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The cortical dynamics in building syntactic structures of sentences: An MEG study in a minimal-pair paradigm

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ABSTRACT

The importance of abstract syntactic structures and their crucial role in analyzing sentences have long been emphasized in contemporary linguistics, whereas the linear order model, in which next-coming words in a sentence are claimed to be predictable based on lexico-semantic association or statistics alone, has also been proposed and widely assumed. We examined these possibilities with magnetoencephalography (MEG) and measured cortical responses to a verb with either object–verb (OV) or subject–verb (SV) sentence structures, which were tested in a minimal-pair paradigm to compare syntactic and semantic decision tasks. Significant responses to the normal OV sentences were found in the triangular part of the left inferior frontal gyrus (F3t) at 120–140 ms from the verb onset, which were selective for explicit syntactic processing. The earliest left F3t responses can thus be regarded as predictive effects for the syntactic information of the next-coming verb, which cannot be explained by associative memory or statistical factors. Moreover, subsequent responses in the left insula at 150–170 ms were selective for the processing of the OV sentence structure. On the other hand, responses in the left mediofrontal and inferior parietal regions at 240–280 ms were related to syntactic anomaly and verb transitivity, respectively. These results revealed the dynamics of the multiple cortical regions that work in concert to analyze hierarchical syntactic structures and task-related information, further elucidating the top-down syntactic processing that is crucial during on-line sentence processing.

Introduction

It has been proposed that syntactic computation, which recursively embeds phrases within phrases to produce hierarchical sentence structures, is a critical component of the uniquely human faculty of language (Chomsky, 1995; Hauser et al., 2002). The initial step toward clarifying such formal computation in systems neuroscience would be distinguishing between syntactic (form) and semantic (content) processes in the brain. Earlier functional imaging studies reported the distinction between syntax and semantics in the left frontal regions (Stromswold et al., 1996; Dapretto and Bookheimer, 1999; Kang et al., 1999); however, different words were used for two contrasting conditions, and thus the distinction might be simply explained by lexical factors. To overcome this problem, we have developed a minimal-pair paradigm, in which the same set of words was used to make normal and anomalous sentences for each condition. Using this paradigm, our functional magnetic resonance imaging (fMRI) study has clarified that explicit syntactic processing, as compared with explicit semantic and phonological processing, selectively enhances the activation in the left inferior frontal gyrus (IFG) (Suzuki and Sakai, 2003). Using transcranial magnetic stimulation (TMS) in the same minimal-pair paradigm, we have also reported selective priming effects on syntactic decisions when TMS was administered to the left IFG at 150 ms after the verb onset (Sakai et al., 2002). These results suggest the critical involvement of the left IFG in syntactic processing, but more detailed temporal aspects of syntactic processing must be further elucidated.

Recent fMRI and magnetoencephalography (MEG) studies have suggested that the left IFG activation is modulated by various linguistic factors, including grammaticality (Friederici et al., 2000a), the structure of the relative clause (Stromswold et al., 1996; Indefrey et al., 2001), and canonicity (Röder et al., 2002; Ben-Shachar et al., 2004; Bornkessel et al., 2005; Grewe et al., 2006; Kinno et al., 2008). As a possible common operation among these linguistic computations that are subserved by the left IFG, we propose here that merging a pair of syntactic objects is most crucial, which is indeed a fundamental operation for building syntactic structures of a sentence (Chomsky, 1995). In the present MEG study, we thus focus on the structure of a minimal sentence, which is formed by merging a single pair of noun and verb. Figs. 1a, b show the basic structures of object–verb (OV) and subject–verb (SV) sentences we used, respectively. In the OV sentence, a noun phrase (NP) with an accusative case particle (Acc) *-o* is combined with a transitive verb (vt) to form a verb phrase (VP). Note

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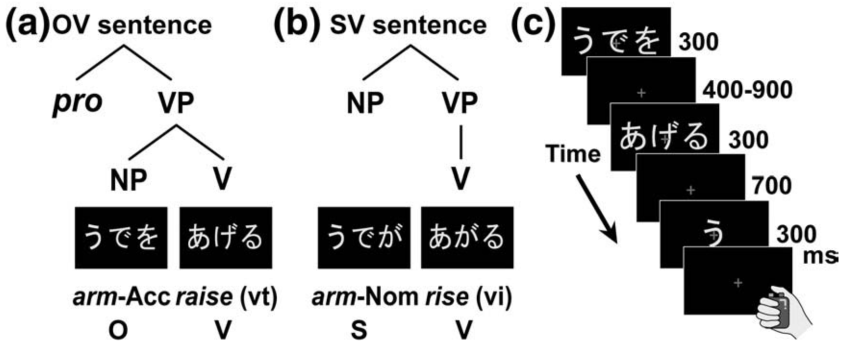

Fig. 1. A minimal-pair paradigm with a minimum sentence consisting of a noun phrase and a verb. A pair of sentences including an object–verb (OV) sentence ('*ude-o ag-e-ru*') (a) and a subject–verb (SV) sentence ('*ude-ga ag-ar-u*') (b) is shown. The same noun was used for both sentences; a transitive verb (vt) and an intransitive verb (vi) were morphologically related in a pair (Table 1). For both sentence structures, a sentence is divided into a subject (OV: pronominal element, *pro*; SV: a noun phrase, NP) and a predicate (verb phrase, VP). The VP is further divided into an NP and V under the OV sentence condition, leading to a more complex structure than the structure under the SV sentence condition. (c) Single trial of a task. All tasks used the same set of visual stimuli, consisting of an NP, which was either O or S, and a V, which was either vt or vi. One kana letter (e.g., '*u*') was presented after a V to inform participants to initiate a response. For the explanation of a syntactic decision (Syn) task and a semantic decision (Sem) task, see Table 2.

that Japanese is a verb-final language, and that the phonetically null subject (pro-drop) is allowed in Japanese, as well as in Spanish and Italian (Jaeggli, 1981). As shown in Fig. 1a, the presence of an empty category (EC) has been proposed as a pronominal element (*pro*) (Chomsky, 1981), which is combined with a VP to form a whole sentence (Saito and Fukui, 1998). In the SV sentence, in contrast, an NP with a nominative case particle (Nom) *-ga* is combined with a VP, and indirectly with an intransitive verb (vi), to form a whole sentence (Fig. 1b). The following examples clarify the distinction between these basic structures:

a) *Mary will raise her hand, and John will do so*,
b) *Mary will rise, and John will do so*,

as '*do so*' substitutes for the entire VP in both sentences.

The distinction between vt and vi, i.e., verb transitivity, is one of the universal aspects of syntactic features, present in English, Japanese, and other natural languages. In Japanese, there are a number of morphologically related vt–vi pairs (e.g., '*ag-e-ru*' and '*ag-ar-u*'; Table 1) that are primarily determined by morphosyntax (Shibatani, 1990), similar to the distinction of *raise/rise, fell/fall, lay/lie,* and *set/sit* in English. Each pair of OV and SV sentences was prepared with an identical noun in the present study, in which the verbs were also semantically related (Table 1). By simply exchanging the verbs within a vt–vi pair, a minimal pair of syntactically normal (N) and anomalous (A) sentences was produced under each of the OV and SV sentence conditions (Table 2). This experimental paradigm is one of the novel merits of the present study.

