When a sentence loses semantics: Selective involvement of a left anterior temporal subregion in semantic processing

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Title

When a sentence loses semantics: Selective involvement of a left anterior temporal subregion in semantic processing

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Abstract

Although the left anterior temporal lobe (ATL) has been associated with semantic processing, the role of this region in syntactic structure building of sentences remains a subject of debate. Functional neuroimaging studies contrasting well-formed sentences with word lists lacking syntactic structure have produced mixed results. The current functional magnetic resonance imaging study examined whether the left ATL is selectively involved in semantic processing or also plays a role in syntactic structure building by manipulating syntactic complexity and meaningfulness in a novel way. To deprive semantic/pragmatic information from a sentence, we replaced all content words with pronounceable meaningless placeholders. We conducted an experiment with a 2 × 2 factorial design with factors of SEMANTICS (natural sentences [NAT]; sentences with placeholders [SPH]) and SYNTAX (the basic Japanese Subject-Object-Verb [SOV] word order; a changed Object-Subject-Verb [OSV] word order). A main effect of SEMANTICS (NAT > SPH) was found in the left ATL, as well as in the ventral occipitotemporal regions. The opposite contrast (SPH > NAT) revealed activation in the dorsal regions encompassing Brodmann area 44, the premotor area, and the parietal cortex in the left hemisphere. We found no main effect of SYNTAX (OSV > SOV) in a subregion of the left ATL that was more responsive to natural sentences than meaningless sentences. These results indicate selective involvement of a subregion of the left ATL in semantic/pragmatic processing.

Introduction

The function of the anterior temporal lobe (ATL) during sentence processing has been a longstanding question. A growing body of evidence supports the view that the ATL represents domain-general semantic knowledge (Rogers *et al.*, 2006; Lambon Ralph *et al.*, 2009) and integrates semantic information (Jung-Beeman, 2005; Wilson *et al.*, 2014), thereby serving as a semantic hub (Patterson *et al.*, 2007; Lambon Ralph *et al.*, 2017). However, some studies have implicated the left ATL in syntactic structure building (Mazoyer *et al.*, 1993; Noppeney & Price, 2004; Humphries *et al.*, 2005; Humphries *et al.*, 2006; Rogalsky & Hickok, 2009; Bemis & Pylkkänen, 2011; Brennan *et al.*, 2012), in contrast to the view that the left Brodmann area (BA) 44 and the posterior middle temporal gyrus (pMTG) are brain regions responsible for hierarchical syntactic structure building (Just *et al.*, 1996; Dapretto & Bookheimer, 1999; Ben-Shachar *et al.*, 2003; Friederici *et al.*, 2003; Ben-Shachar *et al.*, 2004; Caplan *et al.*, 2008; Makuuchi *et al.*, 2009; Makuuchi *et al.*, 2012; Makuuchi *et al.*, 2013; Tyler *et al.*, 2013; Zaccarella & Friederici, 2015; Zaccarella *et al.*, 2015; Zaccarella *et al.*, 2017; Iwabuchi *et al.*, 2019). Neuropsychological studies have also provided mixed results. Several studies have associated lesions in Broca's area and/or the left pMTG with syntactic deficits (Wilson & Saygin, 2004; Tyler *et al.*, 2011; Jakuszeit *et al.*, 2013), while others have reported syntactic processing impairment after left ATL damage (Dronkers *et al.*, 2004; Magnusdottir *et al.*, 2012).

These conflicting results regarding the function of the ATL may have arisen from shortcomings in the experimental paradigms of previous studies. Many studies have contrasted well-formed sentences with word-lists lacking syntactic structure to reveal the neural substrates of syntactic structure building (Mazoyer *et al.*, 1993; Stowe *et al.*, 1998; Friederici *et al.*, 2000; Vandenberghe *et al.*, 2002; Humphries *et al.*, 2005; Humphries *et al.*, 2006; Rogalsky & Hickok, 2009). These studies indicated that the left ATL was more active for sentences than for word-lists, suggesting that the region is a center of syntactic structure building. Furthermore, some of these studies found no significant activation in the left BA 44 for structure building (Mazoyer *et al.*, 1993; Stowe *et al.*, 1998; Vandenberghe *et al.*, 2002; Humphries *et al.*, 2005; Humphries *et al.*, 2006; Rogalsky & Hickok, 2009). However, as Friederici (2011) insightfully pointed out, the word-lists used in these studies might allow an unwanted automatic syntactic structuring process, which can increase activation in the left BA 44 to a level as high as, or even higher than, that achieved by well-formed sentences.

Another line of research has indicated an association between the left ATL and semantic integration by comparing semantically natural sentences with “Jabberwocky” sentences in which words were replaced with pseudo-words (Röder *et al.*, 2002; Fedorenko *et al.*, 2010; Pallier *et al.*, 2011; Fedorenko *et al.*, 2012; Redcay *et al.*, 2016; Matchin *et al.*, 2017; Matchin *et al.*, 2018). However, studies that contrasted Jabberwocky sentences with lists of pseudo-words have provided contradictory findings in terms of syntactic processing; some have suggested an involvement of the left ATL in syntactic processing (Humphries *et al.*, 2006; Fedorenko *et al.*, 2010; Bedny *et al.*, 2011; Fedorenko *et al.*, 2012), while others have not (Pallier *et al.*, 2011; Goucha & Friederici, 2015). Thus, whether the activity in the left ATL is reactive to syntactic structure building, even when all contents words in a sentence are replaced with meaningless items, remains an open question.

