博士論文

論文題目 Syntactic predictive effects for sentence structures in the left inferior frontal gyrus

(左下前頭回における文構造への統辞的予測効果)

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Syntactic predictive effects for sentence structures in the left inferior frontal gyrus

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List of Abbreviations

A	anomalous
ACC	anterior cingulate cortex
Acc	accusative case marker
BA	Brodmann's area
Cong	congruent
Eva	evaluation
(f)MRI	(functional) magnetic resonance imaging
F3t	triangular part of the left inferior frontal gyrus
F3op	opercular part of the left inferior frontal gyrus
IFG	inferior frontal gyrus
Incong	incongruent
IPL	inferior parietal lobule
MCC	midcingulate cortex
MEG	magnetoencephalography
Mem	memory
MNE	minimum norm estimate
MNI	Montreal Neurological Institute
MTG	middle temporal gyrus
N	normal
Nom	nominative case marker
NP	noun phrase
OFC	orbitofrontal cortex
OV	object-verb
PCC	posterior cingulate cortex
pro	pronominal element
rANOVA	repeated measures analysis of variance
ROI	region of interest
RT	reaction time
Sem	semantic decision
SMG	supramarginal gyrus
Syn	syntactic decision
SV	subject-verb
TMS	transcranial magnetic stimulation
vi	intransitive verb
VP	verb phrase
vt	transitive verb

1. General Introduction

Human language consists of more than linear strings of words: it is constructed based on hierarchical syntactic structures by recursively merging a pair of syntactic objects (Chomsky, 1995). Such syntactic computation is a critical component of the uniquely human faculty of language. 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 (Dapretto and Bookheimer, 1999; Kang *et al.*, 1999; Stromswold *et al.*, 1996); 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 previous functional magnetic resonance imaging (fMRI) study has clarified that explicit syntactic processing of object-verb (OV) sentences, 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. Understanding the role of syntactic structures in language comprehension is crucial for elucidating the neural mechanisms underlying the human language faculty.

Recently, computational parsing theories with incremental predictions based on syntactic structures have been developed (Hale, 2011; Levy, 2008). According to these theories, the difficulty of processing a given phrase can be quantitatively explained by deviations from a prediction about the syntactic features of upcoming words in a sentence, which are based on the incrementally constructed syntactic structures. According to these theories, the difficulty of processing a given phrase can be quantitatively explained by deviations from a prediction about the syntactic features of upcoming words in a sentence, which are based on the incrementally constructed syntactic structures. In our recent magnetoencephalography (MEG) study using Japanese sentences, we have shown that a preceding noun phrase (NP) with a case marker (dative or accusative) provides information about the argument structures of a sentence-final verb, and that this process enhances syntactic processing of the verb (Inubushi *et al.*, 2012).

To clarify predictive syntactic processing in the left IFG, I incorporated subject-verb (SV) sentences into the above mentioned minimal pair-paradigm. I further examined automaticity of predictive syntactic processing by testing the effects of subliminal stimuli on such processing. By utilizing a high temporal resolution (about 10-20 ms) of MEG equipped with superconducting quantum interference devices (SQUIDs), we recorded the magnetic fields generated by the neural activity.

2. Experiment 1: The cortical dynamics in building syntactic structures of sentences

2.1. Introduction

Recent fMRI and 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 (Indefrey *et al.*, 2001; Stromswold *et al.*, 1996), and canonicity (Ben-Shachar *et al.*, 2004; Bornkessel *et al.*, 2005; Grewe *et al.*, 2006; Kinno *et al.*, 2008; Röder *et al.*, 2002). 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 (Iijima *et al*., 2009), we thus focus on the structure of a minimal sentence, which is formed by merging a single pair of noun and verb.