Based on this minimal-pair paradigm, we tested two main linguistic tasks (Table 2): a syntactic decision (Syn) task and a semantic decision (Sem) task. In the Syn task, participants judged whether sentences were syntactically correct or not (Fig. 1c). To solve the Syn task, the identification of vt or vi, as well as the linguistic knowledge of a syntactic relationship between a case particle and a verb, was required. Moreover, the Syn task could not be solved on the basis of the lexico-semantic relationship between a noun and a verb, because it was always correct for both syntactically normal sentences and anomalous sentences. For the Sem task, we made semantically anomalous sentences by exchanging verbs among the whole set of sentences. Here we focused on the lexico-semantic relationship (selectional restrictions) between a noun and a verb. For example, '*ude*' (gloss: *arm*) and '*ag-e-ru*' (vt, gloss: *raise*) are semantically associated, whereas '*ude*' and '*tam-e-ru*' (vt, gloss: *collect*) have little association. In the Sem task, participants judged whether sentences were semantically normal or anomalous, while the presented sentences were always syntactically correct with respect to the usage of vt and vi.

In our paradigm under the OV sentence condition, the preceding NP case-marked with an Acc predicts the syntactic information of vt *within* the VP, because vt is the only possible verb type within the VP (Fig. 1a). Since the Syn task involved the judgment on a syntactic relationship between an NP and the next-coming verb, greater predictive effects for the syntactic information of the next-coming verb are expected in the Syn task than the Sem task. Under the SV sentence condition, in contrast, the preceding NP with a Nom specifies a VP, but not vi itself (Fig. 1b). Thus, the Syn-selective predictive effects would be more distinct under the OV sentence condition than the SV sentence condition.

Besides the structural account of sentence processing, an alternative hypothesis is the linear order model for word sequences, which

Table 1
A list of 48 normal sentences

Group	Object–Verb (OV) sentence		Subject–Verb (SV) sentence		Translation of SV sentence
	Noun-Acc	vt	Noun-Nom	vi	
I	*ude-o*	*ag-e-ru*	*ude-ga*	*ag-ar-u*	*the arm rises*
	kagi-o	*kak-e-ru*	*kagi-ga*	*kak-ar-u*	*the lock engages*
	waza-o	*kim-e-ru*	*waza-ga*	*kim-ar-u*	*techniques succeed*
	neji-o	*shim-e-ru*	*neji-ga*	*shim-ar-u*	*the screw gets tight*
	nuno-o	*som-e-ru*	*nuno-ga*	*som-ar-u*	*the cloth gets dyed*
	oyu-o	*tam-e-ru*	*oyu-ga*	*tam-ar-u*	*hot water collects*
	ase-o	*tom-e-ru*	*ase-ga*	*tom-ar-u*	*sweat ceases*
	ana-o	*um-e-ru*	*ana-ga*	*um-ar-u*	*the hole is filled*
II	*hada-o*	*ar-as-u*	*hada-ga*	*ar-e-ru*	*someone's skin gets rough*
	uso-o	*bar-as-u*	*uso-ga*	*bar-e-ru*	*the lie is exposed*
	kabi-o	*hay-as-u*	*kabi-ga*	*ha(y)-e-ru*	*mold grows*
	hara-o	*hiy-as-u*	*hara-ga*	*hi(y)-e-ru*	*someone's stomach gets cold*
	kizu-o	*huy-as-u*	*kizu-ga*	*hu(y)-e-ru*	*the number of scratches increases*
	ine-o	*kar-as-u*	*ine-ga*	*kar-e-ru*	*the rice withers*
	nabe-o	*kog-as-u*	*nabe-ga*	*kog-e-ru*	*the pot gets burnt*
	koe-o	*mor-as-u*	*koe-ga*	*mor-e-ru*	*the voices are heard*
	maki-o	*moy-as-u*	*maki-ga*	*mo(y)-e-ru*	*firewood gets burnt*
	kutsu-o	*nur-as-u*	*kutsu-ga*	*nur-e-ru*	*the shoes get wet*
	netsu-o	*sam-as-u*	*netsu-ga*	*sam-e-ru*	*the fever wanes*
	yuki-o	*tok-as-u*	*yuki-ga*	*tok-e-ru*	*snow melts*
	yuka-o	*yur-as-u*	*yuka-ga*	*yur-e-ru*	*the floor shakes*
III	*tsume-o*	*nob-as-u*	*tsume-ga*	*nob-i-ru*	*someone's nails grow*
	zure-o	*nao-s-u*	*zure-ga*	*nao-r-u*	*the difference is corrected*
	kaji-o	*ok-os-u*	*kaji-ga*	*ok-i-ru*	*the fire starts*

Morphologically related vt and vi are paired for each row. According to Shibatani (1990), the verbs are divided into three groups: groups I (*-e-ru*/*-ar-u*), II (*-as-u*/*-e-ru*), and III (others). There was no significant difference regarding the co-occurrence frequency of adjacent NP and verb between the normal OV and SV sentences, according to either *Google* (http://www.google.co.jp/) [$t(23)=-0.37$, $P=0.7$ (paired t-test)] or *Yahoo* (http://www.yahoo.co.jp/) [$t(23)=0.91$, $P=0.4$].

Table 2
Examples of sentences used in a minimal-pair paradigm

Task	Sentence structure	Anomaly	
		Normal (N)	Anomalous (A)
Syntactic decision task (Syn)	OV	*'ude-o ag-e-ru'*[a] *arm*-Acc *raise* (vt)	*'ude-o ag-ar-u'*[b] *arm*-Acc *rise* (vi)
	SV	*'ude-ga ag-ar-u'*[c] *arm*-Nom *rise* (vi)	*'ude-ga ag-e-ru'*[d] *arm*-Nom *raise* (vt)
Semantic decision task (Sem)	OV	*'ude-o ag-e-ru'* *arm*-Acc *raise* (vt)	*'ude-o tam-e-ru'* *arm*-Acc *collect* (vt)
	SV	*'ude-ga ag-ar-u'* *arm*-Nom *rise* (vi)	*'ude-ga tam-ar-u'* *arm*-Nom *collect* (vi)

We designed this minimal-pair paradigm so that anomalous sentences in the Syn task violated the syntactic relationship between a case particle and a verb, whereas anomalous sentences in the Sem task were unacceptable regarding the lexico-semantic relationship between a noun and a verb. The Syn task thus explicitly required syntactic processing but implicitly involved semantic processing, whereas the Sem task explicitly required semantic processing but implicitly involved syntactic processing. We did not use sentences with dual errors, such as *'ude-o tam-ar-u'* and *'ude-ga tam-e-ru'*. In both tasks, the accusative (Acc) and nominative (Nom) case particles corresponded to OV and SV sentence structures, respectively.

[a] *someone raises one's own arm.*

[b] The sentence is syntactically incorrect since vi does not take an object, whereas the lexico-semantic relationship between the noun and verb is correct as in the case of the normal SV sentence[c].

[c] *the arm rises* (e.g., while breathing deeply).

