Language Abilities as a Function of Lateralization of Language-Specific Brain Networks

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Language abilities as a function of lateralization of language-specific brain networks

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Communication is one of the most important abilities that humans have; through language, we relate, create, and cooperate with one another. While language development proceeds effortlessly, and through highly predictable milestones for most infants, some individuals have impairments in the timing and ultimate attainment of language fluency. There are distinct ways in which language development can go awry, such as developmental language disorder, dyspraxia, autism spectrum disorder (ASD) and many others (Snowling et al., 2020; Whitehouse & Bishop, 2008). The myriad of specific problems that can arise during language development suggests that a variety of different systems and mechanisms work together to produce fluent, functional language. One indicator thought to drive language impairment is language lateralization, meaning that one side of the brain is more engaged during language tasks than the other. For most right-handed, typically developing individuals, the left hemisphere is dominant for language. Furthermore, some individuals showing less asymmetry of lateralization also show significant language impairment (Illingworth & Bishop, 2009). However, this developmental phenomenon has to date not been demonstrated in adults; specifically, studies have to date failed to document a relationship between strength of lateralization and language development. Thus, we have no real consensus on the role of language lateralization in healthy individuals. The goal of the current study is to document an association between indices of language ability, including syntactic complexity and receptive vocabulary, and degree of lateralization of language-specific brain networks.

Language networks. Language networks encompass many areas of the brain. Bernal and colleagues (2015) conducted a pooling-data connectivity study, meaning that they sourced data from fMRI studies reporting BA44 (also known as Broca’s Area) network activations, resulting
in a pool of 57 papers and 883 subjects. They analyzed this pooled data for statistical
significance of clusters using the activation likelihood estimate (ALE) method. The ALE maps
aimed to describe the core expressive language networks associated with Broca’s area and
revealed 16 significant clusters of activation. The main cluster included BA44 and adjacent
regions, including anterior insula, inferior and middle frontal gyri, and pre-central gyrus. The left
inferolateral frontal gyrus and anterior insula were particularly important in expressive language,
as the researchers found dense connectivity between these areas. This study also highlighted the
importance of supplementary motor areas (SMA) for verbal fluency and initiation of speech,
noting a significant cluster in the left pre-SMA and anterior cingulate gyrus (BA6 and 32). A
second distinct cluster included the left superior and inferior parietal lobule, which is implicated
in verbal working memory. These clusters were all left-lateralized.

Interestingly, subjects with right hemisphere dominance for language were nonetheless
left-lateralized in the left arcuate fasciculus. Dick and colleagues (2014) discuss the role of the
arcuate fasciculus in their literature review. It has been accepted that the SLF/AF (superior
longitudinal fasciculus/arcuate fasciculus) has terminations in both Broca’s and Wernicke’s
areas. The fact that right-lateralized individuals still have dominance in their left arcuate fasciculi
suggests that lateralization may be more complex than we think, and that different language
areas may lateralize differently. This hypothesis is supported by Bernal and colleagues’ (2015)
conclusion that the networks related to Broca’s area have a myriad of functions supporting
expressive language, such as verbal working memory, syntactic memory, mirror neuron activity,
and motor programming.

The importance of the left inferior frontal gyrus (IFG) in regulating the recovery of
semantic information further supports the notion of language lateralization to the left. Whitney et
al. (2011) conducted a semantic judgement Transcranial Magnetic Stimulation (TMS) study where participants had to retrieve dominant and non-dominant aspects of semantic knowledge. Participants ($n = 16$) were shown a cue word above three target words, one of which was related to the cue word. They were instructed to choose the related word with their right hand. The dominant/strong association condition included cue-target pairings such as “banana-peel” or “salt-pepper,” whereas the weak/non-dominant condition included pairings such as “banana-slip” or “salt-grain.” Results indicated that stimulation of the pMTG (posterior middle temporal gyrus) led to an equal disruption of executively demanding semantic decisions as compared to stimulation of the left IFG. It was postulated that the pMTG is recruited when additional control is needed to restrain language output from choosing distractor items. These findings were supported when the researchers found impaired regulation of semantic control in patients suffering from left temporoparietal and/or prefrontal infarction.