Figures 2.1a and 2.1b show the basic structures of OV and SV sentences, 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 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. 2.1a, 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),

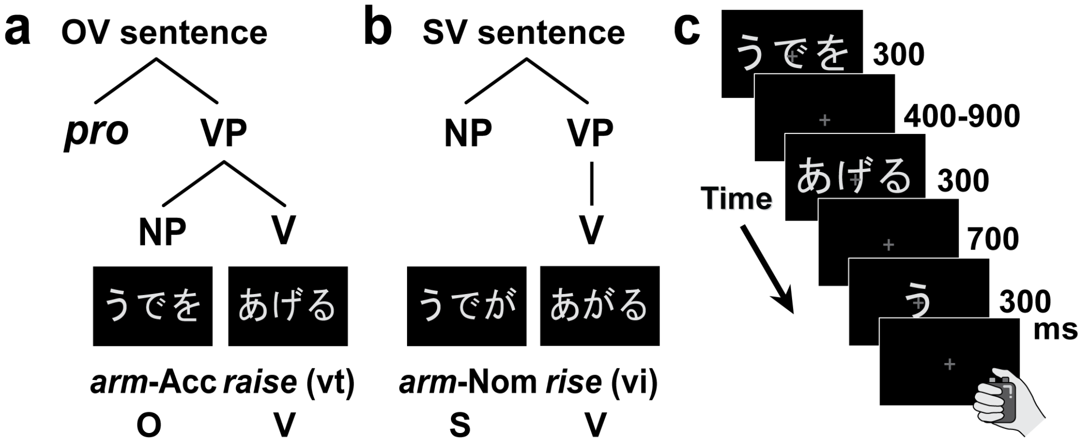


Fig. 2.1. A minimal-pair paradigm with a minimum sentence consisting of a noun phrase and a verb. A pair of sentences including an object-verb (OV) sentence (‘*ude-o ag-e-ru*’) **(a)** and a subject-verb (SV) sentence (‘*ude-ga ag-ar-u*’) **(b)** is shown. The same noun was used for both sentences; a transitive verb (vt) and an intransitive verb (vi) were morphologically related in a pair (Table 2.1). 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 2.2.

to form a whole sentence (Fig. 2.1b). 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 2.1) 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 2.1). 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 2.2). 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 2.2): 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. 2.1c). To solve the Syn task, the identification of vt or vi, as well as the linguistic knowledge of a syntactic relationship between a case marker 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 the normal sentences and anomalous sentences. For the Sem task, we made semantically incorrect sentences by exchanging verbs among a 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.

Table 2.1. 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 2.2. 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’* [1] *arm*-Acc *raise* (vt)	*‘ude-o ag-ar-u’* [2] *arm*-Acc *rise* (vi)
	SV	*‘ude-ga ag-ar-u’* [3] *arm*-Nom *rise* (vi)	*‘ude-ga ag-e-ru’* [4] *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 marker 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 marker corresponded to OV and SV sentence structures, respectively. On the other hand, the distinction between transitive verb (vt) and intransitive verb (vi), i.e., verb transitivity, 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.

[1] *someone raises one’s own arm*.

[2] 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[3].

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

[4] The sentence is syntactically incorrect because there is a wrong case marker when compared with the normal OV sentence[1]. 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 2.1).

In this 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. 2.1a). 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. 2.1b). 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 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 2.1). 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. 2.1c). 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.

2.2. Materials and Methods

2.2.1. 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.

2.2.2. 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 marker) or verb (Fig. 2.1c), 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).

2.2.3. 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. 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 (Table 2.2).

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-o kim-e-ru*’ (*techniques succeed*) is positive, and ‘*hada-o ar-as-u*’ (*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 were fully randomized and counterbalanced. Only trials with participants’ correct responses were used for analyzing RTs.

2.2.4. 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. 2.2). 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 × 1 × 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

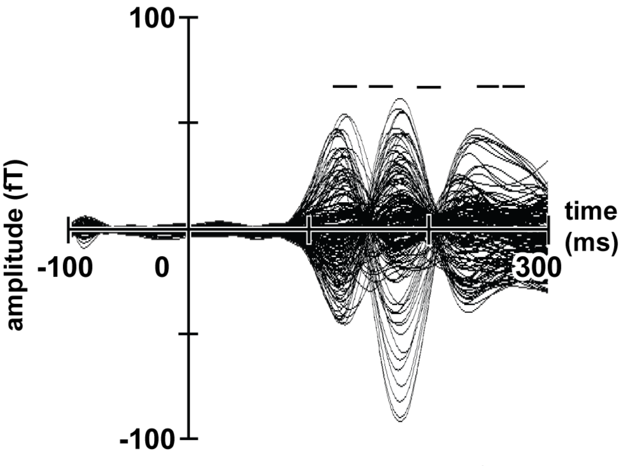


Fig. 2.2. The averaged MEG signals for all trials from ten participants, shown for each sensor. The black bars above the waveforms indicate the time windows, where significant responses were observed in the contrasts shown in Table 2.3 and Figs. 2.3-2.6.