We aimed to clarify whether the left ATL engages in the syntactic structure building during sentence processing, using functional magnetic resonance imaging (fMRI). Our hypothesis was the existence of a subregion in the left ATL that is uniquely involved in semantic/pragmatic processing but insensitive to the cost of syntactic structure building. We invented meaningless sentences by replacing all content words in Japanese sentences with pronounceable placeholders (e.g., AA, BB, CC, etc.). The sentences with placeholders required readers to build hierarchical structures similar to those in natural sentences while inhibiting any semantic/pragmatic computation to obtain the sentential meaning. Replacing the content words in sentences with meaningless placeholders provides two advantages over using pseudo-words. One is that it eliminates the cognitive cost of a vain lexical search for pseudo-words in the mental lexicon. Since pseudo-words are designed to look like real words (e.g., pandesteek, swarbing) (Goucha & Friederici, 2015; Fedorenko *et al.*, 2016), the readers must search their mental lexicon thoroughly to judge whether the word actually exists. This exhaustive but unsuccessful search burdens the readers more than real words do. In contrast, our "XX"-type stimuli did not resemble Japanese words at all and served as mere placeholders, thereby suppressing the extra lexical search that pseudo-words would require. The other advantage of the XX-type placeholders is that they prevent unpredictable lexical and semantic processing that "word-like" pseudo-words might elicit. These XXs are never used as lexical items in Japanese, so the readers could immediately recognize these signs as meaningless placeholders of sentence constituents. Since it silences useless lexical search and unwanted semantic/pragmatic processing, the XX-type placeholder is an excellent alternative to pseudo-words in studies of syntactic sentence processing.

We also manipulated the syntactic processing cost using Japanese sentences with either the basic Subject-Object-Verb (SOV) order or a changed Object-Subject-Verb (OSV) order to identify the neural loci of syntactic structure building. Changing the word order from SOV to OSV adds one more hierarchy to the linguistic tree structure, thereby increasing the cost of hierarchical structure building (Iwabuchi *et al.*, 2019). A 2 × 2 factorial design crossing SEMANTICS (natural sentences [NAT], sentences with placeholders [SPH]) with SYNTAX (SOV, OSV) allowed us to disentangle the neural correlates of semantic processing from those of syntactic processing. The contrasts of NAT > SPH and OSV > SOV can provide the answer to the critical question of whether the left ATL is exclusively involved in the processing of sentences with semantic/pragmatic information or is also responsive to the cost of syntactic structure building.

Materials and Methods

Participants

Twenty-four native Japanese speakers (17 female, 7 male; 18–35 years old, mean age 22.7 years old) took part in the fMRI experiment. No participants had a history of neuropsychiatric disorders, and all had normal or corrected-to-normal vision. They were all right-handed, as assessed by the Japanese-translated version of the FLANDERS handedness questionnaire (range 90–100, mean 99.5, SD 2.0) (Nicholls *et al.*, 2013; Okubo *et al.*, 2014). The study was approved by the ethics committee of the National

Rehabilitation Center for Persons with Disabilities in Japan. Written informed consent was provided by all participants.

Experimental design and stimuli

We used a 2 × 2 factorial design with SYNTAX (the basic order SOV; the changed order OSV) and SEMANTICS (NAT; SPH) as variables. We created noun phrases used in natural sentences by selecting five concrete nouns (*sootoku*, the governor; *daijin*, the minister; *kanryoo*, the bureaucrat; *kaichoo*, the chairperson; *chookan*, the administrator). All these nouns comprised four morae, and were written with two kanji characters. Two of the five nouns were used as either the subject or object in a sentence stimulus. A subject or object noun phrase was created by combining a selected noun and a Japanese nominative case marker "*ga*" or accusative case marker "*o*," respectively (e.g., *sootoku-ga*, governor[SUBJECT]; *daijin-o*, minister[OBJECT]). Two adjectives (*ranboo-na*, wild; *gooman-na*, arrogant) and four transitive verbs (*nagutta*, punched; *tataita*, hit; *sikatta*, scolded; *niranda*, stared) were also chosen to compose sentences. All verbs were in the past tense. By combining these elements (a subject noun phrase, an object noun phrase, an adjective, and a verb), we created 40 sentences that were syntactically and semantically natural (i.e., the NAT stimuli). Each natural sentence comprised a subject noun phrase with an attached adjective, an object noun phrase, and a verb (e.g., *ranboo-na sootoku-ga daijin-o nagutta*. [The wild governor punched the minister.]). Sentences had either the canonical SOV order or the changed OSV word order. The corresponding nonsensical sentences were created by replacing all open-class lexical items (i.e., nouns, adjectives, and verbs) in the NAT sentences with pronounceable meaningless placeholders that convey no semantic meanings (the SPH stimuli). We used five pairs of two uppercase letters (AA, BB, CC, DD, and EE) as placeholders for nouns. In a SPH stimulus, two of these placeholders were combined with either the nominative ("*ga*") or the accusative case marker ("*o*"). Two meaningless adjectives were created by combining two uppercase letters with the Japanese suffix "*na*" (i.e., PP-*na* and QQ-*na*), which generates an adjective when attached to a noun. Each of the four placeholders for verbs was composed of an uppercase letter and a light verb in the past tense -*sita* (N-*sita*, N-PAST; V-*sita*, V-PAST; S-*sita*, S-PAST; Y-*sita*, Y-PAST), which is combined with a noun to create a novel verb. The numbers of characters (two for each noun, three for each adjective, and three for each verb) and morae (four for each noun, five for each adjective, and four for each verb) were strictly controlled between the NAT and SPH conditions. The sentences provided below are examples (see also Figure 1):

(NAT-SOV) *ranboo-na sootoku-ga daijin-o tataita*.

[wild governor-SUBJECT][minister-OBJECT][hit]

“The wild governor hit the minister.”

(SPH-SOV) PP-*na* AA-*ga* BB-*o* V-*sita*.

[PP-ADJECTIVE AA-SUBJECT][BB-OBJECT][V-PAST]

“PP$_{\text{adjective}}$-AA V-PAST BB.”

(NAT-OSV) *daijin-o ranboo-na sootoku-ga tataita*.

[minister-OBJECT][wild governor-SUBJECT][hit]

“The wild governor hit the minister.”

(SPH-OSV) BB-*o* PP-*na* AA-*ga* V-*sita*.

[BB-OBJECT][PP-ADJECTIVE AA-SUBJECT][V-PAST]

“PP$_{\text{adjective}}$-AA V-PAST BB.”

