Greater Leftward Lateralization of the Inferior Frontal Gyrus in Second Language Learners with Higher Syntactic Abilities

Arihito Nauchi,[1,2] and Kuniyoshi L. Sakai[1,2]*

[1]*Department of Basic Science, Graduate School of Arts and Sciences, The University of Tokyo, Komaba, Tokyo, Japan*
[2]*CREST, Japan Science and Technology Agency, Kawaguchi-shi, Japan*

Abstract: There is a great individual variability for acquiring syntactic knowledge in a second language (L2). Little is, however, known if there is any anatomical basis in the brain for individual differences in syntactic acquisition. Here we examined brain structures in 95 nonnative speakers of English, including 78 high-school students and 17 adult international students. We found a significant correlation between the performance of a syntactic task and leftward lateralization of a single region in the triangular part (F3t) of the inferior frontal gyrus, which has been proposed as the grammar center. Moreover, this correlation was independent of the performance of a spelling task, age, gender, and handedness. This striking result suggests that the neural basis for syntactic abilities in L2 is independent of that for lexical knowledge in L2, further indicating that the individual differences in syntactic acquisition are related to the lateralization of the grammar center. *Hum Brain Mapp 30:3625–3635, 2009.* © 2009 Wiley-Liss, Inc.

Key words: brain anatomy; lateralization; frontal cortex; human; language acquisition; syntax

INTRODUCTION

Why does the ability to master a L2 differ considerably among individuals, while anyone can master a first language (L1)? Recent functional imaging results have shown that both L1 and L2 are processed in the same cortical regions [Perani and Abutalebi, 2005; Sakai, 2005], indicating that the L2 acquisition mechanisms may be partly shared with L1 acquisition mechanisms. Voxel-based morphometry (VBM) studies have reported that the relative gray matter (GM) density of the inferior parietal cortex or the bilateral posterior supramarginal gyri was correlated with individual vocabulary scores [Lee et al., 2007; Mechelli et al., 2004]. However, the previous anatomical studies have examined the linguistic proficiency only at the word level. Functional imaging studies have also clarified the distinct activation patterns for lexico-semantics in left parieto-temporal regions and those for syntax in left frontal regions [Price, 2000; Sakai, 2005], suggesting differential neural correlates for acquiring lexical and syntactic knowledge. There are a large number of functional studies that have attempted to localize brain regions engaged in syntactic processing, although the interpretation of these studies varies [Caplan, 2001]. For instance, the anterior portion of the superior temporal gyrus and the left angular gyrus, as well as the inferior frontal gyrus (IFG), have been implicated as being engaged

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*Correspondence to: Kuniyoshi L. Sakai, Department of Basic Science, Graduate School of Arts and Sciences, The University of Tokyo, Komaba, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8902, Japan. E-mail: sakai@mind.c.u-tokyo.ac.jp

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TABLE I. Demographic details of each group

	High-school students	Adult students
N	78 (43 females)	17 (9 females)
Age		
Range	14–18	20–41
Mean ± SD	15 ± 1.4	28 ± 5.6
AOE		
Range	12–13	6–19
Mean ± SD	13 ± 0.3	11 ± 4.0
DOE		
Range	1.7–4.7	6–28
Mean ± SD	2.6 ± 1.4	17 ± 6.7
LQ		
Range	29–100	60–100
Mean ± SD	81 ± 16	87 ± 14

N, number of participants; AOE, age of first exposure to English; DOE, duration of exposure to English; LQ, laterality quotient of handedness.

in syntactic processes during sentence comprehension [Caplan et al., 2001; Friederici et al., 2003; Meyer et al., 2000]. Given this uncertainty about the regional specificity, the data from VBM studies are expected to shed new light on the critical roles of these cortical regions in syntactic processes. Therefore, we employed the VBM technique to clarify which regions are actually related to the individual differences of syntactic abilities in L2.

In our recent functional magnetic resonance imaging (fMRI) study for L2 learners, who were in two groups with different age of first exposure (AOE) to English (mean: 12.6 and 5.6 years for *late* and *early* learners, respectively), we examined the cortical activations involved in processing English sentences containing either syntactic or spelling errors, where the testing ages and task performances of both groups were matched [Sakai et al., in press]. Two forced-choice error-detection tasks were contrasted using the same set of English sentences: a syntactic (Syn) task and a spelling (Spe) task. The Syn task directly tested the correct use of English verbs in sentences [Levin, 1993], whereas the Spe task served as a control not only for the word-level knowledge and the reading abilities, but for the overall developmental and educational differences (e.g., experiences and exposures in L2). We found distinct activation patterns in two regions of the left IFG that correlated differentially with the performances of the late and early learners. Specifically, activations of the triangular part (F3t, Brodmann's area (BA) 45) of the left IFG correlated *positively* with the accuracy of the Syn task for the late learners, while activations of the left ventral F3t correlated *negatively* with the accuracy for the early learners. In contrast, activations of the orbital part (F3O, BA 47) of the left IFG correlated *positively* with the reaction times (RTs) of the Syn task for the late learners, whereas those activations correlated *negatively* with the RTs for the early learners. These results provide a functional basis for individual differences in L2 acquisition. The next goal is to examine whether there is also an anatomical basis for individual differences in the acquisition of syntactic knowledge, probably involving the left IFG such as F3t and F3O.

In this study, we used the same English stimuli and tasks of Syn and Spe. We acquired high-resolution MR images from 95 nonnative speakers of English in two groups: Japanese high-school students and adult international students. The latter group was added to exclude the possibility that the results were dependent on particular age or L1 backgrounds (Tables I and II). To examine any difference between these two groups is *not*, however, within the scope of this study. By examining the performance of the linguistic tasks, as well as all possible factors including age, gender, and handedness throughout both groups, truly biologically relevant individual variability on syntactic abilities will be elucidated in the brain.