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 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 (Dale and Sereno, 1993; Hämäläinen *et al.*, 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 Figures 2.3-2.5 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 results for each time bin were further corrected for multiple comparisons across the whole cortical patches ($P_{\mathrm{corr}} < 0.05$), 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.

2.2.5. Procedures of identifying selective responses

We first compared the tasks under the *normal* sentence conditions, in which *identical* sentences were presented (Table 2.2). 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 $P_{\mathrm{corr}} < 0.05$. 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 2.2), was performed for the cortical patch with a maximum t-value (Table 2.3). To examine any

Table 2.3. A list of statistical analysis

Paired *t*-test	rANOVA	Figure
Syn – Sem, (OV, N, vt)	task × sentence structure × anomaly	2.3
Syn, (*OV*, N, *vt*) – (*SV*, N, *vi*)	sentence structure × verb transitivity	2.4
Syn, (*SV*, *A*, vt) – (*OV*, *N*, vt)	syntactic anomaly × sentence structure	2.5
Syn, (SV, *A*, *vt*) – (SV, *N*, *vi*)	verb transitivity × syntactic anomaly	2.6

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

Sem-selective responses, we also started with Sem – (Eva + Mem) / 2 (uncorrected $P < 0.005$), and then performed Sem – Syn ($P_{\mathrm{corr}} < 0.05$).

We next focused on three factors included in the Syn task: sentence structure (OV, SV), syntactic anomaly (N, A), and verb transitivity (vt, vi; see Table 2.2). 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 ($P_{\mathrm{corr}} < 0.05$). 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 2.3). 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 2.2). 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 2.3).

2.3. Results

2.3.1. Behavioral data

For each task, behavioral data of accuracy and RTs are shown in Table 2.4. 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 ($P > 0.2$). 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 2.4). 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).

Table 2.4. Behavioral data for each task

Task	Sentence structure	Anomaly	
		Normal (N)	Anomalous (A)
Syntactic decision task (Syn)	OV	92.9 ±1.4 575 ± 64	92.5 ± 1.9 611 ± 63
	SV	96.7 ± 1.1 572 ± 70	93.1 ± 1.9 609 ± 64
Semantic decision task (Sem)	OV	92.5 ± 2.1 589 ± 67	95.7 ± 1.3 601 ± 71
	SV	94.5 ± 1.6 565 ± 69	95.8 ± 1.2 598 ± 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, reaction times (RTs) (ms).

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.

2.3.2. 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 2.2). If the normal OV and SV sentences were separately analyzed, the task selectivity would be thus properly elucidated. 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 triangular part of the IFG (F3t) [Talairach coordinates, $(x, y, z) = (–47, 35, 9)$; Brodmann's area (BA) 45; $P_{\text{corr}} = 0.025$] at 120-140 ms after the verb onset (Fig. 2.3a).

The temporal changes in this region confirmed the earliest Syn-selective responses, which peaked around 130 ms (Fig. 2.3b).