[d] The sentence is syntactically incorrect because there is a wrong case particle when compared with the normal OV sentence[a]. Note, however, that the sentence becomes grammatical in a rare case when an arm itself can be regarded as an *animate subject*, e.g.,'[*robotto-no*] *ude-ga* [*iwa-o*] *ag-e-ru*' ([*robot*'s] *arm raises* [*a rock*]). Other nouns are clearly *inanimate subjects* in SV sentences (Table 1).

predicts next-coming words based on lexico-semantic association or statistics, i.e., transition probabilities between single words in a sentence (Cleeremans and McClelland, 1991; Elman, 1991). Greater predictive effects for the lexico-semantic information of the next-coming verb are expected in the Sem task than the Syn task, irrespective of sentence structures, because the Sem task required the linear order processing of associated words. However, a differential effect on the cortical responses between the normal OV and SV sentences, if any, cannot be explained by such associative memory or statistical factors alone, because there was no difference between the normal OV and SV sentences regarding the co-occurrence frequency of adjacent NP and verb pairs (Table 1). To examine both the syntactic and semantic predictive effects on the cortical responses to *verbs*, we directly compared the Syn and Sem tasks under each of the normal OV and SV sentence conditions. For this purpose, we focused on the cortical responses to a verb from the verb onset. The interval between an NP and a verb was varied, so that the responses to verbs were not confounded with those to NPs (Fig. 1c). A direct comparison of the Syn and Sem tasks on the normal sentences is also useful for clarifying the predictive effects independently from syntactic or semantic anomaly.

Materials and methods

Participants

The participants in the present study were 12 native Japanese speakers. Two participants, whose data contained large amount of noise due to eye movement or blinking (noise-free data during −100–300 ms: 70.3 and 76.2% each for the excluded participants, 80.9–99.8% for the others), were discarded from the analysis, leaving a total of 10 participants (2 females, 19–31 years). The 10 participants showed right-handedness (laterality quotients: 86–100) as determined by the Edinburgh inventory (Oldfield, 1971). Informed consent was obtained from each participant after the nature and possible consequences of the studies were explained. Approval for these experiments was obtained from the institutional review board of the University of Tokyo, Komaba.

Stimuli

Visual stimuli were presented in yellow letters against a dark background, which were projected from outside of the shield room onto the translucent screen (within the visual angle of 5.7°). For fixation, a red cross was always shown at the center of the screen. Each visual stimulus was either an NP (a noun and a case particle) or verb (Fig. 1c), which always consisted of three letters (three moras or syllables) spelled in kana letters (Japanese phonograms) to ensure a consistent reading time among words. Each stimulus was presented for 300 ms, and the interstimulus interval (ISI) between an NP and a verb was randomly varied for 400, 500, 600, 700, 800, and 900 ms. One kana letter was also presented 1000 ms after the verb onset to inform participants to start pushing one of two buttons according to a task instruction. The identity of a kana letter is relevant only in a memory (Mem) task, but we presented a kana letter in the other tasks to keep stimuli identical. The inter-trial interval was randomly varied within the range of ±10% at 4 s to reduce any periodical noises. Stimulus presentation and behavioral data collection were controlled using the LabView software and interface (National Instruments, Austin, TX).

Tasks

Each of the Syn and Sem tasks was performed in a separate MEG run. In each run of the Syn task, there were 24 trials and 24 different sentences for each of normal OV, normal SV, syntactically anomalous OV, and syntactically anomalous SV sentences. In each run of the Sem task, there were 24 trials and 24 different sentences for each of normal OV, normal SV, semantically anomalous OV, and semantically anomalous SV sentences. As shown in Table 2, verb transitivity (vt, vi) was related to both sentence structure (OV, SV) and anomaly (N, A) in the Syn task, whereas verb transitivity corresponded to sentence structure alone in the Sem task. In this paper, the normal OV sentence condition, for example, is denoted as (OV, N, vt). In both of the Syn and Sem tasks, a kana letter following a verb was chosen randomly from six letters of the stimuli in the same trial. The Syn task explicitly required syntactic processing but implicitly involved semantic processing, and vice versa in the Sem task.

Two additional tasks regarding the control of reading, evaluation, and memorization processes involved in the Syn and Sem tasks were tested in separate runs: an evaluation (Eva) task and a Mem task. In the Eva task, participants judged whether the impression of each sentence was positive or negative based on pragmatics, while the presented sentences were always normal in terms of syntax and lexico-semantics. For example, '*waza-ga kim-ar-u*' (*techniques succeed*) is positive, and '*hada-ga ar-e-ru*' (*someone*'s *skin gets rough*) is negative. Correct answers in the Eva task were determined by a pilot study performed before the experiments. We used the Eva task for analyzing reaction times (RTs) and task selectivity of cortical responses alone. A kana letter was presented in the same manner as in the Syn and Sem tasks. In each run of the Eva task, there were 24 trials and 12 different sentences for each of positive OV (a half of the 24 normal OV sentences), negative OV (the other half of the 24 normal OV sentences), positive SV (a half of the 24 normal SV sentences), and negative SV (the other half of the 24 normal SV sentences) sentences. In the Mem task, participants judged whether or not a kana letter following a verb *matched* one of the six letters of the normal sentence in the same trial. In contrast to other tasks, the decision in the Mem task was delayed until the presentation of a kana letter. We used the Mem task for analyzing the accuracy and task selectivity of cortical responses alone. In each run of the Mem task, there were 24 trials and 24 different sentences for each of the matched OV, mismatched OV (with sentences identical to those for the matched OV), matched SV, and mismatched SV (with sentences identical to those for the matched SV) sentences. For all participants, four runs were tested for each of these four tasks, in which the orders of tasks, and sentence structures

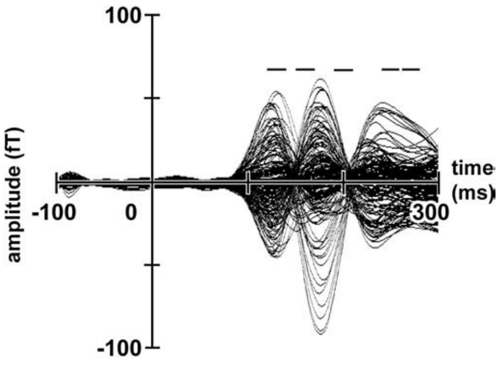

Fig. 2. The averaged MEG signals for all trials from ten participants, shown for each sensor. The black bars above the waveforms indicate the time windows, where significant responses were observed in the contrasts shown in Table 3 and Figs. 3–6.

were fully randomized and counterbalanced. Only trials with participants' correct responses were used for analyzing RTs.