Procedure

Visual stimulus presentation was controlled by the Presentation software (Neurobehavioral Systems, Inc., Albany, CA, USA). Sentences were presented using the rapid serial visual presentation paradigm (600 ms duration per word and a 100 ms blank screen between words). Each sentence always started with the same temporal adverbial phrase consisting of two words (*kinoono yoruosoku* [yesterday late-evening]). Thus, the duration of each sentence stimulus, including the leading phrase, was fixed at 4.1 s. Prior to the fMRI sessions, participants underwent practice sessions outside the scanner room. The experiment with fMRI scanning was divided into two sessions. Twenty sentences were presented for each of the four main conditions per session. In 60% of the trials, a probe sentence (e.g., "*sootoku-ga tataita*." [The governor hit (someone).]) was presented after 1,100 ms from the offset of the last word of the previous sentence (i.e., a verb in Japanese). Half the probes matched the content of the previously presented sentence, whereas the other half did not. Participants were asked to judge whether the content of a probe was consistent with the previously presented sentence during the probe presentation period (3,000 ms). They reported their judgments by pressing response buttons with the right index (yes) or middle (no) finger as quickly as possible. Assignments of probes were pseudo-randomized for each session and each participant. For each session, the presentation orders of the experimental conditions and the inter-trial intervals were pseudo-randomized and optimized by the optseq program (Dale, 1999) (available at http://surfer.nmr.mgh.harvard.edu/optseq/).

Practice session

Participants performed two to four practice sessions outside the scanner room prior to the fMRI sessions. Each of these sessions comprised 24 trials. The practice session procedures were mostly the same as the fMRI session procedures, but participants were requested to answer the probe-matching task for 100% of the trials. In the practice sessions, we did not use any of the content words or placeholders that appeared in the fMRI sessions. In the first practice session, each word of a sentence was presented for 900 ms with a 100 ms interval between the words. When the participants' correct responses reached 80% or they completed two sessions, participants proceeded to the second type of practice session where the duration of each word was set to 600 ms. The fMRI sessions began after participants finished the second practice sessions with the same criteria as the first practice sessions.

fMRI data acquisition

MRI data were collected with a 3 T MRI scanner (MAGNETOM Skyra; Siemens, Erlangen, Germany). For each fMRI session, we obtained 585 functional scans with a gradient-echo echo-planner imaging (EPI) sequence that lasted approximately 19.5 min. The acquisition order was ascending, and the following parameters were used: repetition time = 2,000 ms, echo time = 30 ms, flip angle = 90 degrees, field of view = 192 × 192 mm, matrix 64 × 64, 35 axial slices, and slice thickness = 3 mm with a 1-mm gap. The slices were aligned to the anterior commissure - posterior commissure (AC-PC) plane, covering the whole brain. T1-weighted high-resolution structural images were also acquired (MPRAGE sequence, TR = 2,300 ms, TE = 2.98, inversion time = 900 ms, flip angle = 9 degree, field of view = 256 × 256 mm, matrix 256 × 256, sagittal 224 slices, 1-mm isotropic resolution).

Preprocessing of fMRI data

We used the SPM12 software package (available at http://www.fil.ion.ucl.ac.uk/spm/) to process the fMRI data. First, the functional images were realigned to the mean image, and the difference of slice acquisition timing was corrected using the middle slice as the reference. The functional images were then coregistered to the individuals' anatomical images. The spatial normalization to the East Asian brain template was performed in two steps: 1) estimation of normalization parameters via segmentation and 2) writing the normalized images with the parameters. All functional images were transformed into the Montreal Neurological Institute (MNI) stereotaxic space to allow multi-subject analyses. The functional images were resampled into 3 × 3 × 3 mm^3 voxels with the seventh-degree B-spline interpolation, and smoothed with a 6-mm full width at half maximum (FWHM) Gaussian kernel.

fMRI data analysis

After preprocessing, the condition effects in each voxel were estimated per participant by a general linear model. Sentence presentation periods (4.1 s) and probe presentation periods (3 s) were separately modeled with box-car functions, and both were convolved with a hemodynamic response function. Consequently, the design matrix included the eight regressors for the four types of sentences and the probes of the four conditions. The six motion parameters were also included in the design matrix as covariates of no interest to account for movement-related variance. Low-frequency noise was removed using a high-pass filter with a cut-off period of 128 s. Temporal correlations in fMRI time series were estimated by an autoregressive AR(1) model, which was used to correct for non-sphericity during statistical inference.

For group-level random-effects analysis, the four beta maps of experimental conditions that were obtained from the individual-level analysis were submitted to a 2 × 2 full factorial ANOVA with two within-subjects factors of SEMANTICS (NAT; SPH) and SYNTAX (SOV; OSV). The main effects of SEMANTICS and SYNTAX were identified with t tests. The statistical maps were initially thresholded at $p = 0.01$ (uncorrected for multiple comparisons at the voxel level) with a cluster-size threshold of at least 50 voxels. Then, the significance for statistical inference was thresholded at $p < 0.05$ with family-wise error (FWE) correction at the cluster level.

Volume of interest (VOI) analyses

We performed analyses on the four VOIs in the left hemisphere (BA 44, BA 45, the ATL, and the pMTG), because these regions have all been pinpointed as neuroanatomical sites associated with syntactic and/or semantic processing by several reviews or meta-analyses (Hagoort & Indefrey, 2014; Rodd *et al.*, 2015; Zaccarella *et al.*, 2017; Walenski *et al.*, 2019). To define these VOIs, we created anatomical masks using the Neuromorphometrics atlas in SPM12 (Neuromorphometrics, Inc. http://www.neuromorphometrics.com/). We used the anatomical labels of the opercular part of the IFG and the triangular part of the IFG in the Neuromorphometrics atlas as the masks of BA 44 and BA 45, respectively. For the pMTG, we generated a mask by removing an area anterior to the y-coordinate -25 from the region labeled as the left middle temporal gyrus in this atlas. Then, we used SPM12 to conduct an automatic search for individual local maxima within these masks based on the T-contrast of experimental sentences (i.e., NAT-SOV, NAT-OSV, SPH-SOV, SPH-OSV) vs. rest, with a threshold of 0.001 uncorrected for multiple comparisons. Within a 12 mm radius sphere centered at those individual local maxima in each region's mask, voxels showing significant activation for the same T-contrast (i.e., four experimental conditions > rest; $p < 0.001$ uncorrected) were defined as an individual VOI.