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 [$t(9) = 3.2$, $P =$

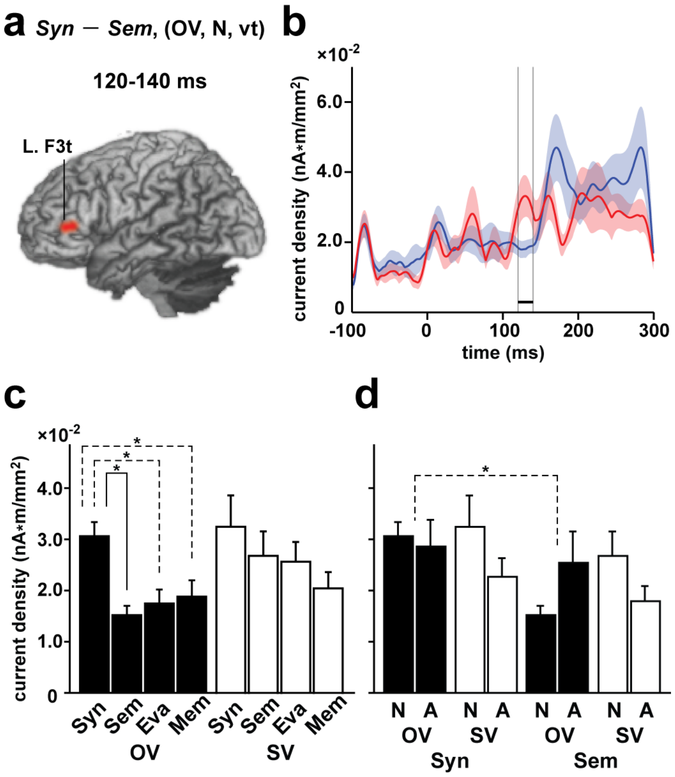


Fig. 2.3. Selective responses to the Syn task. (a) The cortical responses to Syn and Sem were compared with a paired t-test under the normal OV sentence condition, and mapped on the transformed standard brain shown in the left panels ($P_{\mathrm{corr}} < 0.05$). Note the significant responses in the 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.

0.010] (Fig. 2.3c). 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 2.2. 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. 2.3d). 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 (SV, N, vi), 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 Figure 2.3b, 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 ($P_{\mathrm{corr}} > 0.17$) reached significance under the normal OV sentence condition.

2.3.3. Cortical responses to sentence structure or verb transitivity

Following the elucidation of the Syn-selective responses described above, we examined the effect of sentence structure (OV, SV) or verb transitivity (vt, vi), while syntactic anomaly (N) was held constant (Table 2.3). In Syn, (OV, N, vt) – (SV, N, vi), we found selective responses in the left insula [(–33, 8, 19); $P_{\mathrm{corr}} = 0.031$] at 150-170 ms (Fig. 2.4a). The temporal changes in this region showed transient selective responses to the normal OV sentences (Fig. 2.4b). 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 2.3). 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. 2.4c). 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): $t(9) = 2.6$, $P = 0.029$].

At 190-210 ms, we also observed significant selective responses in the left supramarginal gyrus (SMG) [(–59, –23, 23); BA 40; $P_{\mathrm{corr}} = 0.025$] (Fig. 2.4d-e). 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 [$F(1, 9) = 1.0$, $P = 0.3$]. 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