MEG data acquisition and analyses

The raw MEG data were acquired with a 160-channel whole-head system (MEGvision, Yokogawa Electric Corporation, Kanazawa-city, Japan), and they were digitized with an on-line bandwidth of 0.3 Hz to 1000 Hz and a sampling rate of 2000 Hz. Using the BESA 5.1 software (MEGIS Software, Munich, Germany), the MEG signals evoked by a verb from −100 to 300 ms were analyzed, where the signals from −100 to 0 ms were used as a baseline (Fig. 2). Only artifact-free trials (peak-to-peak amplitude <2500 fT) with participants' correct responses were averaged for each condition, and the averaged MEG signals were band-pass filtered in the frequency domain from 2 to 30 Hz to eliminate large eye movement noises. For mapping with the individual brain, high resolution T1-weighted MR images (repetition time, 30 ms; echo time, 8.0 ms; flip angle, 60°; field of view, 256×256 mm^2; resolution, $1 \times 1 \times 1$ mm^3) were acquired using a 1.5-T Scanner (Stratis II, Premium; Hitachi Medical Corporation, Tokyo, Japan). The sensor positions were coregistered to the MR images by aligning the five fiducial markers with their visible locations on the head surface, and final adjustments were completed by using a least-squares fit algorithm (MEG Laboratory, Yokogawa Electric Corporation, Kanazawa-city, Japan). Using the BrainVoyager QX software (Brain Innovation, Maastricht, Netherlands), each individual brain was normalized to the image of the Montreal Neurological Institute (MNI) standard brain, which was already transformed into the Talairach space (Talairach and Tournoux, 1988). In order to perform a cortex-based data analysis, the gray and white matter of the transformed standard brain was segmented, and their boundary was then

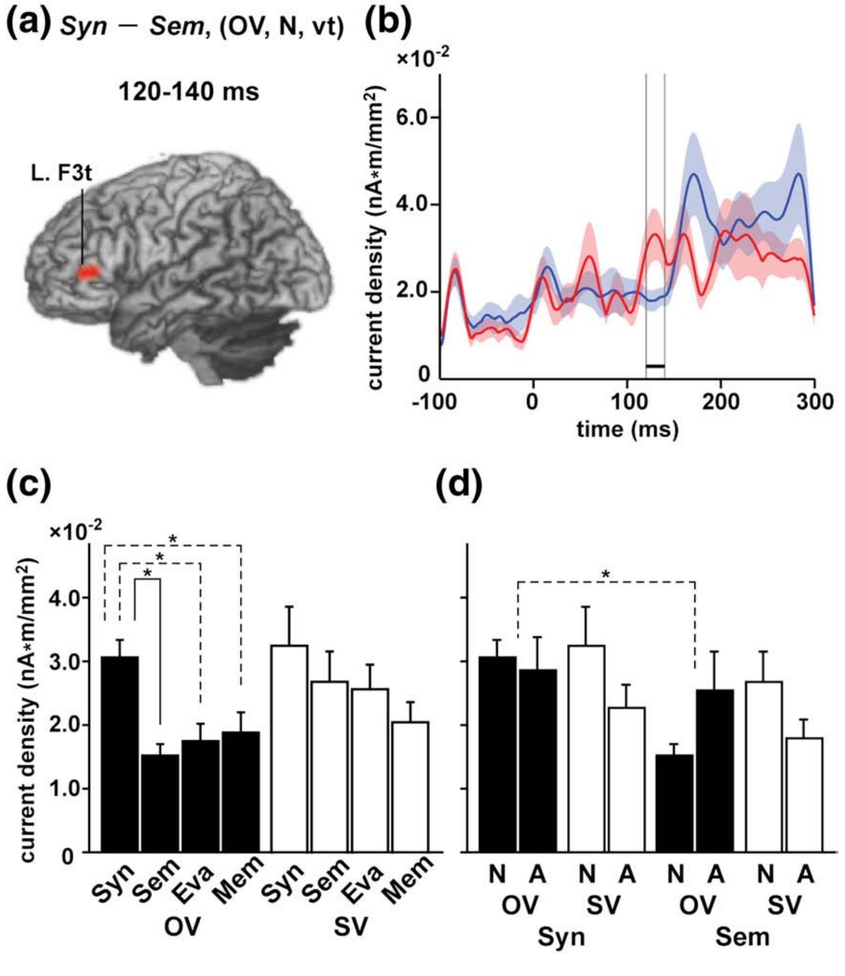

Fig. 3. Selective responses to the Syn task. (a) The cortical responses to Syn and Sem were compared with a paired *t*-test under the normal OV sentence condition, and mapped on the transformed standard brain ($P_{corr} < 0.05$). Note the significant responses in the left (L.) F3t. (b) The averaged temporal changes of the current density for the left F3t. The red and blue lines correspond to the current density for Syn, (OV, N, vt) and Sem, (OV, N, vt), respectively. Their SEMs are shown as shaded bands ($n = 10$). The interval which resulted in significant differences is shown with a bar. (c) Histograms for the current density (mean ± SEM) under each normal sentence condition for the left F3t. (d) Histograms for the current density, including the anomalous sentences for Syn and Sem. Filled and open bars denote the current density under the OV and SV sentence conditions, respectively. The solid and dashed lines with asterisks above pairs of bars correspond to the significant contrasts used for the statistical parametric maps and other significant contrasts ($P < 0.05$, paired *t*-test), respectively.

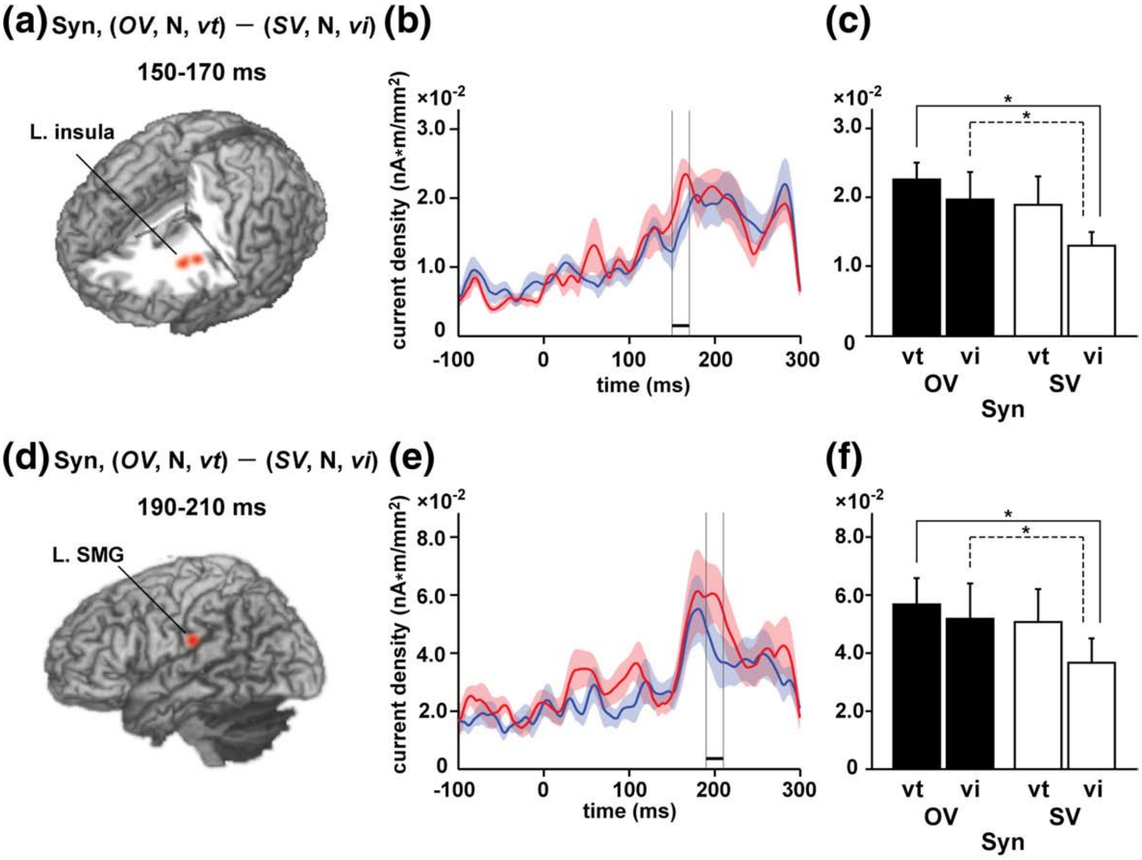

Fig. 4. Cortical responses to sentence structure or verb transitivity. (a, d) The OV and SV sentence conditions were compared within the Syn task (Table 3). Note the significant responses in the left insula and left supramarginal gyrus (SMG). (b, e) The averaged temporal changes of the current density for the left insula and left SMG, respectively. The red and blue lines correspond to the current density for Syn, (OV, N, vt) and (SV, N, vi), respectively. (c, f) Histograms for the current density under each condition are shown for the left insula and the left SMG, respectively. Filled and open bars denote the current density under the OV and SV sentence conditions, respectively.

partitioned into 3256 cortical patches with a mean distance of 5.5 mm (Kriegeskorte and Goebel, 2001).