MATERIALS AND METHODS

Participants

We recruited 95 healthy nonnative English speakers in two groups. The high-school students ($N = 78$) were native speakers of Japanese, who had passed an entrance examination at the age of 12, and they were in the second or fifth academic years. They had studied English as L2 only in Japan and the age at which they had begun studying English was 13 years; they had never studied a third language (L3). The adult international students ($N = 17$) had L1 backgrounds other than English (e.g., Bulgarian, Chinese, Croatian, Indonesian, Lithuanian, Mongolia, Persian, Philippine (Cebuano and Tagalog), and Turkish), and they had studied English as L2 in their non-English speaking countries at least until 15 years old. They also varied

TABLE II. Participants' behavioral data for each group

Task	High-school students	Adult students
Syn		
Accuracy (%)		
Range	41–90	60–91
Mean ± SD	59 ± 11	77 ± 12
RTs (ms)		
Range	2,832–5,804	3,809–5,557
Mean ± SD	4,651 ± 578	4,496 ± 515
Spe		
Accuracy (%)		
Range	48–98	75–98
Mean ± SD	77 ± 13	90 ± 7.1
RTs (ms)		
Range	2,875–5,716	3,614–5,100
Mean ± SD	4,371 ± 604	4,273 ± 534

Only trials with correct responses were used for reaction times (RTs). The accuracy of Syn for the high-school students was significantly higher than the chance level at 50 % ($t(77) = 7.7$, $P < 0.0001$).

in their skills of the Japanese language as L3. All participants of these two groups were right-handed and their laterality quotients of handedness (LQs) were above 20 according to the Edinburgh inventory [Oldfield, 1971]. Informed consent was obtained from all participants, as well as from the parents/guardians of the high-school students, and the study was approved by the Secondary Education School attached to the Faculty of Education of the University of Tokyo and by the review board of The University of Tokyo, Komaba.

Stimuli and Tasks

We selected 42 high-frequency English verbs (20 transitive and 22 intransitive, including 12 unergatives and 10 unaccusatives [Yusa, 2003]), and made 100 sets of sentence stimuli using these verbs, as listed previously [Sakai et al., in press]. Each set consisted of a key sentence and its associated sentence, which was either syntactically normal or anomalous. The syntactic errors used in the Syn task were basically related to argument structures of English verbs. For instance, as in the example of "*Do you often meet Mary? - Yes, I often meet*.", L2 learners tend to make a mistake of omitting an object. This is because objects of transitive verbs can be omitted quite freely in many languages other than English [Cole, 1987; Park, 2004]. Similarly, the null-subject (pro-drop) is allowed in Japanese, as well as in Spanish and Italian [Hyams, 1989], and Spanish speakers often accept English sentences without overt subjects [White, 1985]. Even if these aspects of English grammar are normally taught at school, such syntactic knowledge is hard to acquire for the students. Because the present paradigm explicitly requires judgment on the grammaticality of sentences, the acquisition of argument structures and their associated syntactic knowledge will be properly assessed. In the Spe task, on the other hand, a typographical error was included in each set for half of the same sets, to test the English orthography of words.

All behavioral data were acquired outside the MR scanner. At the initiation of every trial of 7 s, a cue, indicating whether the task was Syn or Spe, was shown for 400 ms, followed by a set of two English sentences for 6,400 ms. The participants were instructed to read the two sentences silently from first to last before responding, and they indicated whether or not the sentences contained an error by pushing one of two buttons. In a single session, there were two Syn and two Spe task blocks (five trials each), and each session was repeated five times. The order of these two task blocks was counterbalanced across each participant. In calculating the accuracy of each task, we included trials with no responses as incorrect ones, and excluded trials with premature responses (button press within 2 s); no further adjustment for correct or incorrect responses was made.

The high-school students received 10 brief training sessions from their English teachers as a part of the normal lessons, in which the correct usage of English verbs was taught with the 100 sets. During the training, each set consisted of a key sentence followed by its associated two sentences, one of which contained a syntactic error in some cases. The students first tried to guess their grammaticality, and a teacher then provided them with the correct answers and a brief explanation. After the training sessions, 100 new sets of sentences with the same English verbs were used for the Syn and Spe tasks to ensure whether they had actually acquired the knowledge of syntactic structures, rather than merely memorizing the sentence examples used for the training. The accuracy of Syn improved significantly after the training (paired-t test: $t(77) = 7.7$, $P < 0.0001$), and we used these data (Table II) for the present analyses, together with the MRI data also acquired after the training.

MR Image Acquisition and Analyses

Using a 1.5-Tesla MRI system (STRATIS II, Premium; Hitachi Medical Corporation, Tokyo, Japan), high-resolution T1-weighted images of the whole brain (160 axial slices; $1.0 \times 1.0 \times 1.0$ mm^3) were acquired with a radio frequency spoiled steady-state acquisition with a rewound gradient echo (RF-Spoiled SARGE) sequence (repetition time, 30 ms; echo time, 8.0 ms; flip angle, 60°). MR images were first skull-stripped with a Brain Extraction Tool (BET) [Smith, 2002] in MRIcro software [Rorden and Brett, 2000] (http://www.sph.sc.edu/comd/rorden/ mricro.html), and the data were further analyzed with SPM5 software [Friston et al., 1995] (http://www.fil.ion.ucl.ac.uk/spm). A symmetrical GM template was made by averaging GM maps of the standard brain and its mirrored image [Luders et al., 2004]. The VBM preprocessing [Ashburner and Friston, 2005] (http://dbm.neuro.uni-jena.de/vbm/) combined bias correction, spatial normalization with the symmetrical template, and segmentation with a hidden Markov random field model [Cuadra et al., 2005]. The results presented below were replicated also with a conventional asymmetric template, but the symmetric template is more appropriate to use in the present study for comparing the corresponding regions in the left and right hemispheres.

To evaluate the absolute volume of GM, the segmented GM images were further modulated by multiplying the voxel values by the relative voxel volumes (i.e., the Jacobian determinants of the deformation field derived from spatial normalization) [Ashburner and Friston, 2000]. The modulated GM images were then smoothed with an isotropic Gaussian kernel of 12 mm at full-width half-maximum (FWHM) [Lee et al., 2007]. To avoid possible edge effects (partial volume effects) around the border of the GM, voxels with a value greater than 0.05 (maximum, 1.0) were used for analyzing the modulated GM images. Using the same procedures, we also examined volumes of the white matter (WM) across the whole brain. For the anatomical identification of cortical regions, we used the automated anatomical labeling (AAL) method [Tzourio-Mazoyer et al., 2002] on SPM5.