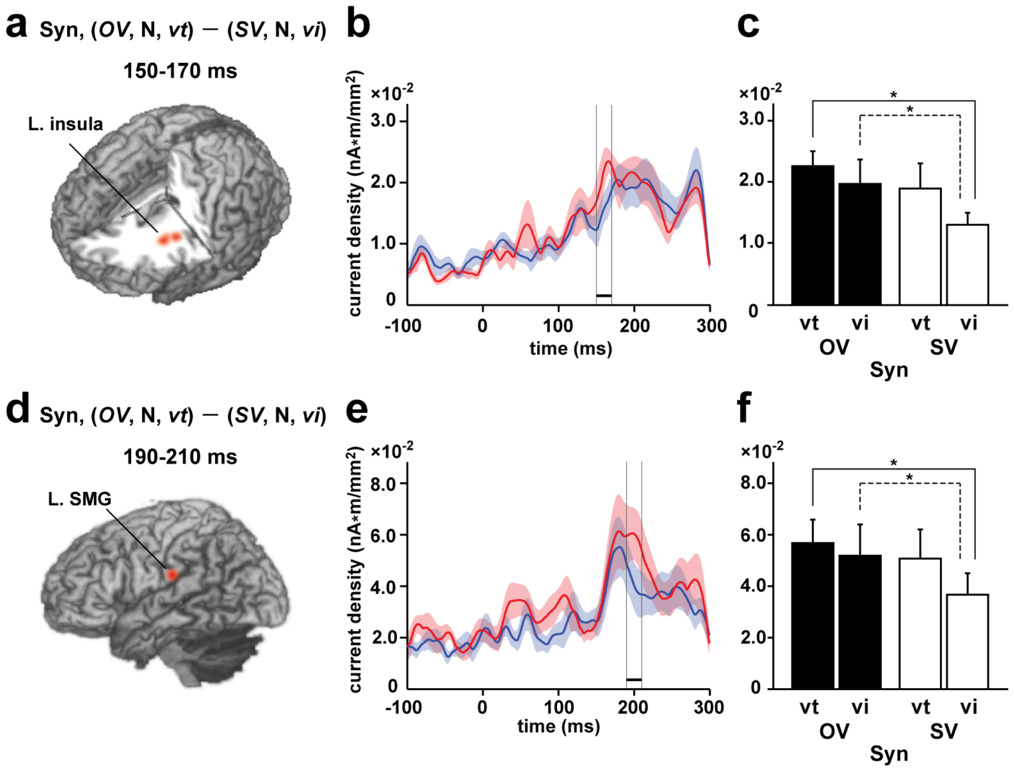


Fig. 2.4. Cortical responses to sentence structure or verb transitivity. (a, d) The OV and SV sentence conditions were compared within the Syn task (Table 2.3). Note the significant responses in the left insula and left supramarginal gyrus (SMG). **(b, e)** The averaged temporal changes of the current 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. Filled and open bars denote the current density under the OV and SV sentence conditions, respectively.

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).

2.3.4. 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 2.3). 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. 2.5a). In Figure 2.5b, Syn, (SV, A, vt) might have also enhanced the responses in the left ACC during 170-220 ms, but Syn, (SV, A, vt) – (OV, N, vt) 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. 2.5c). 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).

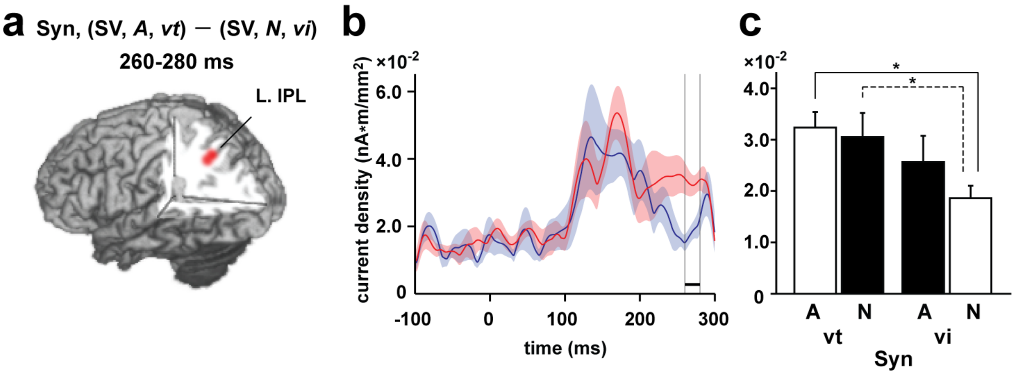


Fig. 2.5. Cortical responses to syntactic anomaly or sentence structure. (a) The anomalous and normal sentence conditions were compared within the Syn task (Table 2.3). A parasagittal section ($x = –7$) is shown for the left anterior cingulate cortex (ACC) and left orbitofrontal cortex (OFC). **(b)** 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.

2.3.5. 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 2.3). 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. 2.6a). The temporal changes in this region showed distinct differences between two SV sentence conditions (Fig. 2.6b). 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. 2.6c). 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.

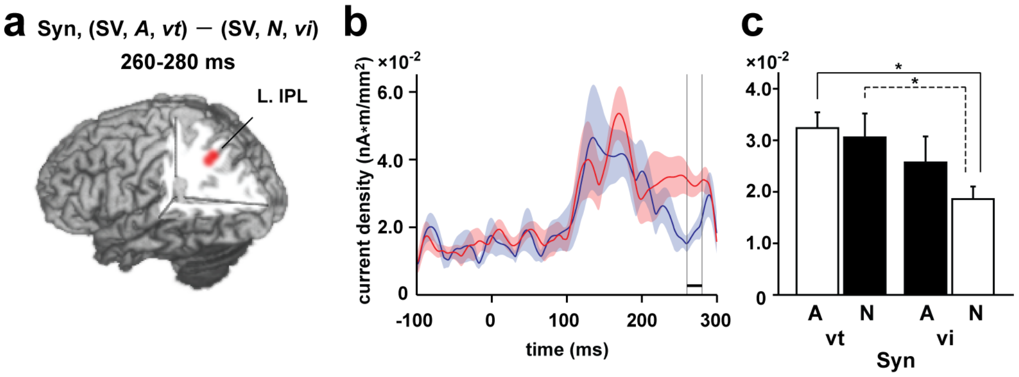


Fig. 2.6. Cortical responses to verb transitivity or syntactic anomaly. (a) The vt and vi sentence conditions were compared within the Syn task (Table 2.3). Note the significant responses in the left inferior parietal lobule (IPL). **(b)** The averaged temporal changes of the current density for the 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.