For each participant, the MEG signals of each channel were averaged for a bin of 20 ms; the time bin was moved in 10 ms steps over the 100–300 ms period after the presentation of a verb. The distribution of cortical activation underlying the averaged MEG signals was modeled with the minimum norm estimates (MNEs) of currents using BESA 5.1. A current dipole was perpendicularly placed at the center of each cortical patch, approximating any spatial distributions of currents on the cortex without assuming particular positions of the dipole sources. (Hämäläinen et al., 1993; Dale and Sereno, 1993). The current density at each cortical patch was calculated by dividing the current strength by the mean area of the cortical patches. The MNEs of currents without averaging for a bin of 20 ms were also obtained and shown in Figs. 3–6 as the temporal changes of the current density.

Across all participants, a paired *t*-test on the current density was performed for two contrasting conditions (see below). The statistical

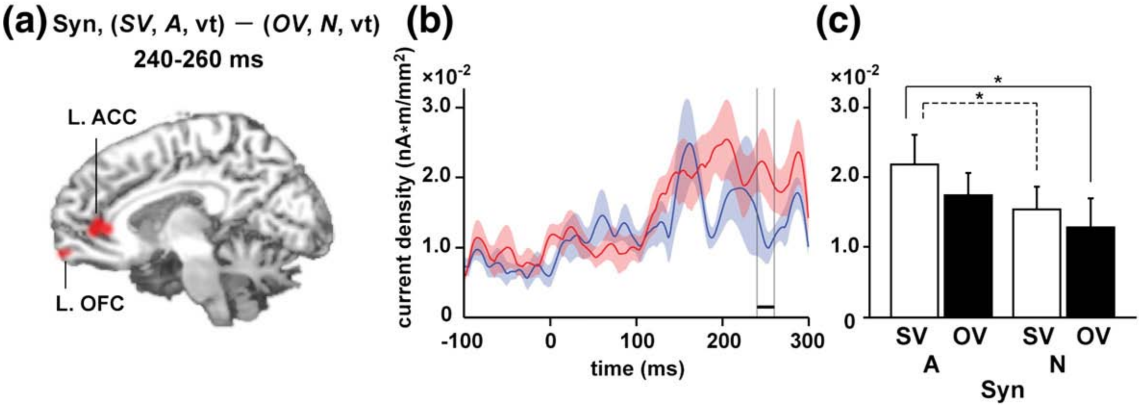

Fig. 5. Cortical responses to syntactic anomaly or sentence structure. (a) The anomalous and normal sentence conditions were compared within the Syn task (Table 3). A parasagittal section ($x=-7$) is shown for the left anterior cingulate cortex (ACC) and left orbitofrontal cortex (OFC). (b) The averaged temporal changes of the current density for the left ACC. The red and blue lines correspond to the current density for Syn, (SV, A, vt) and (OV, N, vt), respectively. (c) Histograms for the current density under each condition are shown for the left ACC; the left OFC showed a similar tendency.

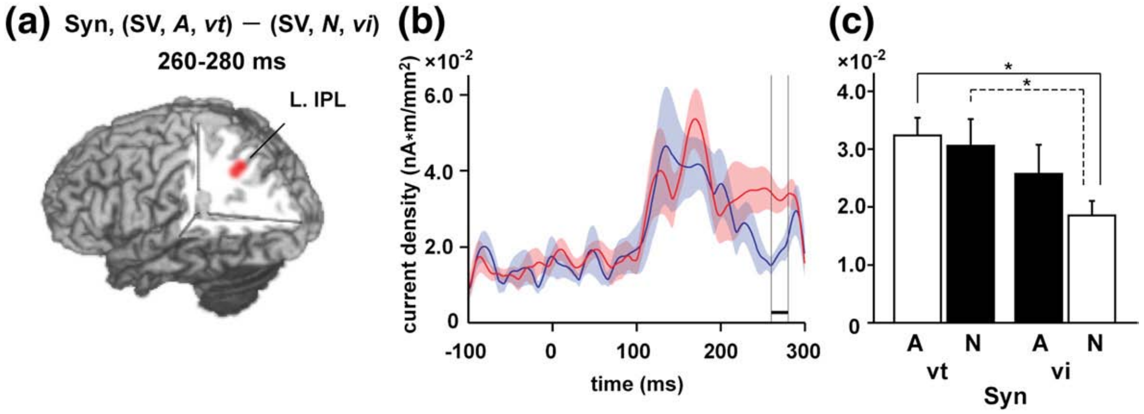

Fig. 6. Cortical responses to verb transitivity or syntactic anomaly. (a) The vt and vi sentence conditions were compared within the Syn task (Table 3). Note the significant responses in the left inferior parietal lobule (IPL). (b) The averaged temporal changes of the current density for the left IPL. The red and blue lines correspond to the current density for Syn, (SV, A, vt) and (SV, N, vi), respectively. (c) Histograms for the current density under each condition are shown for the left IPL.

results for each time bin were further corrected for multiple comparisons across the whole cortical patches ($P_{corr}<0.05$), using a permutation procedure for the current density of two conditions (Karniski et al., 1994; Pantazis et al., 2005). For example, in the comparison between the Syn and Sem tasks, the data of all cortical patches were exchanged between the two tasks in some of the participants. For such a permutation, a maximum t-value was determined among the cortical patches. There were $2^{10}=1024$ permutations for 10 participants, which produced a reference distribution of t-values for determining the corrected P-values. Correction for multiple comparisons using t-values, each of which is a mean difference normalized by a variance, is superior in sensitivity than that using simple mean differences of the current density (Nichols and Holmes, 2002). Note that this method requires no assumption of a normal distribution or of the correlation structure of the data requiring correction (Karniski et al., 1994). The dipoles with statistical significance were identified, each of which was further represented by a sphere with a diameter of 6 mm using ImageJ software (http://rsb.info.nih.gov/ij/). Using the MRIcro software (http://www.mricro.com/), a spatial Gaussian filter was applied to these spheres (full width of half maximum, 8 mm), which were then superimposed onto the transformed standard brain as a statistical parametric map of the cerebral cortex.