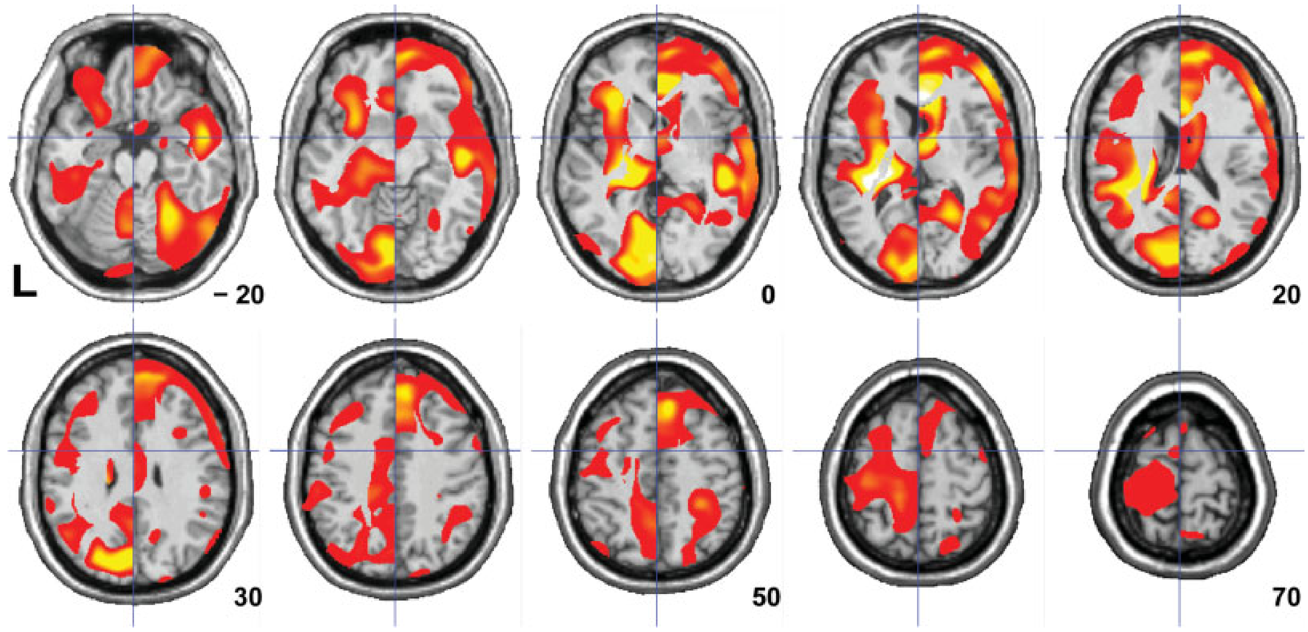


Figure 1.

The overall lateralization of cortical regions ($N = 95$). Cortical regions with the significantly positive regional asymmetry index (AI) are shown (from red to yellow) on the axial slices (z coordinates are denoted) of the symmetrical standard brain, which was normalized to the symmetrical template (L, left). The symmetrical gray matter (GM) template (GM value > 0.05) was also used as an inclusive mask. The cross hairs denote the position of the anterior commissure ($x = y = 0$). Note that both lateral and medial frontal regions show rightward lateralization, whereas the deeper frontal structures show leftward lateralization.

The voxel-based asymmetry of the *regional* GM was estimated by calculating the asymmetry index (AI) for a pair of original and mirrored GM images:

AI = 2 × (original GM – mirrored GM)/(original GM + mirrored GM)

The modulated GM images were used for this calculation, and the resultant AI images were then smoothed with a 12-mm FWHM kernel [Luders et al., 2004]. The positive AI in the left and right hemispheres correspond to leftward and rightward lateralization, respectively.

RESULTS

Here we set out our main line of analyses by explaining the motivation of each analysis and the method used to carry it out. First, we characterize the AI in the whole brain to show the overall left or right lateralization of cortical regions. We then present the results of the AI analyses for all participants, employing a multiple regression analysis to examine the effects of five standardized factors on the AI: the accuracy of Syn, the accuracy of Spe, age, gender, and LQ (Fig. 2B). In this analysis, no particular correlation between the AI and the global volume is expected. If any locus shows a significant correlation with one factor, we further perform a partial correlation analysis with the standardized AI at this locus and the standardized value of this factor to confirm the selective and reliable correlation. To fully characterize the lateralization of this locus, we need to clarify whether this correlation emerges because of the regional GM in one hemisphere, thereby employing both multiple regression and partial correlation analyses. We will then proceed to the separate analyses of each group using the same procedures, followed by the examination for any effects of age.

The Overall Lateralization of Cortical Regions

Figure 1 shows the overall lateralization of cortical regions with the significantly positive AI ($P < 0.05$, false discovery rate (FDR) corrected for multiple comparisons). It is notable that both lateral and medial frontal regions, as well as the superior and middle temporal regions, showed rightward lateralization. In contrast, leftward lateralization was observed in the deeper frontal structures including IFG and the insula, as well as lateral and medial occipital regions. The AAL method indicated that the regions with leftward lateralization included most of putamen, thalamus, and the Heschle gyrus as well. The general pattern of volume differences between left and right hemispheres are consistent with previous reports [Luders et al., 2004; Toga and Thompson, 2003].