Early lateralization studies. Early research on lateralization initially supported the notion that language is lateralized to the left hemisphere. Rasmussen and Milner (1977) utilized the intracarotid amobarbital test (also known as the “Wada test”) in order to effectively inactivate one hemisphere of the brain and observe the effects it had on language. In this test, a catheter is inserted into the internal carotid artery. 175 mg of Amytal in a 10% solution is then injected into the catheter, which temporarily deactivates one hemisphere of the brain, causing the contralateral arm and leg to fall. If the injected hemisphere is non-dominant for speech, the subject will be able to count and perform verbal tasks during the hemiparesis. However, if the injected hemisphere is dominant, then the patient will become aphasic or markedly dysphasic until the injection wears off in about four to ten minutes. They found that lateralization was predictably left lateralized in most right-handed individuals, as 96% of their right-handed patients showed
speech disturbance when the left hemisphere was deactivated. A majority of left-handed and
ambidextrous patients were also left-lateralized (70%). Within the non-right-handed sample,
15% showed significant speech disturbance after injection in either side of the brain, suggesting
language functions representing bilaterally as a function of handedness.

Loring and colleagues (1990) utilized the intracarotid amobarbital test on epileptic
patients \( n = 103 \), finding that 91% of the dextral (i.e., right-handed) patients were left-
hemisphere dominant for language, 4% were right-hemisphere dominant, and 4% were mixed
dominant. Following injection, they saw 21% display varying degrees of impairment on a battery
of language tasks. They concluded that right hemisphere language dominance is rare, and that in
cases where language is not solely left-hemisphere dominant, some degree of bilateral
representation should be expected. This aligns with the hypothesis that language functions can be
dissociated between hemispheres. It is important to remember that all of the patients in this study
were epileptic. The authors suggest that their results indicate that left- and mixed- hand
preference could be a marker of atypical cerebral dominance in language, however, it is possible
that there is a unique trajectory of brain development in epileptic patients that could have
influenced the results of this study. Future research should continue to examine samples with
epilepsy and early brain legion to study their effects on the development of brain lateralization.

_Differing models of typical lateralization._ Assuming that most individuals show some
degree of language lateralization, it is of interest to understand whether lateralization leads to
superior language skills. Interestingly, one study reported an association between right-
hemispheric brain activation and better language performance (van Ettinger-Veenstra et al.,
2010). Fourteen right-handed subjects completed behavioral tasks, an fMRI sentence completion
paradigm, and a dichotic listening test. Analyses focused on areas that are commonly thought to
be left-lateralized for language, including the frontal temporal lobe, posterior temporal lobe, IFG, anterior cingulate, and superior parietal lobe. When subjects were asked to recall one stimulus (i.e. the syllable they perceived the best), there was an advantage to having bilateral cingulate cortex activation. This suggests that the monitoring of behaviorally motivated stimuli involves both hemispheres during language tasks. Additionally, they found a negative correlation between the lateralization of the posterior temporal cortex and reading task performance, suggesting that the right hemisphere may be important for reading. It is possible that this is due to the visuospatial demands of reading. However, the researchers also noted that this is the right-hemisphere homologue of Wernicke’s area and postulated that it may be important in integrating lexical and syntactic information.

In an fMRI study, Bartha-Doering and colleagues (2018) found surprising evidence for bilateral language representation being associated with better language skills. In their sample of 30 right-handed children and adolescents, they found a significant negative correlation between expressive vocabulary and laterality index of the mesial temporal lobe (MTL). Specifically, bilateral MTL involvement was advantageous for vocabulary skills. This corroborates their previous finding that unilateral MTL epilepsy can lead to deficits in semantic fluency and expressive vocabulary regardless of the hemisphere affected (Bartha & Trinka, 2014). The MTL’s bilateral function in vocabulary suggests that only certain areas implicated for language may be left-lateralized.

