapretto, M., Katzir, T., Starr, A., Bramen, J., Kan, E., Bookheimer, S., & Sowell, E. R. (2011). fMRI of syntactic processing in typically developing children: structural correlates in the inferior frontal gyrus. *Developmental cognitive neuroscience*, 1(3), 313-323. doi:<https://doi.org/10.1016/j.dcn.2011.02.004>
- Oldfield, R. C. (1970). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113. doi:10.1016/j.ijpsycho.2013.12.002
- Osterhout, L., & Holcomb, P. J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language*, 31, 785-806. doi:[https://doi.org/10.1016/0749-596X\(92\)90039-Z](https://doi.org/10.1016/0749-596X(92)90039-Z)
- Qi, Z., & Legault, J. (2020). Neural hemispheric organization in successful adult language learning: Is left always right? *Psychology of Learning and Motivation*. doi:<https://doi.org/10.1016/bs.plm.2020.02.004>
- Raja Beharelle, A., Dick, A. S., Josse, G., Solodkin, A., Huttenlocher, P. R., Levine, S. C., & Small, S. L. (2010). Left hemisphere regions are critical for language in the face of early left focal brain injury. *Brain*, 133(6), 1707-1716. doi:<https://doi.org/10.1093/brain/awq104>
- Ringo, J. L., Dony, R. W., Demeter, S., & Simard, P. Y. (1994). Time Is of the essence: a conjecture that hemispheric specialization arises from

- interhemispheric conduction delay. *Cerebral Cortex*, 4(4), 331-343.
doi:<https://doi.org/10.1093/cercor/4.4.331>
- Seghier, M. L., Kherif, F., Josse, G., & Price, C. J. (2011). Regional and hemispheric determinants of language laterality: implications for preoperative fMRI. *Human brain mapping*, 32(10), 1602-1614.
doi:<https://doi.org/10.1002/hbm.21130>
- Spencer, K. M., & Banich, M. T. (2005). Hemispheric biases and the control of visuospatial attention: an ERP study. *BMC Neuroscience*, 6(51).
doi:<https://doi.org/10.1186/1471-2202-6-51>
- Steinhauer, K., Alter, K., & Friederici, A. D. (1999). Brain potentials indicate immediate use of prosodic cues in natural speech processing. *Nature Neuroscience*, 2(2), 191-196. doi:<https://doi.org/10.1038/5757>
- Tanner, D., & Van Hell, J. G. (2014). ERPs reveal individual differences in morphosyntactic processing. *Neuropsychologia*, 56, 289-301.
doi:<https://doi.org/10.1016/j.neuropsychologia.2014.02.002>
- Thiel, A., Herholz, K., Koyuncu, A., Ghaemi, M., Kracht, L. W., Habedank, B., & Heiss, W.-D. (2001). Plasticity of language networks in patients with brain tumors: a positron emission tomography activation study. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, 50(5), 620-629. doi:<https://doi.org/10.1002/ana.1253>
- Thiel, A., Schumacher, B., Wienhard, K., Gairing, S., Kracht, L. W., Wagner, R., Haupt, W. F., & Heiss, W.-D. (2006). Direct demonstration of transcallosal disinhibition in language networks. *Journal of Cerebral Blood Flow & Metabolism*, 26(9), 1122-1127. doi:<https://doi.org/10.1038/sj.jcbfm.9600350>
- Tyler, L. K., Shafto, M. A., Randall, B., Wright, P., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010a). Preserving syntactic processing across the adult life span: the modulation of the frontotemporal language system in the context of age-related atrophy. *Cerebral Cortex*, 20(2), 352-364.
doi:<https://doi.org/10.1093/cercor/bhp105>
- Tyler, L. K., Wright, P., Randall, B., Marslen-Wilson, W. D., & Stamatakis, E. A. (2010b). Reorganization of syntactic processing following left-hemisphere brain damage: does right-hemisphere activity preserve function? *Brain*, 133(11), 3396-3408. doi:<https://doi.org/10.1093/brain/awq262>
- Tzourio-Mazoyer, N., Petit, L., Razafimandimby, A., Crivello, F., Zago, L., Jobard, G., Joliot, M., Mellet, E., & Mazoyer, B. (2010b). Left hemisphere

lateralization for language in right-handers is controlled in part by familial sinistrality, manual preference strength, and head size. *The Journal of Neuroscience*, 30(40), 13314–13318.

doi:<https://doi.org/10.1523/JNEUROSCI.2593-10.2010>

Tzourio-Mazoyer, N., Simon, G., Crivello, F., Jobard, G., Zago, L., Perchey, G., Hervé, P.-Y., Joliot, M., Petit, L., Mellet, E., et al. (2010a). Effect of familial sinistrality on planum temporale surface and brain tissue asymmetries. *Cerebral Cortex*, 20(6), 1476–1485. doi:<https://doi.org/10.1093/cercor/bhp209>

Weng, Y.-L., & Lee, C.-L. (2020). Reduced right-hemisphere P600 responses to syntactic word class violations are associated with greater right-hemispheric inhibition: evidence from right-handers with familial sinistrality. *Brain Research*, 1738(1). doi:<https://doi.org/10.1016/j.brainres.2020.146815>

Wey, T. V., Cook, N. D., Landis, T., Regard, M., & Graves, R. E. (1993). Lateralized lexical decisions and the effects of hemifield masks: A study of interhemispheric inhibition and release. *International Journal of Neuroscience*, 71(1-4), 37-44.

doi:<https://doi.org/10.3109/00207459309000590>