The Structural Basis for Individual Syntactic Abilities in L2

According to a multiple regression analysis on the AI, we found a significant correlation between the accuracy of Syn and the AI in a focal region of the left F3t ($x = -32$, $y = 31$, $z = 12$; 554 voxels; Z-score = 5.0; $P = 0.013$, FDR corrected), which was one and only region in the whole brain (Fig. 2A). At this locus, the AI was significantly positive, ranging from −0.23 to 0.41 (mean ± SEM: 0.067 ± 0.012; $t = 5.7$, $P < 0.0001$). Remarkably, this region is just *medial* to the functionally critical region of the Syn task (three loci: $x = -42$, $y = 27$, $z = 0$; $x = -57$, $y = 24$, $z = 15$; $x = -51$, $y = 27$, $z = 24$) indicated by our fMRI study using the same paradigm [Sakai et al., in press]. At the locus of the left F3t in this study, the regression coefficients of the AI were significant for the accuracy of Syn (0.077 ± 0.014, $P < 0.0001$) and age (−0.031 ± 0.013, $P = 0.016$) only (other coefficients, $P > 0.28$) (Fig. 2C). It is striking to note that the accuracy of Syn is one and only factor with a significantly positive correlation. The selective contribution of syntactic abilities is thus clear from this significant interaction between the AI in the left F3t and the five factors, because the AI can be predicted by the accuracy of Syn alone, independently of the accuracy of Spe, gender, and LQ. Indeed, there was no significant correlation (i.e., neither positive nor negative correlation) between the accuracy of Spe and the AI in the whole brain (corrected $P > 0.05$).

By using the standardized AI at this locus of the left F3t, we also performed a partial correlation analysis with the standardized accuracy of Syn, after the effects of all other factors had been removed from each of these two parameters. The standardized AI was significantly correlated with the standardized accuracy of Syn ($r = 0.50$, $P < 0.0001$) (Fig. 2D). In contrast, the standardized AI was not correlated with the standardized accuracy of Spe at all ($r = -0.008$, $P = 0.9$) (Fig. 2E), even when both parameters were standardized in the same manner as the case of Syn. These results clearly demonstrate that the leftward lateralization of the F3t is specific and critical for the performance of the Syn task.

To fully characterize the leftward lateralization of the F3t, which correlated significantly with the accuracy of Syn, we need to show whether this correlation emerges because of a relatively larger volume of the regional GM in the left hemisphere and/or a smaller volume of the regional GM in the right hemisphere. We thus employed a multiple regression analysis to examine the effects of six standardized factors on the regional GM: the accuracy of Syn, the accuracy of Spe, age, gender, LQ, and the total GM. In this analysis, the positive correlation between the regional GM and the total GM is expected. We found a significant correlation between the accuracy of Syn and the regional GM in the left F3t ($x = -35$, $y = 27$, $z = 11$; Z-score = 3.0; $P = 0.039$, FDR corrected) when a small volume correction (SVC) (5.5-mm radius sphere at $x = -32$, $y = 31$, $z = 12$) was applied. At the locus of the left F3t ($x = -32$, $y = 31$, $z = 12$), the regression coefficients of the regional GM were significant for the accuracy of Syn (0.012 ± 0.005, $P = 0.011$) and the total GM (0.025 ± 0.004, $P < 0.0001$) (Fig. 3A). Moreover, the standardized regional GM in the left F3t was significantly correlated with the standardized accuracy of Syn ($r = 0.23$, $P = 0.023$) (Fig. 3B). In contrast, at the locus of the right F3t ($x = 32$, $y = 31$, $z = 12$), the regression coefficients of the regional GM were significant for the total GM (0.026 ± 0.005, $P < 0.0001$), but not for the accuracy of Syn (−0.008 ±0.005, $P = 0.10$) (Fig. 3C). The standardized regional GM in the right F3t was not significantly correlated with the standardized accuracy of Syn ($r = -0.18$, $P = 0.080$). These results suggest that the larger volume of the left regional GM contributes more to the selective correlation between syntactic abilities and the AI in the left F3t. Regarding the regional WM, there was no significant correlation with the accuracy of Syn or Spe (corrected $P > 0.05$).

The Structural Basis for Individual Syntactic Abilities in L2 for the High-School Students

Next we examined the data from the high-school students alone ($N = 78$) to exclude the possibility that the observed effects were due to the inclusion of the adult international students, who widely varied in age, duration of exposure (DOE) to English, L1 background, and skills of the Japanese language. Note, however, that for the adult group ($N = 17$) none of the regression coefficients of the AI in the left F3t ($x = -32$, $y = 31$, $z = 12$) were significant ($P > 0.3$). The absence of significance for this group would be due to the smaller sample size, as well as the narrower range of the accuracy of Syn (Table II). Using exactly the same procedures of analyses described above, we further checked whether all of the main findings were robust and exactly replicated even for the high-school students alone, who were relatively homogeneous individuals with respect to age, AOE, DOE, and L1 background (Table I).

According to a multiple regression analysis to examine the effects of the same five standardized factors on the AI, we found a significant correlation between the accuracy of Syn and the AI in a focal region of the left F3t ($x = -33$, $y = 32$, $z = 11$; 579 voxels; Z-score = 5.1; $P = 0.009$, FDR corrected), which was one and only region in the whole brain. At this locus of the left F3t, the AI was significantly positive, ranging from −0.26 to 0.27 (0.063 ± 0.012; $t = 5.1$, $P < 0.0001$), and the regression coefficients of the AI were significant for the accuracy of Syn (0.069 ± 0.012, $P < 0.0001$) alone (other coefficients, $P > 0.17$) (Fig. 4A). There was no significant correlation between the accuracy of Spe and the AI in the whole brain (corrected $P > 0.05$).