The crowding hypothesis (or functional crowding hypothesis) suggests that left-lateralization for language function is advantageous because right-hemisphere language lateralization could result in poorer visual-spatial functioning (Lansdell, 1969; Teuber, 1974). The hypothesis refers to “crowding” because language and visuospatial information processing
neurons would be competing for space in one hemisphere. Groen and colleagues (2012) carried out a Functional transcranial Doppler sonography (fTCD) study of 58 children ages 6 – 13 years. In fTCD, cognitively induced changes of blood flow velocity in the middle cerebral arteries (MCA) are measured with an ultrasonic apparatus noninvasively resting on the scalp. Results indicated that children with more left-lateralized language had higher vocabulary and nonword reading scores. However, this study compared performance on tests of nonverbal cognitive ability, vocabulary, reading, and phonological short-term memory for children with unilateral language representation against those of children with bilateral language representation, and they found no significant differences. Based on this result they did not support the functional crowding hypothesis. They concluded that it was unlikely that the lateralization of visuospatial skill has any effect on the lateralization or performance of language, and that bilateral representation was not necessarily a disadvantage.

Danguecan & Smith (2019) aimed to test the functional crowding hypothesis and analyzed retrospective data from 91 children with left-sided focal epilepsy who underwent assessment of language dominance from October 1981 to March 2017. 57 patients showed left language lateralization (typical group) and 34 showed bilateral or right language lateralization (atypical group). Results of three visual tasks and three verbal tasks were analyzed in order to determine the relative contributions of seizure onset, handedness, seizure localization, and language dominance on verbal versus visuospatial cognitive skills. Results indicated that the left-lateralized group had significantly higher verbal performance than the bilateral/right- lateralized group. Furthermore, the atypical group showed significantly worse performance on the visual measures, offering support for the crowding hypothesis. Similar to the aforementioned study by Loring and colleagues (1990), this epileptic sample also contained a relatively high number of
patients with bilateral or right language lateralization. Again, it seems that epileptic patients’
brains may develop differently in order to accommodate from the seizure activity. Here, this
could likely be the case since these participants had left-sided focal epilepsy.

Another intriguing possibility is that there is a nonlinear relationship between
hemispheric lateralization and cognitive performance. Hirnstein and colleagues (2010) conducted
visual half-field tasks consisting of word matching and face decision on 140 women and 90 men.
Most of the participants showed a moderate degree of lateralization, suggesting that the
relationship can be better described by an inverted U-shaped curve, with better word-matching
accuracy associated with moderate lateralization. Quadratic regressions in the word-matching
task showed that optimal cognitive performance was associated with low negative laterality
indices. The favoring of a quadratic rather than a linear model suggests that there would be an
optimal performance at a medium level of lateralization, but performance would deteriorate
toward both ends of extreme lateralization. The caveat for this type of study is that a visual half-
field study may not yield as accurate results as a study that directly measures brain activity
would. Thus, it is important that the authors’ hypothesis is tested with fMRI measures in order to
produce higher-quality evidence.

_Lateralization in language impairment_. Several studies examine language lateralization
in language-impaired individuals, offering insights into how the brain might compensate in
atypical conditions. There is a suggestion in the literature that individuals with Specific
Language Impairment (SLI), now more often referred to as Developmental Language Disorder
(DLD), present with non-left language lateralization (Badcock et al., 2012; Waldie et al., 2013;
Whitehouse & Bishop, 2008; Illingworth & Bishop, 2009). This pattern seems to be unique to
DLD. Whitehouse & Bishop (2008) report that right or bilateral lateralization was not seen in
participants who have a history of SLI or a language impairment from ASD. So, it seems that hemispheric dominance is not implicated in every case of poor language and therefore cannot be used as an absolute indicator. Rather, they hypothesized that lateralization was not a cause of language impairment, but a consequence of it. This hypothesis is supported by the findings of Illingworth & Bishop (2009), who conducted an fTCD study comparing dyslexic individuals ($n = 30$) to typical controls ($n = 30$). Overall, the dyslexic group demonstrated reduced leftward asymmetry compared to controls. However, they asserted that most people with dyslexia still showed left lateralization ($n = 23$), and most people in the general population who express right or bilateral language do not have language problems. Thus, non-left lateralization may be a marker of impairment rather than a cause.