Procedures of identifying selective responses

We first compared the tasks under the *normal* sentence conditions, in which *identical* sentences were presented (Table 2). To examine any Syn-selective responses, we adopted a two stage procedure with a statistical parametric map (a paired t-test), starting with contrasting the current density in the Syn task and the two control tasks, i.e., Syn−(Eva+Mem)/2, with a liberal statistical threshold of uncorrected $P<0.005$. To exclude false positive responses, we then focused on Syn-selective responses, i.e., Syn − Sem, at the level of $P_{corr}<0.05$. Once Syn-selective responses were found at a particular time bin, a three-way repeated measures analysis of variance (rANOVA), further incorporating the factors of sentence structure and anomaly (Table 2), was performed for the cortical patch with a maximum t-value (Table 3). To examine any Sem-selective responses, we also started with Sem−(Eva+Mem)/2 (uncorrected $P<0.005$), and then performed Sem − Syn ($P_{corr}<0.05$).

We next focused on three factors included in the Syn task: sentence structure (OV, SV), syntactic anomaly (N, A), and verb transitivity (vt, vi). To examine any selective responses to these factors, a statistical parametric map (a paired t-test) was obtained by contrasting the current density under two conditions ($P_{corr}<0.05$). For example, with Syn, (OV, N, vt) – (SV, N, vi), we examined the effect of sentence structure (OV, SV) or verb transitivity (vt, vi), while syntactic anomaly (N) was held constant (Table 3). Once selective responses were found at a particular time bin, a two-way rANOVA was performed for the cortical patch with a maximum t-value. In the rANOVA of sentence structure × verb transitivity, the remaining factor of syntactic anomaly (held constant for a paired t-test) corresponds to an interaction of two main effects of interest (see the Syn task in Table 2). Similarly, Syn, (SV, A, vt) – (OV, N, vt) and Syn, (SV, A, vt) – (SV, N, vi) were also performed, in which two factors were selected in a cyclic manner (Table 3).

Table 3
A list of statistical analyses

Paired *t*-test	rANOVA	Figure
Syn − *Sem*, (OV, N, vt)	task × sentence structure × anomaly	3
Syn, (*OV*, N, *vt*) – (*SV*, N, *vi*)	sentence structure × verb transitivity	4
Syn, (*SV*, *A*, vt) – (*OV*, *N*, vt)	syntactic anomaly × sentence structure	5
Syn, (SV, *A*, *vt*) – (SV, *N*, *vi*)	verb transitivity × syntactic anomaly	6

The italicized factors in each condition for a paired t-test are main effects of interest. See the Materials and methods for each analysis.

Results

Behavioral data

For each task, behavioral data of accuracy and RTs are shown in Table 4. We focused on the normal sentence conditions, in which *identical* normal sentences were presented. Regarding the accuracy for normal sentences, a two-way rANOVA [task (Syn, Sem, Mem) × sentence structure (OV, SV)] showed marginal main effects of task [$F(2,\ 18)=3.4$, $P=0.055$] and sentence structure [$F(1,\ 9)=4.7$, $P=0.058$] with a significant interaction [$F(3,\ 27)=5.8$, $P=0.012$]. By analyzing the accuracy data separately for each sentence structure, paired t-tests showed no significant difference in accuracy among the tasks under the normal OV sentence condition ($P>0.5$). Under the normal SV sentence condition, the accuracy of Syn was significantly higher than Sem [$t(9)=2.4$, $P=0.040$] and Mem [$t(9)=4.7$, $P=0.0011$], and that of Sem was also higher than Mem [$t(9)=2.2$, $P=0.054$]. Regarding the RTs for normal sentences, a two-way rANOVA [task (Syn, Sem, Eva) × sentence structure (OV, SV)] showed a significant main effect of task [$F(2,\ 18)=6.9$, $P=0.0060$] with neither main effect of sentence structure [$F(1,\ 9)=2.3$, $P=0.2$] nor interaction [$F(2,\ 18)=2.1$, $P=0.1$]. The RTs of Syn were significantly shorter than Eva [OV: $t(9)=2.6$, $P=0.028$; SV: $t(9)=2.6$, $P=0.029$]; the RTs of Sem were also significantly shorter than Eva [OV: $t(9)=2.6$, $P=0.031$; SV: $t(9)=3.1$, $P=0.013$]. In contrast, there was no significant difference in RTs between Syn and Sem ($P>0.2$).

Table 4
Behavioral data for each task

Task	Sentence structure	Anomaly	
		Normal (N)	Anomalous (A)
Syntactic decision task (Syn)	OV	92.9 ± 1.4	92.5 ± 1.9
		575 ± 64	611 ± 63
	SV	96.7 ± 1.1	93.1 ± 1.9
		572 ± 70	609 ± 64
Semantic decision task (Sem)	OV	92.5 ± 2.1	95.7 ± 1.3
		589 ± 67	601 ± 71
	SV	94.5 ± 1.6	95.8 ± 1.2
		565 ± 69	598 ± 70
Evaluation task (Eva)	OV	89.6 ± 2.4	
		630 ± 63	
	SV	88.7 ± 2.0	
		625 ± 67	
Memory task (Mem)	OV	92.3 ± 1.3	
		789 ± 33	
	SV	91.5 ± 1.6	
		780 ± 32	

Data are shown as mean ± SEM. Upper row, accuracy (%); lower row, RTs (ms).

These behavioral results indicate that the main linguistic tasks of Syn and Sem were comparable to or easier than the control tasks of Eva and Mem. Therefore, selective responses in Syn or Sem, if any, cannot be explained by task difficulty.

We next focused on the effects of sentence structure and syntactic anomaly within the Syn task (Table 4). Regarding the accuracy of Syn, a two-way rANOVA [sentence structure (OV, SV) × syntactic anomaly (N, A)] showed a significant main effect of sentence structure [$F(1, 9) = 6.1$, $P = 0.036$; SV > OV] and a marginal main effect of syntactic anomaly [$F(1, 9) = 4.8$, $P = 0.057$; N > A] with no interaction [$F(1, 9) = 3.7$, $P = 0.09$]. Paired t-tests further revealed that the accuracy under the normal SV sentence condition (SV, N, vi) was significantly higher than the other conditions [(OV, N, vt): $t(9) = 3.0$, $P = 0.015$; (OV, A, vi): $t(9) = 2.9$, $P = 0.016$; (SV, A, vt): $t(9) = 2.5$, $P = 0.032$], whereas there was no other significant difference in the accuracy ($P > 0.5$). This result indicates that the normal SV sentence condition was the least demanding among the four conditions. Regarding the RTs of Syn, there was a significant main effect of syntactic anomaly [$F(1, 9) = 10$, $P = 0.011$; A > N] with neither main effect of sentence structure [$F(1, 9) = 0.13$, $P = 0.7$] nor interaction [$F(1, 9) < 0.1$, $P > 0.9$]. Paired t-tests showed that the RTs under the anomalous OV sentence condition (OV, A, vi) were significantly longer than the normal sentence conditions [(OV, N, vt): $t(9) = 3.3$, $P = 0.0087$; (SV, N, vi): $t(9) = 2.5$, $P = 0.032$]; the RTs under the anomalous SV sentence condition (SV, A, vt) were also significantly longer than the normal sentence conditions [(OV, N, vt): $t(9) = 3.0$, $P = 0.016$; (SV, N, vi): $t(9) = 2.5$, $P = 0.036$]. These results indicate that the anomalous OV and SV sentences were more demanding than the normal sentences. The longer RTs for the anomalous sentences, which are consistent with our previous studies using the same paradigm (Sakai et al., 2002; Suzuki and Sakai, 2003), may be due to the reanalysis of anomalous sentences.