VOI time series data were extracted as eigenvariates from the VOIs. The time series data were adjusted for the F-contrast for the effect of interest (i.e., the contrast for activation in at least one of the four experimental conditions; $p<0.001$ uncorrected for multiple comparisons) by removing variance caused by effects of no interest such as head motion parameters. We used the same technique as in our previous studies (Makuuchi *et al.*, 2013; Iwabuchi *et al.*, 2019) to calculate the trial time courses (TTCs) for each participant's preprocessed (realigned, slice time corrected, coregistered, normalized, and upsampled to every 0.5 s) time series data. For each VOI, we defined the time window for statistical testing based on peak latency, and carried out two-way ANOVAs with within-subjects factors of SEMANTICS (NAT and SPH) and SYNTAX (SOV and OSV). Peak latency was calculated from the TTC averaged across the four experimental conditions.

Results

Behavioral data

Nineteen participants (13 female, 6 male; 18–35 years old, mean 22.7 years old) were included in data analyses. One participant was excluded from the fMRI and behavioral analyses because the experiment was ceased during a session due to bad physical condition of the participant. Four participants were excluded due to low performances in the probe matching task (below 65% accuracy). Figure 2 shows the summary of accuracy and reaction time data of the analyzed participants in the probe matching task (mean accuracy, 81.8%; accuracy range, 66.7–98.9%). We used a logistic mixed-effects model and a linear mixed-effects model to analyze accuracy and reaction time, respectively. We included SEMANTICS (NAT; SPH), SYNTAX (SOV; OSV), and their interaction as the fixed effects. We specified the maximal random effects structure (Barr *et al.*, 2013), including the by-subject and by-item random slopes for SEMANTICS, SYNTAX, and their interaction as well as the by-subject and by-item random intercepts. Data fitting was performed with Stata MP 15.1 (StataCorp, College Station, TX). Reaction times for the SOV sentences were significantly shorter than those for the OSV sentences, as indicated by a significant effect of SYNTAX (coefficient = 78.2, standard error [SE] = 35.0, z = 2.24, $p = 0.025$). We also found that SEMANTICS had a significant effect on reaction time (coefficient = 130.8, SE = 35.2, z = 3.71, $p < 0.001$), which suggests that participants responded faster when presented with sentences that were semantically natural than with those that were meaningless. The interaction between SEMANTICS and SYNTAX was not significant for reaction time (coefficient = -9.66, SE = 43.6, z = -0.22, *p* = 0.83). As for accuracy, since the model with maximal random effects structure failed to converge, we simplified the model by excluding by-subject and by-item random slopes for the interaction between SEMANTICS and SYNTAX. The analysis of accuracy revealed a significant effect of SEMANTICS (coefficient = -0.59, SE = 0.22, z = -2.72, *p* = 0.007), which indicates higher accuracy in the NAT conditions than in the SPH conditions. The effect of SYNTAX and the interaction between SEMANTICS and SYNTAX did not have significant influence on accuracy (SYNTAX: coefficient = -0.30, SE = 0.22, z = -1.35, *p* = 0.18; interaction: coefficient = -0.05, SE = 0.27, z = 0.19, *p* = 0.85). Altogether, the behavioral results indicate that the SPH and OSV sentences were more difficult than the NAT and SOV sentences, respectively.

fMRI data

In the group-level whole-brain analysis, the contrast of NAT > SPH revealed significant activation in the left ATL, the left BA 47, and the left pMTG as well as the bilateral fusiform gyrus and the bilateral inferior occipital gyrus, whereas the left supramarginal gyrus, the bilateral superior parietal lobule, the left premotor area, and the left middle/inferior occipital gyrus were activated by the contrast of SPH > NAT ($p < 0.01$ uncorrected, $k > 50$) (Figure 3 and Table 1). For the former comparison, the left BA 47 and pMTG did not survive the multiple comparison correction at the cluster level. We found no significant activation when we compared the OSV condition to the SOV condition, while the medial part of the right superior frontal gyrus was activated by the contrast of SOV > OSV (Table 2).

Subsequently, we conducted VOI analyses for the left BA 44, BA 45, ATL, and pMTG. The VOI images, which were created by summing VOI masks across participants, were overlaid onto a rendered brain surface in Figure 4. For two participants, we found no significant peak in the left ATL for the T-contrast of experimental sentences > rest, and hence these participants were excluded from the VOI analysis of the left ATL. Means and ranges of VOI sizes (i.e., the numbers of voxels contained) were as follows: BA 44, 121.7 (53–190); BA 45, 85.4 (39–164); the ATL, 34.8 (2–144); and the pMTG, 85.4 (5–150). The mean MNI coordinates for the centers of mass were [-40.8, 14.1, 24.0] for BA 44, [-41.7, 27.9, 6.0] for BA 45, [-45.0, 11.3, -16.8] for the ATL, and [-53.1, -34.1, 0.8] for the pMTG. The VOI of the left ATL was located along the anterior superior temporal sulcus. The left pMTG VOI seemed to contain some voxels in the superior temporal gyrus/sulcus.

The TTCs in these VOIs are also plotted in Figure 4. Peak latencies calculated from averaged TTCs were as follows: mean 6.76 s, 95% confidence interval (CI) 6.36–7.17 s for BA 44; mean 7.00 s, 95% CI 6.36–7.64 s for BA 45; mean 5.14 s, 95% CI 4.51–5.78 s for the ATL; mean 6.29 s, 95% CI 5.85–6.73 s for the pMTG. Based on the 95% CIs of peak latency values, the averaged TTC data were calculated across 6.5–7.0 s for the left BA 44, 6.5–7.5 s for the left BA 45, 5.0–5.5 s for the ATL, and 6.0–6.5 s for the left pMTG. The averaged data in each VOI was then submitted to a two-way within-subjects ANOVA. For the left BA 44, we found that the effect of SEMANTICS was significant (F[1,18] = 5.08, partial eta squared = 0.2203, p = 0.04, Bonferroni corrected q = 0.12), which suggests that BA 44 exhibited a higher response to SPH stimuli compared to NAT stimuli. The effect of SYNTAX (F[1,18] = 0.17, partial eta squared = 0.0095, p = 0.68) and the interaction between SEMANTICS and SYNTAX (F[1,18] = 0.02, partial eta squared = 0.0012, p = 0.88) were not significant in BA 44. In contrast, the analysis revealed a significant main effect of SYNTAX in both the left BA 45 (F[1,18] = 5.17, partial eta squared =0.2231, p = 0.037, Bonferroni corrected q = 0.106) and the pMTG (F[1,18] = 4.55, partial eta squared = 0.2019, p = 0.047, Bonferroni corrected q = 0.14), which indicates that enhanced activation was elicited by OSV sentences compared to SOV sentences. No significant main effect of SEMANTICS and interaction were found for both the left BA 45 (F[1,18] < 0.01, partial eta squared < 0.001, p = 0.99 for