Bradshaw and colleagues (2020) also conducted an fTCD study comparing individuals with language disorder to typical controls. At the group level, all language tasks demonstrated significant left lateralization. However, they observed interesting patterns in individuals showing bilateral representation of language (i.e., inconsistent laterality). Inconsistent laterality itself was predictive of developmental disorder, yet most individuals in the developmental disorder group had consistent laterality, supporting the above hypothesis that atypical laterality does not cause impairment. In the individuals with inconsistent laterality, the most common pattern was left lateralization during phonological decision and sentence generation, but right lateralization for semantic decision. The researchers speculate that this could be due to differing involvement of dorsal and ventral language streams. Sentence generation and phonological decision require more L posterior frontal cortex involvement, while semantic decision utilizes bilateral temporal lobes. This corroborates the finding that semantic knowledge may be represented bilaterally in the temporal lobes (Bartha-Doering et al., 2018, Bradshaw et al., 2020). The bulk of findings in
language impairment suggest that developmental disorder is heterogeneous and that atypical lateralization is one of many factors that can increase the likelihood of an atypical language network.

**Current Study**

The existing literature suggests that understanding the hemispheric lateralization of language may clarify the mechanisms involved in language impairment and developmental disorder. Once this is better understood, using our knowledge of the brain’s plasticity, better and earlier interventions for language disorder could be discovered. The current study aimed to further examine whether increased lateralization in either direction is associated with better language skills. In particular, we included measures of vocabulary skill and syntactic complexity. Our fMRI paradigm targeted pertinent language clusters in order to determine a laterality index (LI) for each participant. We hypothesized that left lateralization would be associated with better functioning, with a small effect size, as Hirnstein and colleagues (2010) demonstrated that extreme LIs are likely not advantageous. The literature suggests that left lateralization is the most common form of language representation, but that it does not necessarily mean that one will have *better* functioning. Adding to the literature on typically developing individuals will help to clarify this hypothesis. Since language is comprised of such complex networks, it can also be expected that some bilateral representation will occur depending on the task. As described by Bradshaw et al. (2020), the syntactic complexity task may engender both left and right activation since both sentence generation and semantic decision are depended upon.

**Methods**

**Participants**
The participants in this study included 25 right-handed undergraduate students at the University of Connecticut. Participation was excluded if the subject had any history of neurological/psychiatric issues including seizure, head injury, schizophrenia, bipolar disorder, or learning disability. They were all enrolled in introductory psychology, PSYC 1100 and PSYC 1103 and received course credit for the initial behavioral evaluation. If they were MRI eligible, they were invited to participate, and received $40 for completing the MRI scan, along with an image of their brains.

**Materials**

*Nonverbal IQ.* For the measure of nonverbal IQ (NVIQ), participants completed the Fluid Reasoning subtest of the Stanford-Binet Intelligence Scale (Roid & Pomplun, 2012). In the Matrices activity, the participant is required to determine the rules and patterns underlying pieces of information, such as visual objects.

*Receptive vocabulary.* Participants completed the Peabody Picture Vocabulary Test, Fourth Edition (PPVT-4) (Dunn et al., 2007), a reliable measure of receptive vocabulary in English that yields age-based standard scores. The participant hears a word and sees four different pictures in the test booklet. The participants indicated to the examiner which picture best resembles the definition of each word.

**Procedure**

In one visit, participants completed the Cartoon Narration, NVIQ, receptive vocabulary, and grammaticality judgement assessments. If eligible, they were invited to do the MRI scan at a later date.
Cartoon narration. When participants arrived, they watched a Looney Tunes clip called “Canary Row.” After, they stood in front of a camera with their hands by their sides and retold as much of the story as they could remember. Videos were subsequently transcribed for analysis.