2.4. 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 normal 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. 2.3). 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. 2.4). 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. 2.5 and 2.6). Taken together, these results support the linguistic account of sentence processing, rather than the linear order model for word sequences.

The direct comparison between the Syn and Sem tasks revealed that the normal 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 (Dapretto and Bookheimer, 1999; Embick *et al.*, 2000; Hashimoto and Sakai, 2002; Kang *et al.*, 1999; Stromswold *et al.*, 1996). The present study further demonstrated that the cortical responses of the left F3t are selectively modulated by explicit syntactic processing under the OV sentence condition as early as 120-140 ms. Cortical responses to visual words in this time window are often regarded to represent 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. 2.1a, see 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.

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; Friederici *et al.*, 2006; Newman *et al.*, 2003; Suzuki and Sakai, 2003; Tatsuno and Sakai, 2005), 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. 2.1a), 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.

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 (Botvinick *et al.*, 2004; Bush *et al.*, 2000; O'Doherty *et al.*, 2001; 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 2.2). 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 in the present study, also contribute to the ELAN.

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.

3. Experiment 2: Subliminal facilitation of predictive effects during syntactic processing

3.1. Introduction

In the experiment 1, we showed that responses in the left IFG were enhanced, at 120-140 ms after the verb onset of OV sentences, only in a syntactic decision task but not in other tasks including a semantic decision task (Iijima *et al.*, 2009). We interpreted this enhancement as predictive effects caused by the preceding object with an Acc ("-*o*"), such that vt was the only possible verb type for the sentence-final verb, i.e., grammatical, within a minimal construction of a VP. We also confirmed that the enhancement of the left IFG responses was observed for the OV sentences, but not for SV sentences. The SV sentences would have no predictive effects, because the NP with a Nom ("-*ga*") has little power to specify the verb types including a vi, vt, and nominal/adjectival predicate associated with a copular verb ("*desu*, *da* etc." like "*be* etc." in English). In our paradigm, we used object-vt and subject-vi combinations for normal OV and SV sentences, respectively.

From each of the normal OV and SV sentences, we made a syntactically anomalous sentence, by simply exchanging the verb with the rest of a verb pair, which consisted of morphologically and semantically related vt and vi (Table 3.1). Here we defined *anomalous* OV and SV sentences as those with an object (with "-*o*") and subject (with "-*ga*"), respectively. From a normal OV sentence (e.g., "*yuki-o tok-**as-u*** (= vt)": "(*someone*) *melts snow*"), we made an anomalous OV sentence (e.g., "*yuki-o tok-**e-ru*** (= vi)"), which is ungrammatical, since a vi cannot take an object. From a normal SV sentence (e.g., "*yuki-ga tok-**e-ru*** (= vi)": "*snow melts*"), we made an anomalous SV