SEMANTICS; F[1,18] = 0.02, partial eta squared = 0.0012, p = 0.88 for the interaction) and the pMTG (F[1,18] = 2.51, partial eta squared = 0.1225, p = 0.13 for SEMANTICS; F[1,18] = 0.20, partial eta squared = 0.0110, p = 0.66 for the interaction). Regarding the ATL, the analysis revealed no significant effect or interaction (F[1,16] = 1.28, partial eta squared = 0.0743, p = 0.27 for SEMANTICS; F[1,18] = 0.40, partial eta squared = 0.0243, p = 0.54 for SYNTAX; F[1,18] = 2.49, partial eta squared = 0.1345, p = 0.13 for the interaction).

Additionally, we examined whether we could detect any syntactic effect on brain activity in the individual subregions of the ATL that responded to semantic processing (i.e., NAT > SPH). To do this, we identified individual local maxima within the anatomical mask of the ATL, using the contrast of NAT > SPH (p < 0.01 uncorrected). Then, for each participant, we defined all activated voxels for the contrast within a 12 mm sphere centered at the individual local maximum as the individual VOI. Three participants were excluded from the following analysis because no significant voxel was found within the ATL mask. For this semantic ATL VOI, the TTC was calculated per participant and averaged across the time window of the analysis (3.5-7.5 s) based on the peak latency (mean 5.59 s, 95% CI 3.27–7.91 s; Figure 5A). We found that there was no significant difference between the SOV and OSV conditions in the semantic ATL VOI (t

= 0.68, df = 15, p = 0.51; Figure 5B).

Discussion

The current study confirmed that the left ATL showed higher activity for natural sentences than for sentences deprived of semantic/pragmatic information. Moreover, we showed that the left ATL was not reactive to word order change, a syntactic operation. These results did not corroborate the previous findings regarding the association between the left ATL and hierarchical structure building (Mazoyer *et al.*, 1993; Noppeney & Price, 2004; Humphries *et al.*, 2005; Humphries *et al.*, 2006; Rogalsky & Hickok, 2009; Brennan *et al.*, 2012; Magnusdottir *et al.*, 2012; Brennan & Pylkkänen, 2017). Instead, the present study suggests that the left ATL may build a semantic representation during online sentence processing, thereby providing contextual information to predict the unfolding syntactic structure (Tyler & Marslen-Wilson, 1977; Spivey-Knowlton *et al.*, 1993; Trueswell *et al.*, 1994; Kamide *et al.*, 2003).

The contrast of SPH > NAT revealed significant activation in the dorsal regions, consisting of the left BA 44, premotor cortex, and parietal cortex. The differential neural cost associated with the SPH > NAT contrast may be attributed to syntactic predictions. During online sentence comprehension, readers or listeners make predictions about upcoming syntactic structure under given syntactic and semantic contexts (see Federmeier, 2007 and Kamide, 2008 for reviews of psycholinguistic evidence). As the SPH stimuli allowed predictions about incoming elements based exclusively on syntactic information, the activation for the contrast of SPH > NAT may have reflected syntactic predictions. This is in line with recent studies reporting associations between language-related regions, such as Broca's area, and syntactic prediction (Bonhage *et al.*, 2015; Söderström *et al.*, 2018; Chen *et al.*, 2019; Shain *et al.*, 2020). However, we acknowledge that there are two potential confounding factors for the contrast of SPH > NAT. First, this contrast may be associated with an increased phonological working memory load for meaningless placeholders compared to real words (Hulme *et al.*, 1991; Majerus & Van der Linden, 2003). The dorsal language regions consisting of the premotor, inferior frontal and parietal cortices may subserve auditory-motor control (Hickok, 2001; Rauschecker, 2011), thereby contributing to phonological rehearsal when storing speech information (Jonides *et al.*, 1998; Buchsbaum *et al.*, 2005; Buchsbaum & D'Esposito, 2008). Second, the SPH stimuli may provoke additional grapheme-to-phoneme conversions relative to the NAT stimuli (Kuo *et al.*, 2004; Tan *et al.*, 2005; Wu *et al.*, 2012), and the effect may have been mixed into the observed activation (i.e., red regions in Figure 3). Indeed, prior studies have suggested that the fronto-parietal areas are involved in deciphering phonological information from orthographic inputs (Law et al., 1991; Price et al., 1996; Herbster et al., 1997; Price, 1998). Future studies should disentangle these confounding factors.

To our surprise, we found no main effect of SYNTAX when we compared the OSV with the SOV conditions in the whole-brain analysis, despite repeated observations of activation in Broca's area for word order changes in Japanese (Kinno *et al.*, 2008; Kim *et al.*, 2009; Koizumi *et al.*, 2012; Iwabuchi *et al.*, 2019; Iwabuchi *et al.*, 2020) and in German (Bornkessel *et al.*, 2005; Friederici *et al.*, 2006; Meyer *et al.*, 2012; Makuuchi *et al.*, 2013). This discrepancy may be accounted for by the specific construction of sentences in the current study, in which the subject noun phrase was made "heavier" by adding a modifier. Making the subject noun heavier widens the distance between the filler (i.e., the moved object noun phrase) and the gap (i.e., the original position of the object noun phrase), and increases the syntactic working memory cost. We expected a more increased activity in BA 44 in response to OSV sentences with a heavy subject noun phrase (hS) than with a simple subject phrase. However, this maneuver did not yield the expected effect; indeed, a previous study found that the activity in the left BA 44 was not higher for O-hS-V sentences than for hS-O-V or heavy object (hO)-S-V sentences (Iwabuchi *et al.*, 2019). In fact, this area was more activated for hO-S-V than for hS-O-

V, S-hO-V, and O-hS-V sentences (Iwabuchi *et al.*, 2019). Although we still have no good explanation for the mitigated neural costs for the processing of O-hS-V in BA44, these previous findings are consistent with the absence of a main effect of word order change in the current study. Future research may clarify the effect of noun phrase lengths on hemodynamic response.