Cortical responses to task

First, we focused on the task effects by comparing the four tasks under the *normal* sentence conditions, in which *identical* sentences were presented (Table 2). In order to clarify selective cortical responses to the explicit syntactic processing, we examined a statistical parametric map with a paired t-test for directly contrasting the Syn and Sem tasks (Syn − Sem), first under the normal OV sentence condition (OV, N, vt). We found the earliest Syn-selective responses in the left pars triangularis of the IFG (F3t) [Talairach coordinates, $(x, y, z) = (-47, 35, 9)$; Brodmann's area (BA) 45; $P_{corr} = 0.025$] at 120–140 ms after the verb onset (Fig 3a). The temporal changes in this region also revealed enhanced Syn-selective responses, which started to rise as early as 110 ms (Fig. 3b).

Paired t-tests on the current density of this region under the normal OV sentence condition showed that the responses to Syn were significantly larger than those to Sem [$t(9) = 7.5$, $P < 0.0001$], Eva [$t(9) = 3.4$, $P = 0.0083$], and Mem [$t(9) = 3.2$, $P = 0.010$] (Fig. 3c). On the other hand, there was no significant difference among all task pairs under the normal SV sentence condition ($P > 0.1$). We further tested the task effect, additionally incorporating the factors of sentence structure and anomaly shown in Table 2. A three-way rANOVA [task (Syn, Sem) × sentence structure (OV, SV) × anomaly (N, A)] showed a significant main effect of task [$F(1, 9) = 7.2$, $P = 0.025$; Syn > Sem] with neither other main effects [sentence structure: $F(1, 9) < 0.1$ $P > 0.9$; anomaly: $F(1, 9) = 2.5$, $P = 0.2$] nor interactions ($P > 0.1$) (Fig 3d). Even if the responses to the normal and anomalous sentences were averaged together under the OV sentence condition, the responses to Syn were significantly larger than those to Sem [$t(9) = 2.6$, $P = 0.029$]. Moreover, the responses to Sem under the normal OV sentence condition were significantly smaller than those to Syn under both normal and anomalous OV sentence conditions (i.e., with vt and vi) [Syn, (OV, N, vt): $t(9) = 7.5$, $P < 0.0001$; Syn, (OV, A, vi): $t(9) = 2.4$, $P = 0.042$]. Therefore, the responses of the left F3t were Syn-selective under the OV sentence condition, irrespective of syntactic anomaly or verb transitivity.

During the intervals of 100–120 and 140–300 ms, there was no significant Syn-selective response under the normal OV sentence condition. Regarding the normal SV sentence condition, there was no significant Syn-selective response during the entire searched interval of 100–300 ms. We also confirmed that there was no significant response in *Sem − Syn* under both the normal OV and SV sentence conditions during 100–300 ms. In Fig. 3b, Sem might have enhanced the responses in the left F3t during 150–200 ms, but neither Sem − (Eva + Mem)/2 (uncorrected $P > 0.08$) nor Sem − Syn ($P_{corr} > 0.17$) reached significance under the normal OV sentence condition.

Cortical responses to sentence structure or verb transitivity

Following the elucidation of the Syn-selective responses, we examined the effect of sentence structure (OV, SV) or verb transitivity (vt, vi), while syntactic anomaly (N) was held constant (Table 3). In Syn, (OV, N, vt) – (SV, N, vi), we found significant responses in the left insula [$(-33, 8, 19)$; $P_{corr} = 0.031$] at 150–170 ms (Fig. 4a). The temporal changes in this region showed enhanced responses to the normal OV sentences, which started to rise around 130 ms (Fig. 4b). Next we performed a two-way rANOVA [sentence structure × verb transitivity] on the current density of this region, in which the remaining factor of anomaly corresponded to an interaction (Table 3). This analysis revealed a significant main effect of sentence structure [$F(1, 9) = 13$, $P = 0.0054$; OV > SV] with neither main effect of verb transitivity [$F(1, 9) = 4.0$, $P = 0.08$] nor interaction [$F(1, 9) = 0.39$, $P = 0.6$] (Fig. 4c). Paired t-tests showed that the responses to the SV sentences with vi were significantly smaller than those to the OV sentences [(OV, N, vt): $t(9) = 6.7$, $P < 0.0001$; (OV, A, vi): $t(9) = 2.6$, $P = 0.029$].

In the same contrast, significant responses were also present in the left supramarginal gyrus (SMG) [$(-59, -23, 23)$; BA 40; $P_{corr} = 0.025$] at 190–210 ms (Fig. 4d). The temporal changes in this region showed enhanced responses to the normal OV sentences, which started to rise around 150 ms (Fig. 4e). A two-way rANOVA on the current density of this region showed neither main effects [sentence structure: $F(1, 9) = 2.5$, $P = 0.2$; verb transitivity: $F(1, 9) = 3.0$, $P = 0.1$] nor interaction [$F(1, 9) = 1.0$, $P = 0.3$] (Fig. 4f). Paired t-tests showed that the responses to the SV sentences with vi were significantly smaller than those to the OV sentences [(OV, N, vt): $t(9) = 7.7$, $P < 0.0001$; (OV, A, vi): $t(9) = 2.4$, $P = 0.041$]. During 100–300 ms, we confirmed that there was no significant response in the following contrasts, in which syntactic anomaly was held constant: Syn, (SV, N,

vi) – (OV, N, vt); Syn, (OV, A, vi) – (SV, A, vt); and Syn, (SV, A, vt) – (OV, A, vi).

Cortical responses to syntactic anomaly or sentence structure

We next examined the effect of syntactic anomaly (A, N) or sentence structure (SV, OV), while verb transitivity (vt) was held constant (Table 3). In Syn, (SV, A, vt) – (OV, N, vt), significant responses were observed in the left anterior cingulate cortex (ACC) [(−7, 41, 4); BA 32; $P_{\mathrm{corr}}=0.016$] and orbitofrontal cortex (OFC) [(−4, 56, −9); BA 10; $P_{\mathrm{corr}}=0.020$] at 240–260 ms (Fig. 5a). In Fig. 5b, Syn, (SV, A, vt) might have also enhanced the responses in the left ACC during 170–220 ms, but the same contrast did not reach significance ($P_{\mathrm{corr}}>0.19$). A two-way rANOVA [syntactic anomaly × sentence structure] on the current density of the left ACC at 240–260 ms revealed significant main effects of syntactic anomaly [$F(1, 9)=23$, $P=0.0010$; A>N] and sentence structure [$F(1, 9)=6.9$, $P=0.028$; SV>OV] with no interaction [$F(1, 9)=0.14$, $P=0.7$] (Fig 5c). Paired *t*-tests showed that the responses to the anomalous SV sentences were significantly larger than those to the normal sentences [(OV, N, vt): $t(9)=8.1$, $P<0.0001$; (SV, N, vi): $t(9)=4.1$, $P=0.0028$]. During 100–300 ms, we confirmed that there was no significant response in the following contrasts, in which verb transitivity was held constant: Syn, (OV, N, vt) – (SV, A, vt); Syn, (OV, A, vi) – (SV, N, vi); and Syn, (SV, N, vi) – (OV, A, vi).