Table 3.1. A list of 72 normal sentences

Verb subgroup	Object-Verb (OV) sentence		Subject-Verb (SV) sentence		Translation of SV sentence
	Noun-Acc	vt	Noun-Nom	vi	
I	*tama-o*	*at-e-ru*	*tama-ga*	*at-ar-u*	*the bullet hits (someone)*
II		*sor-as-u*		*sor-e-ru*	*the bullet misses*
I	*huku-o*	*kim-e-ru*	*huku-ga*	*kim-ar-u*	*clothes get chosen*
II		*nur-as-u*		*nur-e-ru*	*clothes get wet*
I	*shiru-o*	*maz-e-ru*	*shiru-ga*	*maz-ar-u*	*sauce mixes*
II		*tar-as-u*		*tar-e-ru*	*sauce drips off*
I	*nuno-o*	*som-e-ru*	*nuno-ga*	*som-ar-u*	*the cloth gets dyed*
II		*moy-as-u*		*mo(y)-e-ru*	*the cloth gets burnt*
I	*oyu-o*	*tam-e-ru*	*oyu-ga*	*tam-ar-u*	*hot water pools*
II		*hiy-as-u*		*hi-e-ru*	*hot water cools*
I	*iki-o*	*tom-e-ru*	*iki-ga*	*tom-ar-u*	*the breath ceases*
II		*mor-as-u*		*mor-e-ru*	*the breath gets out*
I	*ine-o*	*u(w)-e-ru*	*ine-ga*	*uw-ar-u*	*the rice is planted*
II		*kar-as-u*		*kar-e-ru*	*the rice withers*
II	*kabe-o*	*kog-as-u*	*kabe-ga*	*kog-e-ru*	*the wall gets burnt*
III		*nao-s-u*		*nao-r-u*	*the wall gets fixed*
II	*kome-o*	*mur-as-u*	*kome-ga*	*mur-e-ru*	*the rice gets steamed*
III		*nok-os-u*		*nok-or-u*	*the rice remains*
II	*netsu-o*	*sam-as-u*	*netsu-ga*	*sam-e-ru*	*the fever wanes*
III		*kom-e-ru*		*kom-or-u*	*the fever pervades*
II	*yuki-o*	*tok-as-u*	*yuki-ga*	*tok-e-ru*	*snow melts*
III		*ot-os-u*		*ot-i-ru*	*snow drops*
II	*mado-o*	*yur-as-u*	*mado-ga*	*yur-e-ru*	*the window shakes*
III		*mi-se-ru*		*mi-e-ru*	*the window can be seen*
III	*ashi-o*	*hit-as-u*	*ashi-ga*	*hit-ar-u*	*the legs soaks*
I		*mag-e-ru*		*mag-ar-u*	*the legs bend*
III	*waza-o*	*ik-as-u*	*waza-ga*	*ik-i-ru*	*techniques get utilized*
I		*kak-e-ru*		*kak-ar-u*	*techniques succeed*
III	*huta-o*	*maw-as-u*	*huta-ga*	*maw-ar-u*	*the lid gets screwed*
I		*shim-e-ru*		*shim-ar-u*	*the lid gets closed*
III	*mizu-o*	*mit-as-u*	*mizu-ga*	*mit-i-ru*	*water brims in (something)*
I		*tam-e-ru*		*tam-ar-u*	*water pools*
III	*tabi-o*	*nob-as-u*	*tabi-ga*	*nob-i-ru*	*the travel gets extended*
I		*o(w)-e-ru*		*ow-ar-u*	*the travel ends*
III	*boya-o*	*ok-os-u*	*boya-ga*	*ok-i-ru*	*small fire occurs*
I		*tom-e-ru*		*tom-ar-u*	*small fire stops*

In every two rows with the same noun, two pairs of a transitive verb (vt) and an intransitive verb (vi) are shown, where each pair in a row is morphologically related and shares the same meanings. For a single trial, a subliminal verb and a target verb were chosen from each of the two vt-vi pairs (see Fig. 3.1a). According to Shibatani (1990), verb pairs of vt and vi can be divided into three verb subgroups in terms of their morphological/phonological regularity: I (vt/vi: *-e-ru*/*-ar-u*), II (*-as-u*/*-e-ru*), and III (others). Verbs from two different subgroups were selected for each noun.

sentence (e.g., “*yuki-ga tok-**as-u*** (= vt)”), which is ungrammatical, since its error can be immediately corrected by the grammatical counterpart: either “*yuki-ga tok-**e-ru***” (verb type counterpart) or “*yuki-**o** tok-as-u*” (case marker counterpart) for this example. In our paradigm of directly contrasting OV and SV sentences, such a syntactic judgment would thus surpass a judgment on selectional restrictions if any.

In the present MEG study with the syntactic decision task, we hypothesize that the predictive effects caused by the preceding object represent early syntactic processes of determining verb *transitivity* (vt or vi) and associated argument structures of the following verb (“target verb” hereafter). To further confirm the automaticity of the predictive effects, we examined whether a *subliminally* presented verb (“subliminal verb” hereafter) unconsciously, i.e., without awareness, affected the predictive effects (Fig. 3.1a). A subliminal verb was presented for 34 ms between two masks after the NP (Fig. 3.1b). As shown in Figure 3.1a, the target verb was either congruent (Cong) or incongruent (Incong) with the subliminal verb in terms of their verb transitivity, leading to four stimulus conditions: OV-Cong, SV-Cong, OV-Incong, and SV-Incong. The lexico-semantic relationships between the noun and subliminal verb, or between the noun and target verb, were always normal and equivalent among these four stimulus conditions. This strict semantic control is one of the merits of the present study.