Regarding the VOI analysis, we found a main effect of SYNTAX in the left BA 45 and pMTG, although it did not remain significant after multiple comparison correction. It is worth noting, however, that despite the insufficient statistical significance, we consistently found increased activation in the left pMTG for word order change in the present study and a previous study (Iwabuchi *et al.*, 2019). These results may point to the role of this region in the processing of hierarchical syntactic structure, as recently suggested by Matchin and Hickok (2020), although future investigations should further confirm the association between the left pMTG and syntax. Interestingly, the VOI of the left BA 45 had a spatial overlap with the left op9, which is a part of the frontal operculum located medioventrally to the anterior part of BA 45 (Amunts *et al.*, 2010; Amunts & Zilles, 2012). In a previous study, we found an association of the left op9 with syntactic working memory; this region exhibited higher activity for O-hS-V than hO-S-V sentences (Iwabuchi *et al.*, 2019). In O-hS-V sentences, the distance between a syntactically dependent pair (i.e., filler and gap) was longer than in hO-S-V sentences, while the syntactic structure was the same. Therefore, in line with several previous studies (Rogalsky *et al.*, 2015; Matchin, 2018; Matchin & Hickok, 2020), we assume that the enhanced activation in the left BA 45 reflected extra syntactic working memory rather than hierarchical structure building. A further possible interpretation of the neural reaction to word order change is the effect of non-canonicity, which is not mutually exclusive to the cost of hierarchical structure building (Bornkessel *et al.*, 2005). Since OSV sentences are rarely produced in daily Japanese usage, especially when the subject noun phrase is heavier than the object phrase (see Iwabuchi et al., 2019), non-canonicity might impact brain activities. Further studies are needed to segregate the effects of hierarchical structure building and non-canonicity in word order change.

Incidentally, the current data suggest that the neural bases of phonological working memory are dissociable from those of syntactic working memory. The left BA 45 and pMTG exhibited no significant activation when the SPH conditions were compared with the NAT conditions. This suggests insensitivity of these regions to the cost of phonological working memory, in contrast to their involvement in syntactic working memory.

A limitation of the present study is that semantic processing is confounded by lexical retrieval in the NAT stimuli. However, other studies suggest that this is likely not the case. Recent neuroimaging studies comparing natural phrases or sentences with lists of non-compositional natural words found that the left ATL is more responsive to the former stimuli (Bemis & Pylkkänen, 2011; 2013; Matchin *et al.*, 2017). Moreover, the left ATL is implicated in structure building for natural sentences but not for Jabberwocky sentences (Pallier *et al.*, 2011; Goucha & Friederici, 2015). Therefore, we reason that the left ATL plays a role in the integration of semantic information, rather than in lexical retrieval, during sentence comprehension.

We consider that the orthographic differences between the NAT and SPH conditions did not contaminate the activation in the left ATL. While kanji and kana characters were used in the NAT sentences, the content words were replaced with alphabet characters (e.g., AA) in the SPH stimuli. Therefore, comparisons between the two conditions were inevitably subject to visual or orthographic differences. However, previous fMRI studies on the processing of different types of characters (i.e., logograms and phonograms) have identified the effects of visual word perception in the ventral occipitotemporal regions (Bolger *et al.*, 2005; Nakamura *et al.*, 2005; Nakamura *et al.*, 2012), which are located far enough from the left ATL. In contrast, the activation in the middle and inferior occipital regions revealed by the contrast of SPH > NAT is probably attributable to the visual and/or orthographic complexities in the SPH conditions relative to the NAT conditions.

For the left ATL VOI, we observed the highest (but statistically insignificant) activity in the SPH-SOV condition, which was inconsistent with the whole-brain results. Spatial heterogeneity of the individual VOIs may account for the discrepancy between the different types of analyses and the unexpected activation pattern in the left ATL VOIs. As shown in Figure 4, the individual VOIs of the left ATL exhibited considerably less spatial overlap across participants than the other VOIs did. This might suggest the existence of functional subregions within the left ATL and that what we detected is a subregion that is selectively involved in semantic processing. We speculate that mixing the activities of distinct functional subregions may result in the inexplicable activation pattern in the left ATL VOI, such as the highest activity for the SPH-SOV. Further research is needed to construe the functional significance of the divergent spatial distribution of the individual maxima in the left ATL.

Defining another individual VOI of the left ATL based on the contrast of NAT > SPH, we demonstrated that the semantic-related ATL subregion showed no sensitivity to the SPH stimuli and the effect of SYNTAX. Although we should caution that failure to detect a significant effect does not necessarily mean a complete lack thereof, this may indicate that the subregion in the ATL is exclusively involved in semantic, but not syntactic, aspect of sentence processing. The finding seems inconsistent with Blank *et al.* (2016), who suggested that the spatially distributed language-related regions, including the left ATL, are all sensitive to both syntactic (i.e., “object-extracted relative clauses” > “the subject-extracted relative clauses”) and semantic processing. In their study, the functional localizer task was to read natural sentences or unstructured lists of pronounceable non-words, and the language-related regions of interest (ROIs) were defined by the contrast of “sentences > non-word lists” (Blank *et al.*, 2016). This localizer, however, does not allow a clear segregation of regions serving syntactic processing from those serving semantic processing. Thus, the apparent contradiction between the results of Blank *et al.* (2016) and the current results is resolved by assuming the existence of functional subregions in the ATL. A lesson from the comparison of the two studies is the impact of the choice of the localizer task on the results.