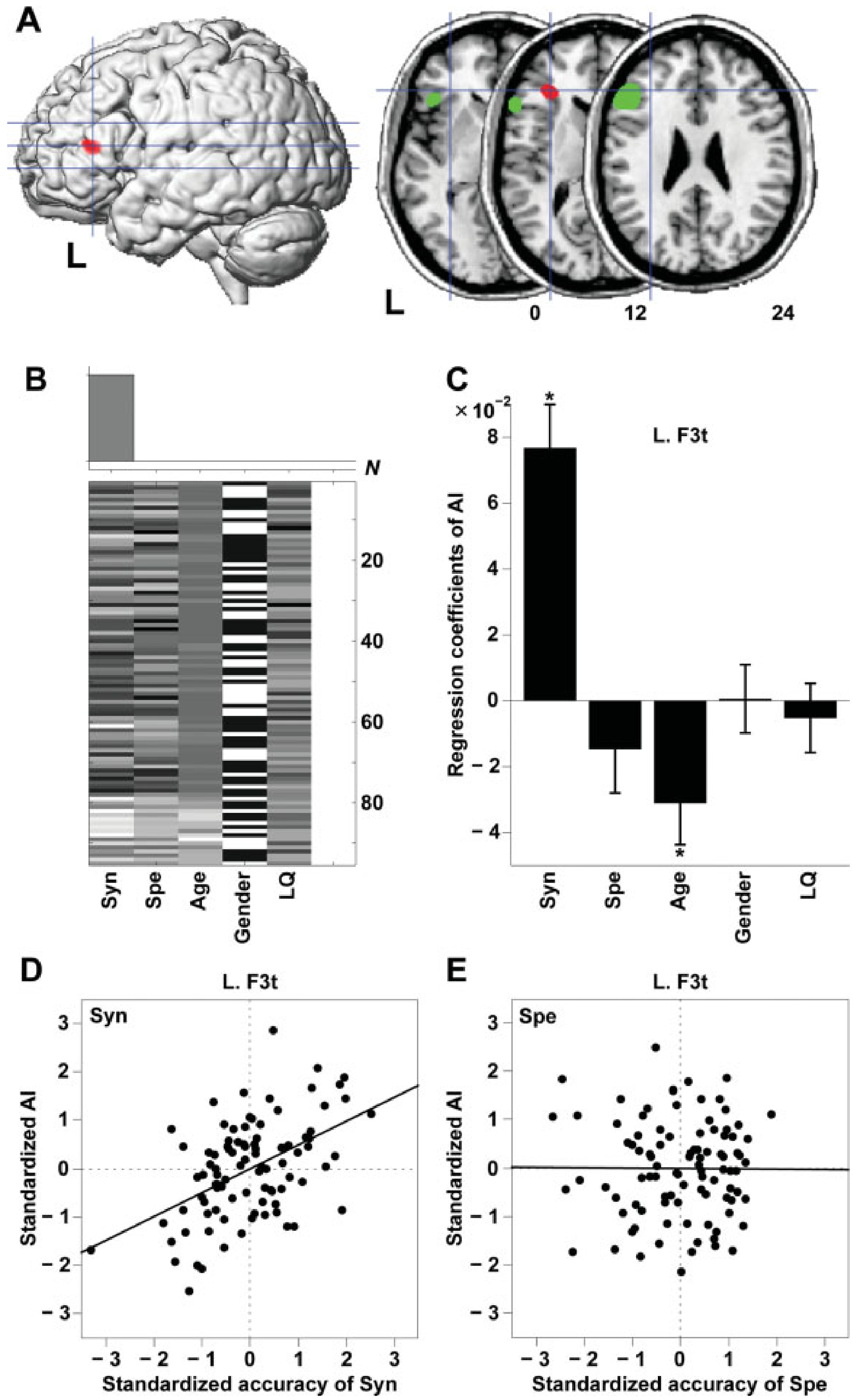
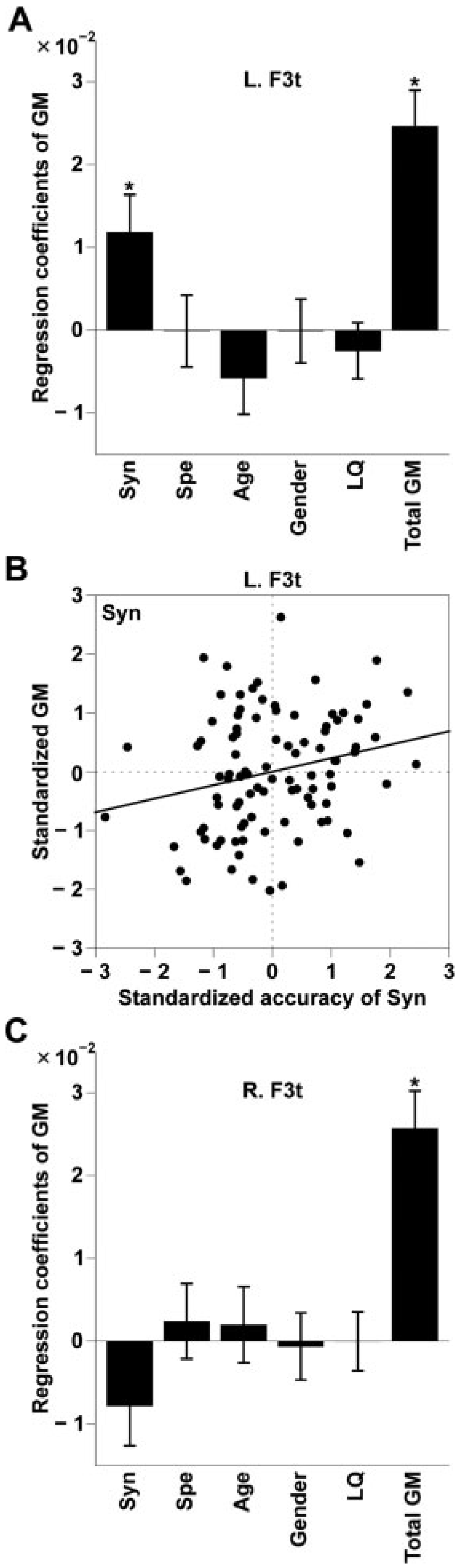


Figure 2.

The structural basis for individual syntactic abilities in L2 ($N = 95$). (**A**) The left F3t with a significant correlation between the accuracy of Syn and the AI. The left (L) lateral surface (horizontal cross hairs at $z = 0, 12, 24$) and axial sections of the symmetrical standard brain are shown for the locus of the left F3t with a significant correlation (red), together with three foci of the left F3t (green) identified by our fMRI study [Sakai et al., in press]. The vertical cross hair on the lateral surface and the horizontal cross hair on the axial sections denote $y = 31$, whereas the vertical cross hairs on the axial sections denote $x = -32$. (**B**) Design matrix used for a multiple regression analysis. The five columns denote the five regressors of the accuracy of Syn, the accuracy of Spe, age, gender, and the laterality quotient of handedness (LQ). (**C**) Regression coefficients of the AI in the left F3t for the five regressors. Error bars indicate the SEM of participants, and asterisks denote the significance level of $P < 0.05$. (**D,E**) A partial correlation between the standardized AI in the left F3t and the standardized accuracy of Syn (D) or Spe (E), after removing the effects of all other factors.