Grammaticality judgement (GJ). Participants listened to short sentences, some of which were grammatically correct. The sentences were not written out on the screen. They were instructed to, as quickly as possible, click whether the sentence they heard was grammatically correct or not. Reaction time and accuracy were recorded.

MRI protocol. Eligible participants initially watched seven minutes of a movie during their structural scan. Next, they completed a language task, in which they were asked to identify pairs of matching words. Then, they completed a social play task used to gauge social perception, where fixations were obtained using eye-tracking; this social MRI task is not included in the current study and is not described further. Finally, they watched another video for eight minutes while their resting state scan was completed.

Participants completed several other behavioral measures which were not relevant to the current study. Altogether, the MRI session lasted 55 minutes and the behavioral assessments lasted about two and a half hours.

Analyses

Syntactic complexity. After transcribing the cartoon narration videos, speech was segmented into C-Units. A C-Unit is an independent clause with all its modifiers, which cannot be further divided without losing its meaning (Miller et al., 2019). Interrater reliability was established by comparing C-Unit classifications for the first author and a graduate student advisor; analyses yielded an intraclass correlation coefficient of .998, considered robust
reliability. In order to capture syntactic complexity, the number of subordinate clauses the participant used was counted. We divided the number of C-Units by the number of subordinate clauses and used this ratio as our measure of syntactic complexity.

**Statistical approach.** Data was analyzed with SPSS. Multiple regression analyses were run for LIs of the inferior temporal region, the superior temporal region, and the frontal region. NVIQ and story length (number of C-Units) were factored out in a single step, and in the second step, syntactic complexity, receptive vocabulary (PPVT-4 Standard Score), GJ reaction time difference between correct and incorrect trials (GJ RT), GJ accuracy score, and number of subordinate clauses were added as predictors of LI.

**Results**

As shown in Table 1, results of the multiple regression analyses indicated that syntactic complexity, receptive vocabulary, grammaticality judgement, and subordinate clause use significantly predicted LIs for the inferior temporal region, \( (F(7, 95) = 6.580, p = .001, R^2 = .730) \), but not for the superior temporal region \( (F(7, 95) = .373, p = .905, R^2 = .133) \), or the frontal region \( (F(7, 95) = 1.226, p = .342, R^2 = .336) \).

For the LI of the inferior temporal region, total number of subordinate clauses, GJ accuracy, and PPVT added statistically significantly to the prediction, presented in Table 2, \( p \)'s < .05. Syntactic complexity was significantly correlated with inferior temporal LI, \( p < .05 \), but was not a significant predictor in the multiple regression model.
Table 1.

<table>
<thead>
<tr>
<th>Statistical significance, linear regression analyses</th>
<th>R Square</th>
<th>F</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inferior Temporal Model</td>
<td>.730</td>
<td>6.580</td>
<td>.001</td>
</tr>
<tr>
<td>Superior Temporal Model</td>
<td>.133</td>
<td>.373</td>
<td>.905</td>
</tr>
<tr>
<td>Frontal Model</td>
<td>.336</td>
<td>1.226</td>
<td>.342</td>
</tr>
</tbody>
</table>

Table 2.

<table>
<thead>
<tr>
<th>Statistical significance of independent variables, inferior temporal model</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syntactic complexity</td>
<td>.102</td>
</tr>
<tr>
<td>Number of subordinate clauses</td>
<td>.015</td>
</tr>
<tr>
<td>GJ RT</td>
<td>.060</td>
</tr>
<tr>
<td>GJ accuracy</td>
<td>.019</td>
</tr>
<tr>
<td>PPVT-4 Standard Score</td>
<td>.005</td>
</tr>
</tbody>
</table>