Using a novel technique to remove semantic/pragmatic information from a sentence without changing its syntactic structure, we found that a subregion of the left ATL was responsive to the processing of natural but not of meaningless sentences. Moreover, we demonstrated that the subregion of the left ATL was indifferent to changes in the syntactic complexity of sentences. Taken together, our findings imply that a subregion in the left ATL is uniquely involved in semantic/pragmatic processing.

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Competing interests

The authors declare no conflict of interest.

Author contributions

TI and MM designed research, performed research, analyzed data, and wrote the manuscript.

Data accessibility

The behavioral and fMRI data collected in the present study are available from the corresponding author upon reasonable request.

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Figure captions

Figure 1. Examples of experimental stimuli.

Sentences were designed with a 2 × 2 factorial design with factors of SEMANTICS and SYNTAX. NAT, natural sentence; SPH, sentence with placeholders; SOV, basic Subject-Object-Verb word order; OSV, changed Object-Subject-Verb word order.

Figure 2. Behavioral results.

The bar plots show the accuracy and mean reaction time in the probe-matching task. Error bars denote standard errors of the mean. NAT, natural sentence; SPH, sentence with placeholders; SOV, basic Subject-Object-Verb word order; OSV, changed Object-Subject-Verb word order.

Figure 3. Brain activation for the effects of SEMANTICS.

Regions exhibiting significant activation for the contrast of NAT > SPH are shown in green, while those activated for SPH compared to NAT are shown in red ($p < 0.05$ family-wise error corrected for multiple comparisons at the cluster level). Color bars denote *t*-statistics. NAT, natural sentence; SPH, sentence with placeholders.

Figure 4. Brain activity in the four hypothetical VOIs.

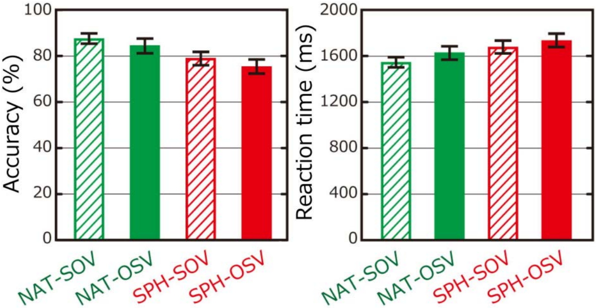
The TTCs in the VOIs of BA 44, BA 45, the ATL, and the pMTG are shown with highlighting of the analyzed time windows (the left side of each panel; green dotted lines, NAT-SOV; green solid lines, NAT-OSV; red dotted lines, SPH-SOV; red solid lines, SPH-OSV). Shaded areas represent standard errors of the mean. The VOIs are overlaid onto a rendered brain surface shown in the center (blue, BA 44; yellow, BA 45; cyan, the ATL; and violet, the pMTG). Color bars denote the number of participants whose VOIs are contained in each voxel. The bar plots show the beta values averaged across the analyzed time windows in the VOIs of BA 44, BA 45, the ATL, and the pMTG (the right side of each panel). Error bars denote standard errors of the mean. TTC, trial time course; VOI, volume of interest; BA 44, Brodmann area 44; BA 45, Brodmann area 45; ATL, anterior temporal lobe; pMTG, posterior middle temporal gyrus; NAT, natural sentence; SPH, sentence with placeholders; SOV, basic Subject-Object-Verb word order; OSV, changed Object-Subject-Verb word order.

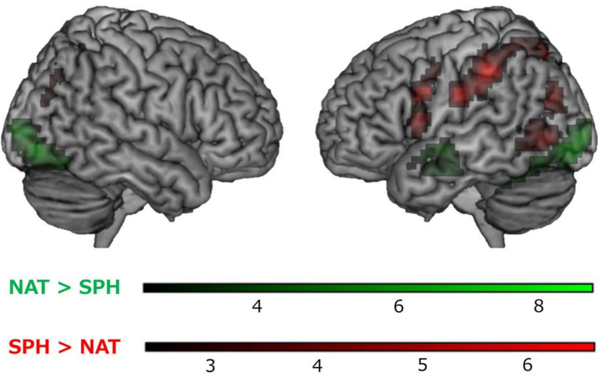
Figure 5. Brain activity in the semantic-related anterior temporal subregion.

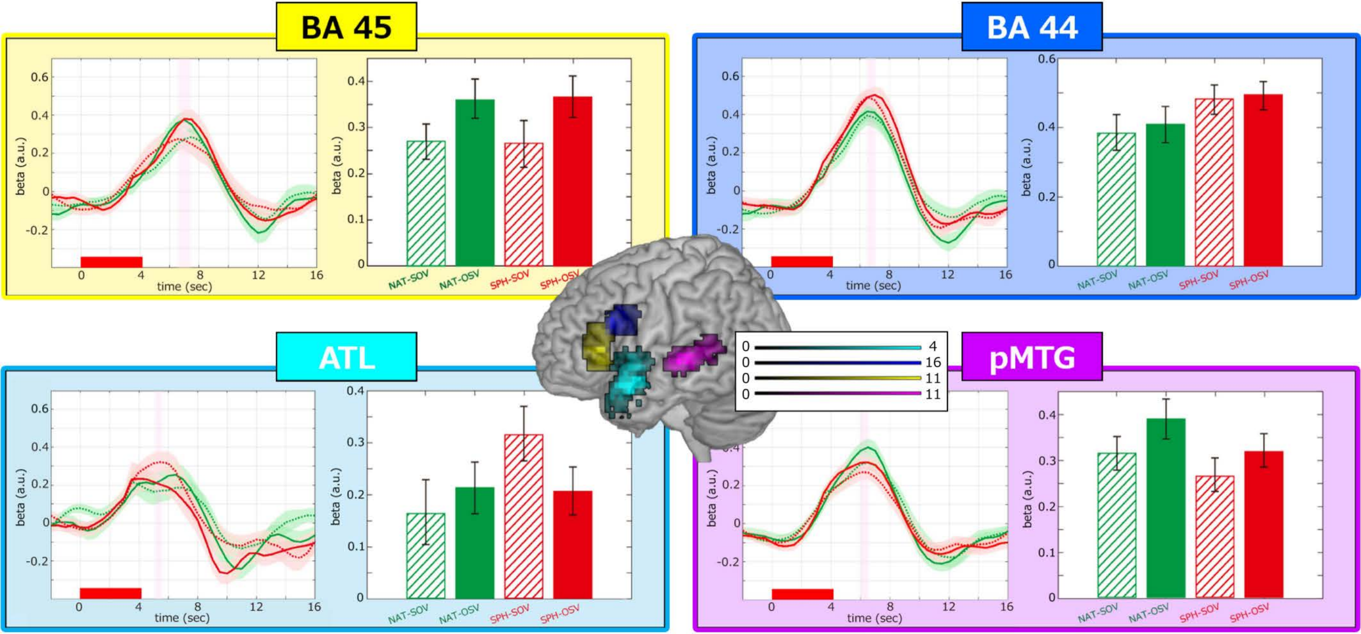
(A) The TTCs in the VOI of the ATL, which was defined individually based on the contrast of NAT > SPH. Green dotted lines, NAT-SOV; green solid lines, NAT-OSV; red dotted lines, SPH-SOV; red solid lines, SPH-OSV. Shaded areas represent standard errors of the mean. The analyzed time window is highlighted. (B) The bar plots show the beta values averaged across the time window. Error bars denote standard errors of the mean. TTC, trial time course; VOI, volume of interest; ATL, anterior temporal lobe; NAT, natural sentence; SPH, sentence with placeholders; SOV, basic Subject-Object-Verb word order; OSV, changed Object-Subject-Verb word order.