According to a partial correlation analysis, the standardized AI at this locus of the left F3t was also significantly correlated with the standardized accuracy of Syn ($r = 0.56$, $P < 0.0001$) (Fig. 4B). In contrast, the standardized AI was not correlated with the standardized accuracy of Spe at all ($r = -0.02$, $P = 0.9$) (Fig. 4C).

We also employed a multiple regression analysis to examine the effects of the same six standardized factors on the regional GM. There was a significant correlation between the accuracy of Syn and the regional GM in the left F3t ($x = -34$, $y = 27$, $z = 11$; Z-score = 2.6; $P = 0.049$, FDR corrected) when a SVC (5.5-mm radius sphere at $x = -33$, $y = 32$, $z = 11$) was applied. At the locus of the left F3t ($x = -33$, $y = 32$, $z = 11$), the regression coefficients of the regional GM were significant for the accuracy of Syn (0.011 ± 0.005, $P = 0.023$) and the total GM (0.026 ± 0.005, $P < 0.0001$). Moreover, the standardized regional GM in the left F3t was significantly correlated with the standardized accuracy of Syn ($r = 0.23$, $P = 0.042$) (Fig. 5A). In contrast, at the locus of the right F3t ($x = 33$, $y = 32$, $z = 11$), the regression coefficients of the regional GM were significant for the total GM (0.030 ± 0.005, $P < 0.0001$), but marginally significant for the accuracy of Syn (-0.009 ± 0.005, $P = 0.059$). It should be noted that the standardized regional GM in the right F3t was significantly correlated with the standardized accuracy of Syn ($r = -0.23$, $P = 0.043$) (Fig. 5B). These results suggest that the larger volume of the left regional GM, as well as the smaller volume of the right regional GM, contributes to the selective correlation between syntactic abilities and the AI in the left F3t. Regarding the regional WM, there was no significant correlation with the accuracy of Syn or Spe (corrected $P > 0.05$).

The Effects of Age

Finally we examined the effects of age, independently of other factors. Regarding the AI images, we conducted the group comparison between the high-school students ($N = 17$ with higher Syn scores) and adult international students ($N = 17$) matched for proficiency ($t(32) = 1.0$, $P = 0.3$), but there was no significant difference (corrected $P > 0.05$). According to a multiple regression analysis for all

Figure 3.
The correlation between the regional GM in the F3t and syntactic abilities in L2 ($N = 95$). (**A**) Regression coefficients of the regional GM in the left F3t for the accuracy of Syn, the accuracy of Spe, age, gender, LQ, and the total GM. Error bars indicate the SEM of participants, and asterisks denote the significance level of $P < 0.05$. (**B**) A partial correlation between the standardized accuracy of Syn and the standardized regional GM in the left F3t, after removing the effects of all other factors. **C**: Regression coefficients of the regional GM in the right F3t for the six regressors.

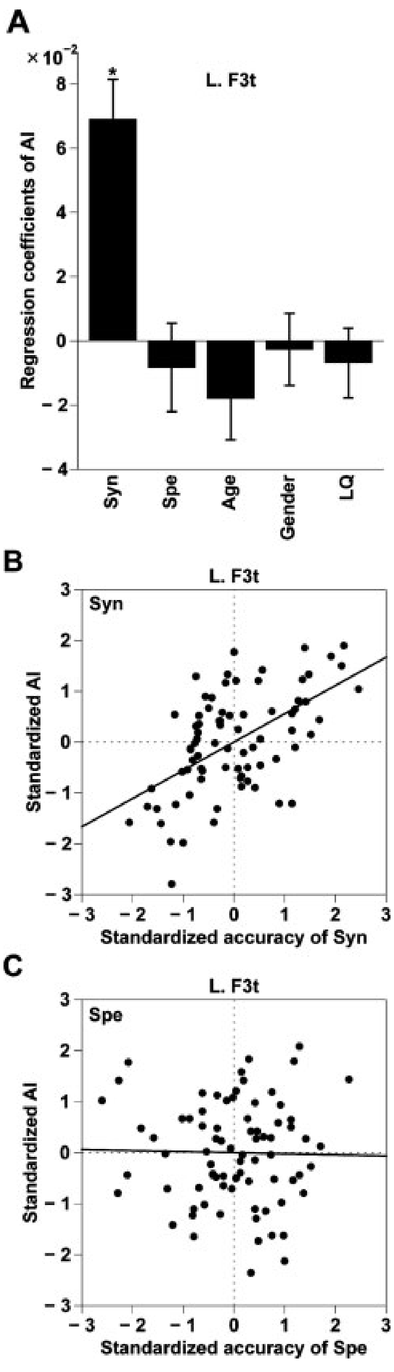


Figure 4.
The structural basis for individual syntactic abilities in L2 for the high-school students ($N = 78$). (**A**) Regression coefficients of the AI for the five regressors. (**B,C**) A partial correlation between the standardized AI in the left F3t and the standardized accuracy of Syn (B) or Spe (C).

participants, there was no significant correlation (i.e., neither positive nor negative correlation) between age and the regional GM, but the regional WM showed a significantly negative correlation with age in the bilateral corona radiata ($x = 28$, $y = -48$, $z = 17$; 14,815 voxels; Z-score = 4.7; $P = 0.017$, FDR corrected) (Fig. 6A). In this analysis, the positive correlation between the regional WM and the total WM is expected. At this locus of the right corona radiata, the regression coefficients of the regional WM