Discussion

The present study examines performance on several language tasks as predictors of lateralization in the inferior temporal, superior temporal, and frontal regions in 25 healthy, right-handed adults without language impairment. Above and beyond NVIQ and length of story told, total number of subordinate clauses \( (p = .015) \), GJ accuracy \( (p = .019) \), and receptive vocabulary \( (p = .005) \) significantly predicted magnitude of lateralization of the inferior temporal region. Performance on the language tasks did not predict lateralization of the frontal or superior temporal regions. Additionally, greater lateralization of the inferior temporal lobe was correlated with higher syntactic complexity \( (p = .036) \). The findings of this study suggest that the inferior temporal lobe has an important role specifically in receptive vocabulary, grammaticality judgement, and syntactic skill. The fact that these language indices were not predictive of
lateralization for the frontal or superior temporal regions, which are also implicated in language, supports the hypothesis that different language functions may lateralize differently. In other words, language skill may not determine the lateralization of all brain areas that are activated during engagement in language.

The main language cluster defined by Bernal and colleagues (2015) primarily lies in the frontal region. Since the LI in these regions did not predict language performance, these areas could either be more pertinent for different functions, or could have a different lateralization pattern. For example, the anterior insula, which is part of the main cluster, could be related to the emotional valence of language (Wattendorf et al., 2016), which was not tested in this study. Given the location of Broca’s Area at the left IFG, it was rather surprising that none of the language tasks in this study predicted lateralization in this area. Future research should continue to explicitly examine which language clusters are associated with better performance. Based on our results, it is possible that the lateralization of the main (frontal) language cluster is not associated with skill level.

The results of the present study suggest that the left inferior temporal lobe is important for skills involving grammar, receptive vocabulary, and syntactic complexity. One possible structure of importance, as described by Whitney and colleagues (2011), is the pMTG. This language area would have been important in all three of the language tasks in the present study because they were constantly having to make semantic choices. The inferior temporal lobe is also thought to be implicated in visual working memory and semantic memory (Hamamé et al., 2012; Visser et al., 2010; Axmancher et al., 2008). The cartoon narration task in the present study required participants to rely on their working memories to recall the events of the story; thus, our task could have tapped into this function of the inferior temporal lobe.
The superior temporal model did not produce any significant predictors of lateralization. Since Wernicke’s area is a more superior temporal region, perhaps our tasks did not involve enough activation of this receptive language area. Additionally, there is evidence that some language functions are represented bilaterally in the temporal lobes (Bartha-Doering et al., 2018, Bradshaw et al., 2020), so it is possible that the inferior temporal region is the only portion where it is advantageous to be left-lateralized. Future research should look more closely at the superior temporal lobe and temporal regions that may benefit from bilateral representation, such as the MTL.

**Limitations**

One limitation of the present study is that “syntactic complexity” can be defined in several ways. We chose to use the ratio of subordinate clauses to C-Units because it was an intuitive way to establish interrater reliability. However, other ways to define this construct could be: utterances; words per C-Unit; types of different subordinate clauses; variability of word choice; and many others. It would be interesting to run the analysis on the same transcripts with different ways of defining syntactic complexity to see if these methods truly differ from one another.

Additionally, our sample size was small and homogeneous, with all participants being college students. Recruiting more adults would have yielded more generalizable results. Furthermore, the transcriptions themselves were short. Most videos were between one and three minutes long. If we had collected a larger language sample from each participant we would have seen a more accurate representation of their typical syntactic complexity. Further, our sample did not include any individuals with language impairment; while the goal of the study was to
investigate this relationship in a healthy, language-intact sample, it would be important to examine the current pattern of results in a more heterogeneous group. Adding in a language-impaired group would allow for an analysis of how different brain abnormalities may affect language representation. As the literature review suggested, examining patients with epilepsy or brain lesions may also yield findings relating to the development of language lateralization.

Finally, for future directions, it would be of interest to examine the interconnectivity between all of the language clusters discussed in this review. For example, there is evidence that the inferior temporal lobe is connected to and mediated by the MTL (Axmacher et al., 2008), which may benefit from bilateral representation. Understanding the circuitry among structures that communicate with one another, yet lateralize differently, will give a clearer answer on the path of linguistic information in the brain. Language studies could be run using technology such as Diffusion Tensor Imaging would be helpful in answering these questions.
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