SYNTAX

		SOV	OSV
SEMANTICS	NAT	乱暴な　総督が　大臣を　叩いた。 ranboo-na sootoku-ga daijin-o tataita. *“The wild governor hit the minister.”*	大臣を　乱暴な　総督が　叩いた。 daijin-o ranboo-na sootoku-ga tataita. *“The wild governor hit the minister.”*
	SPH	ＰＰな　ＡＡが　ＢＢを　Ｖした。 PP-na AA-ga BB-o V-sita. *“$PP_{adjective}$-AA V-PAST BB.”*	ＢＢを　ＰＰな　ＡＡが　Ｖした。 BB-o PP-na AA-ga V-sita. *“$PP_{adjective}$-AA V-PAST BB.”*


Accuracy (%)
100
80
60
40
20
0
NAT-SOV
NAT-OSV
SPH-SOV
SPH-OSV
Reaction time (ms)
2000
1600
1200
800
400
0
NAT-SOV
NAT-OSV
SPH-SOV
SPH-OSV


NAT > SPH
4
6
8
SPH > NAT
3
4
5
6


BA 45
BA 44
ATL
pMTG
beta (a.u.)
time (sec)
0.6
0.4
0.2
0
-0.2
0
4
8
12
16
0.1
0.2
0.3
0.4
0.6
NAT-SOV
NAT-OSV
SPH-SOV
SPH-OSV
0 4
0 16
0 11
0 11

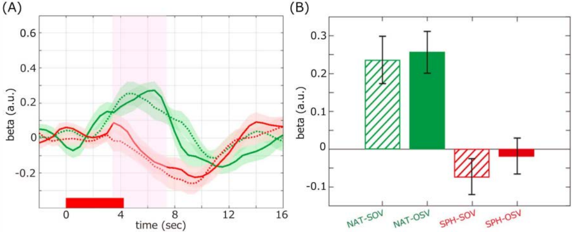

(A)
0.6
0.4
0.2
0
-0.2
beta (a.u.)
0
4
8
12
16
time (sec)
(B)
0.3
0.2
0.1
0
-0.1
beta (a.u.)
NAT-SOV
NAT-OSV
SPH-SOV
SPH-OSV

Table 1. Cortical regions identified by the effects of SEMANTICS ($p < 0.05$ family-wise error corrected for multiple comparisons at the cluster level). Cluster sizes (k) and voxel-level t values are shown.

Anatomical label	**side**	**MNI**			***k***	***t* value**
		x	***y***	***z***		
NAT > SPH						
Fusiform gyrus*	L	-36	-46	-22	525†	8.74
Inferior occipital gyrus*	L	-27	-94	2		4.84
Superior temporal gyrus	L	-57	-7	-6		4.09
Middle temporal gyrus	L	-54	5	-10		3.58
Inferior occipital gyrus*	R	36	-85	-6	320†	5.99
Occipital fusiform gyrus	R	42	-67	-14		4.54
Fusiform gyrus	R	33	-55	-18		3.57
SPH > NAT						
Supramarginal gyrus*	L	-48	-34	42	927†	6.62
Postcentral gyrus*	L	-60	-19	26		5.52
Superior parietal lobule*	L	-24	-64	34		5.50
Superior occipital gyrus*	L	-27	-76	26		5.35
Inferior occipital gyrus	L	-48	-76	-2		4.10
Precentral gyrus*	L	-45	5	30	164†	5.63
Inferior frontal gyrus PO	L	-51	8	10		4.75
Superior parietal lobule	R	27	-64	38	247†	4.81
Middle occipital gyrus	R	36	-79	22		2.64

MNI, Montreal Neurological Institute; R, right; L, left; POrb, pars orbitalis; PO, pars opercularis; NAT, natural sentence; SPH, sentence with placeholders.

*$p < 0.05$, family-wise error corrected for voxel level.

†$p < 0.05$, family-wise error corrected for cluster level.

Table 2. Cortical regions identified by the effects of SYNTAX ($p < 0.05$ family-wise error corrected for multiple comparisons at the cluster level). Cluster sizes (*k*) and voxel-level *t* values are shown.

Anatomical label	**side**	**MNI**			***k***	***t* value**
		x	***y***	***z***		
SOV > OSV						
Superior frontal gyrus	R	24	35	42	556†	4.33
Anterior cingulate cortex	L	0	41	18		3.35
Medial frontal cortex	R	6	41	-14		3.09
Middle frontal gyrus	R	39	26	42		3.05
OSV > SOV						
No significant activation						

MNI, Montreal Neurological Institute; R, right; L, left; SOV, basic Subject-Object-Verb word order; OSV, changed Object-Subject-Verb word order.

†$p < 0.05$, family-wise error corrected for cluster level.