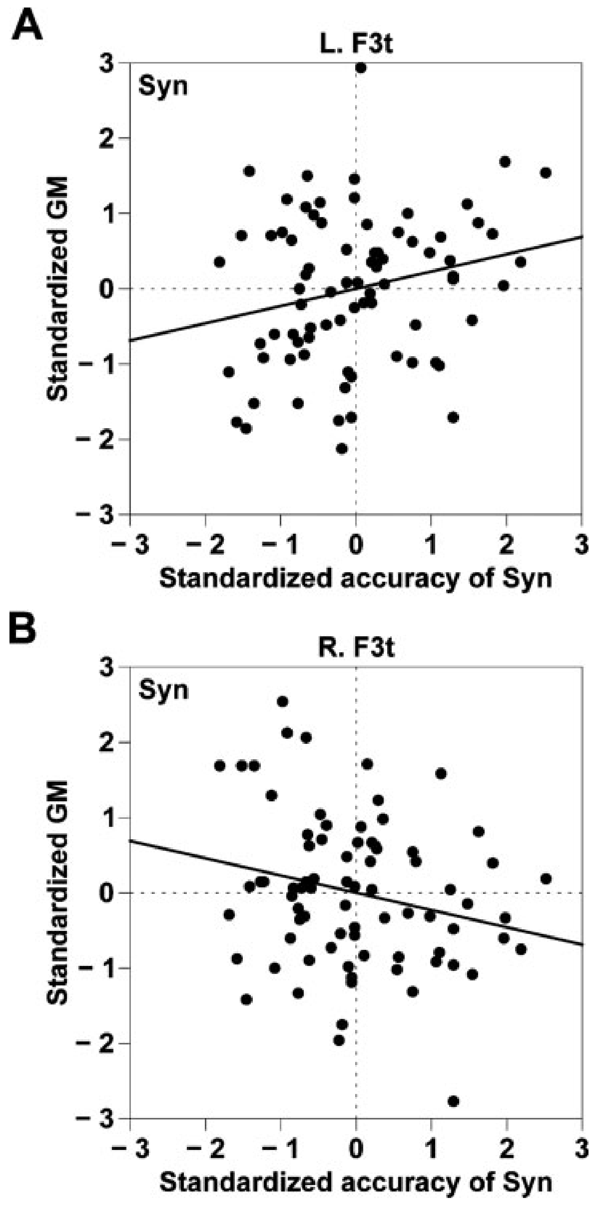


Figure 5.
The correlation between the regional GM in the F3t and syntactic abilities in L2 ($N = 78$). (**A,B**) A partial correlation between the standardized accuracy of Syn and the standardized regional GM in the left F3t (A) or right F3t (B).

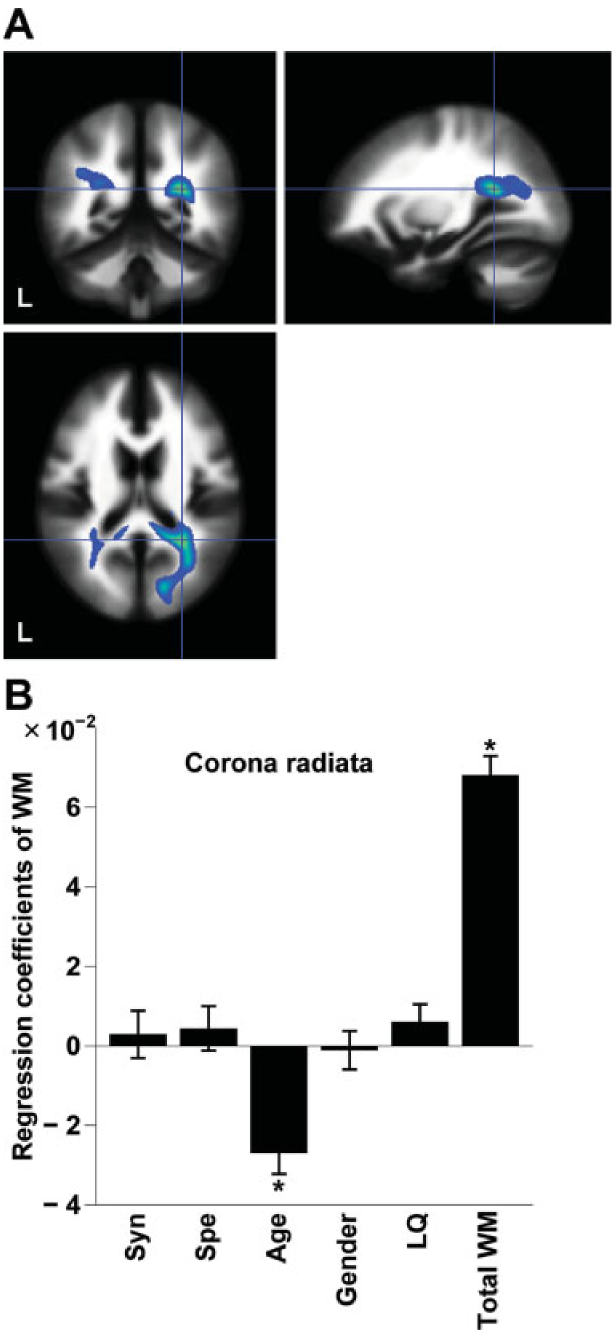


Figure 6.
The effects of age on the white matter (WM) ($N = 95$). (**A**) The bilateral corona radiata with a significantly negative correlation between age and the regional WM. Coronal ($y = -48$), sagittal ($x = 28$), and axial ($z = 17$) slices of the symmetrical WM template are shown. Note the extension of the significant voxels along the fiber bundles. (**B**) Regression coefficients of the regional WM in the right corona radiata for the accuracy of Syn, the accuracy of Spe, age, gender, LQ, and the total WM.

were highly significant for both age (-0.0271 ± 0.005, $P < 0.0001$) and the total WM (0.068 ± 0.005, $P < 0.0001$) (Fig. 6B). This age-dependent negative correlation in the bilateral corona radiata is consistent with the result reported previously [Good et al., 2001].