Cortical responses to verb transitivity or syntactic anomaly

Finally, we examined the effect of verb transitivity (vt, vi) or syntactic anomaly (A, N), while sentence structure (SV) was held constant (Table 3). In Syn, (SV, A, vt) – (SV, N, vi), significant responses were observed in the left inferior parietal lobule (IPL) [(−20, −60, 45); BA 7; $P_{\mathrm{corr}}=0.032$] at 260–280 ms (Fig. 6a). The temporal changes in this region showed distinct differences between two SV sentence conditions (Fig. 6b). A two-way rANOVA [verb transitivity × syntactic anomaly] on the current density of this region revealed a significant main effect of verb transitivity [$F(1, 9)=8.7$, $P=0.016$] with neither main effect of syntactic anomaly [$F(1, 9)=3.1$, $P=0.1$] nor interaction [$F(1, 9)=1.3$, $P=0.3$] (Fig. 6c). Paired *t*-tests showed that the responses to the normal sentences with vi were significantly smaller than those to the sentences with vt [(SV, A, vt): $t(9)=6.5$, $P=0.0001$; (OV, N, vt): $t(9)=3.0$, $P=0.014$]. During 100–300 ms, we confirmed that there was no significant response in the following contrasts, in which sentence structure was held constant: Syn, (SV, N, vi) – (SV, A, vt); Syn, (OV, N, vt) – (OV, A, vi); and Syn, (OV, A, vi) – (OV, N, vt). These results further clarified the specific temporal dynamics of cortical responses selective for sentence structure, syntactic anomaly, and verb transitivity, all of which were included in the Syn task.

Discussion

The present study revealed the dynamics of the multiple cortical regions that are involved in the analysis of hierarchical syntactic structures and task-related information. The Syn-selective responses to the OV sentences suggest that the left F3t may be critically involved in building sentence structures of a sentence as early as 120 ms from the verb onset (Fig. 3). Moreover, we found selective responses to the three factors included in the Syn task: sentence structure, syntactic anomaly, and verb transitivity. Subsequent responses in the left insula at 150–170 ms were selective for the processing of the OV sentence structure (Fig. 4). On the other hand, responses in the left mediofrontal and inferior parietal regions at 240–280 ms were related to syntactic anomaly and verb transitivity, respectively (Figs. 5 and 6). Taken together, these results support the account of sentence processing proposed in contemporary linguistics, rather than the linear order model for word sequences.

Cortical responses to the Syn task

The direct comparison between the Syn and Sem tasks revealed that the OV sentences evoked selective responses to explicit syntactic processing in the left F3t. The syntax-selective activation of the opercular and triangular parts of the left IFG (F3op/F3t), which is a putative grammar center (Sakai, 2005), has been reported by our previous study with a minimal-pair paradigm (Suzuki and Sakai, 2003), as well as by other studies (Stromswold et al., 1996; Dapretto and Bookheimer, 1999; Kang et al., 1999; Embick et al., 2000; Hashimoto and Sakai, 2002). The present study further demonstrated that the responses of the left F3t are selectively modulated by explicit syntactic processing as early as 120–140 ms. Cortical responses to visual words in this time window are often regarded as representing a pre-lexical process, as shown by lexical tasks (Helenius et al., 1998; Pylkkänen and Marantz, 2003). However, in our paradigm under the OV sentence condition, the preceding NP with an Acc already specifies the syntactic information of vt within the VP (Fig. 1a, see the Introduction). The Syn-selective responses of the left F3t can thus be regarded as predictive effects for the syntactic information of the next-coming verb. Under the OV sentence condition of our previous TMS study, we have reported the priming effects on syntactic decisions, when TMS was administered to the left F3op/F3t 150 ms after the verb onset (Sakai et al., 2002). The critical spatio-temporal window of the TMS study is thus consistent with that of the present study, namely, the left F3t and 120–140 ms.

Cortical responses to sentence structure

The activation of the left insula, as well as the adjacent frontal operculum, has been reported in previous fMRI studies focusing on syntactic decision (Friederici et al., 2003; Suzuki and Sakai, 2003; Newman et al., 2003; Tatsuno and Sakai, 2005; Friederici et al., 2006), and in those focusing on sentence comprehension (Homae et al., 2002). In the present study, the selective responses to the OV sentence structures in the left insula may reflect the processing of more complex hierarchical structure of the OV sentences (Fig. 1a), which is consistent with the behavioral results. On the other hand, the left SMG has been implicated in lexical processing (Corina et al., 2005), the activation of which was enhanced more by vt than vi in a lexical decision task (Thompson et al., 2007). In the present study, the responses in the left SMG, showing selectivity to the OV sentences with vt, may reflect the processing of more detailed lexical information for vt.

Cortical responses to syntactic anomaly and sentence structure

As shown by the behavioral data, the syntactically anomalous sentences were more demanding than the normal sentences. Previous studies have suggested that the ACC and OFC are involved in the process of monitoring and choosing between decision options when the outcomes of those decisions are uncertain or conflicting (Bush et al., 2000; O'Doherty et al., 2001; Botvinick et al., 2004; Walton et al., 2004). The effects of syntactic anomaly in the ACC and OFC are consistent with these reports, in that this monitoring process involves an error detection, reanalysis, and correction as in our case of syntactically anomalous sentences, especially for anomalous SV sentences with inanimate subjects and vt (Table 2). On the other hand, it has been reported that the event-related potentials (ERPs) at 100–300 ms, known as early left anterior negativity (ELAN), showed selectivity to the syntactic anomaly, reflecting early phrase structure building processes (Friederici et al., 1993; Hahne and Friederici, 1999). Using MEG, the generators of the ELAN were suggested to be localized in the inferior frontal and anterior temporal cortices (Friederici et al., 2000b), which were selected *a priori* as the seed points. It is possible that the left ACC and/or OFC, which showed greater responses under the syntactic anomalous conditions (Fig. 5b), also contribute to the ELAN.

Cortical responses to verb transitivity

It has been suggested that a lateral region of the IPL [MNI coordinates, (−44, −54, 46)] is critical for vocabulary knowledge (Lee et al., 2007), which may be related to the effect of verb transitivity observed here, i.e., increased responses to the sentences with vt. It is also possible that the decreased responses to the sentences with vi reflected simpler lexical processing with a single argument of a subject, consistent with the behavioral data, in which the condition (SV, N, vi) was the least demanding.

Conclusions

Using MEG with the minimal-pair paradigm to compare the Syn and Sem tasks, we found that the responses to the normal OV sentences in the left F3t at 120–140 ms were selective for explicit syntactic processing. The earliest left F3t responses can thus be regarded as predictive effects for the syntactic information of the next-coming verb, which cannot be explained by associative memory or statistical factors. Moreover, the selective responses to the OV sentence structures in the left insula at 150–170 ms may reflect the processing of more complex hierarchical structure of the OV sentences. The responses in the left SMG at 190–210 ms, showing selectivity to the OV sentences with vt, may reflect the processing of more detailed lexical information for vt. On the other hand, the responses in the left ACC and left OFC at 240–260 ms were related to syntactic anomaly, reflecting an error detection, reanalysis, and correction. The responses in the left IPL at 260–280 ms were related to verb transitivity, probably reflecting lexical processing. These results revealed the dynamics of the multiple cortical regions that work in concert to analyze hierarchical syntactic structures and task-related information, further elucidating the top-down syntactic processing that is crucial during on-line sentence processing.

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