It is interesting to note that the structural basis for syntactic abilities is consistent over a wide range of ages, namely 14–41 years in the present study. Because the DOE of each participant was highly correlated with age ($r = 0.96$, $P < 0.0001$) (see Fig. 7), the result was also robust no matter how short or long the DOE was. The correlation between age and DOE indicates that it is difficult to apportion variance between these variables, not that they are equivalent. In our previous fMRI study, we conducted Japanese (L1) versions of the Syn and Spe tasks, which resulted in the mean accuracy of more than 80% for both tasks [Sakai et al., in press]. Individual differences in L1, as well as age-dependency in L1, are thus difficult to assess with these tasks, and it is another challenging issue for future research.

DISCUSSION

Here we showed that the leftward lateralization of the F3t selectively correlated with the performance of the Syn task, that is, syntactic abilities in L2, independently of lexical knowledge in L2 as tested by the Spe task (Figs. 2 and 4). Moreover, this positive correlation was independent of age or DOE, as well as of gender and handedness. We confirmed that the larger volume of the left regional GM, as well as the smaller volume of the right regional GM,

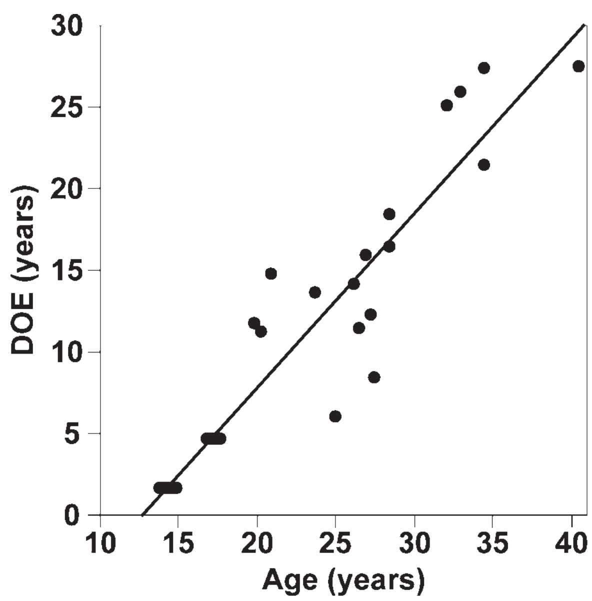


Figure 7.
A correlation between the DOE to English and age for each participant.

contributes to the selective correlation between syntactic abilities and the AI in the left F3t (Figs. 3 and 5). On the other hand, an age-dependent correlation on the regional WM was observed only in the sensory pathway of the bilateral corona radiata, suggesting that the language-dependent variance in the regional GM might be independent of the general architecture of cortical networks for basic sensory-motor functions. Although these correlation data alone cannot allow the causal interpretation, the correspondence of the left F3t between the present anatomical study and our previous functional study using the same paradigm is striking. Given that the syntactic processing in both L1 and L2 is specialized in the left F3t, as shown previously by our fMRI studies [Sakai et al., 2004, in press], the present results further suggest that the anatomical basis for syntactic abilities generally lies in the specificity of the same region.

Accumulating evidence has indicated that the left F3t is specialized in syntactic processing, using various syntactic decision tasks with sentence stimuli [Hashimoto and Sakai, 2002; Iijima et al., 2009; Kinno et al., 2008; Momo et al., 2008; Sakai et al., in press]. The adjacent opercular part (F3op, BA 44) has been also implicated in the syntactic aspect of single words (content or function words) and the complexity of sentences [Friederici et al., 2000, 2006]. Indeed, activation has been sometimes found just on the vertical ramus of the Sylvian fissure, thus covering both the left F3op and F3t, when sentence-level syntax was compared with other linguistic factors including semantics, spelling, unreal rules, and phonology [Dapretto and Bookheimer, 1999; Embick et al., 2000; Musso et al., 2003; Suzuki and Sakai, 2003]. We have previously demonstrated that these regions showed prominent activation for syntactic decision tasks even when they were directly compared with verbal short-term memory tasks [Hashimoto and Sakai, 2002]. The activation of the left F3op/F3t is thus related to the process of analyzing syntactic structures, which cannot be explained either by task difficulty or by verbal short-term memory components. These results consistently indicate an essential and universal role of the left F3op/F3t in syntactic processing. This region can be thus regarded as the "grammar center" [Sakai, 2005]. We should note, however, that all of these syntactic tasks involve executive processes as a part of decision-making component of the tasks. If those executive processes are general in linguistic decisions, our control task of Spe also critically involved the same decision-making component, and thus the Syn-specific leftward lateralization of the F3t cannot be explained by such general executive processes. The involvement of specific linguistic executive processes, such as syntax-semantics interface, should be further examined in the future functional and anatomical studies.

We observed a significantly negative correlation between age and the AI in the left F3t (Fig. 2C), suggesting that this region tends to show more reduced left lateralization when the participant becomes older. Because the ages were not uniformly distributed among the participants in this study, more extensive studies are needed to establish this tendency. A previous cytoarchitectonic study has indicated the opposite direction, such that asymmetry tended to increase with age throughout life, which was significant in BA 45, but not in BA 44 [Amunts et al., 2003]. Because the lateralization itself becomes reversed between the lateral and deeper structures within the F3op/F3t (see Fig. 1), the age-dependent lateralization may be affected by the location of a targeted region and by a proportion of lateral and deeper structures.

One possible explanation for the significance of leftward lateralization of the grammar center is that the larger the AI is, the less the inhibition from the right homologous region becomes, which is controlled through commissural fibers. As a result, the capacity or flexibility of the left F3t activation increases when compared with more symmetrical or right-dominant brain regions. A recent fMRI study has reported that participants with a larger corpus callosum showed more left-lateralized activation in inferior frontal and posterior temporal regions for lexico-semantic tasks [Josse et al., 2008]. It is possible that the relationship between the corpus callosum size and functional lateralization also depends on the location of a targeted region and on specific tasks used. According to an intriguing cytoarchitectonic study, one "language genius" (E.K.), who spoke fluently more than 60 languages in his life, showed the largest asymmetry in the left F3t, when compared with control brains [Amunts et al., 2004]. Our large-scale study of high-school students and adults further suggests that the variable asymmetry of the left F3t is a crucial factor for explaining individual differences on syntactic abilities in L2. Such information about the specific brain structure might be utilized for effectively predicting an individual aptitude for multiple languages.

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