In our paradigm, the predictive effects were caused by a preceding object, and then maintained by a subliminal verb. We expected that the left IFG responses at about 150 ms after the target verb onset, representing predictive effects of the preceding object, would be enhanced under the OV-Cong condition than the SV-Cong condition without such predictive effects, because the transitivity of the target verb, and consequently the grammaticality of the sentence (vt as normal, and vi as anomalous), had been already

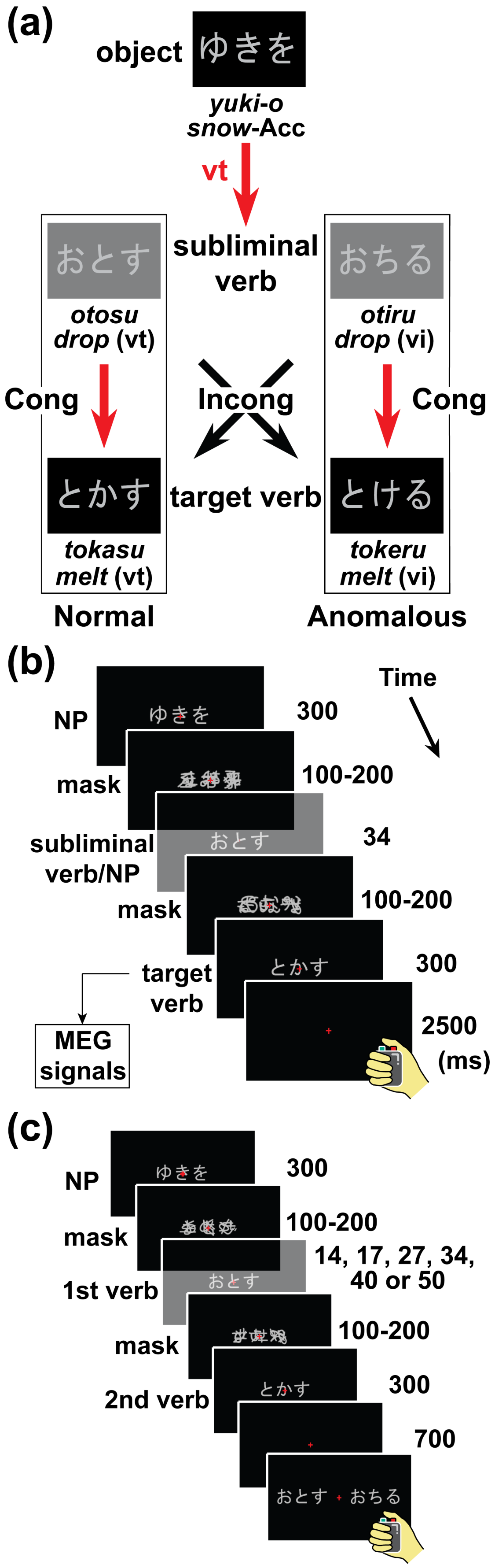


Fig. 3.1. A paradigm with subliminal stimuli. We presented two-word sentences like an object-verb (OV) sentence (e.g., "*yuki-o tokasu*": "(*someone*) *melts snow*") and a subject-verb (SV) sentence (e.g., "*yuki-ga tokeru*": "*snow melts*"). The transitive verb (vt) and intransitive verb (vi) are both morphologically and semantically related (see Table 1), but always *different* words, similar to "*raise*/*rise*" distinction in English. **(a)** Examples of visually presented stimuli of an OV sentence. In a syntactic decision task, participants decided whether a presented sentence was syntactically normal or anomalous. A *supraliminally* presented verb ("target verb") appeared at the end of each trial to be responded by participants. A *subliminally* presented verb ("subliminal verb") was inserted between an object and the target verb. The target verb was either congruent (Cong) or incongruent (Incong) with the subliminal verb in terms of their verb transitivity (vt or vi). Red arrows indicate a *prediction* about the verb, provided by an object with an accusative case marker (Acc), such that the following vt is normal, and that the following vi is anomalous. **(b)** A single trial in the syntactic decision task. We sequentially presented an NP, a subliminal verb or NP, and a target verb, together with a forward mask and a backward mask before and after the subliminal verb, respectively. We focused on MEG signals to target verbs, and we presented the masks with random intervals between 100 and 200 ms, so that MEG signals to target verbs were not confounded with those to the other stimuli. **(c)** A single trial in a forced-choice recognition task to assess the visibility of a masked first verb. At the end of this task, two stimuli were presented, and participants simply chose which stimulus had actually appeared as a first verb with a different interval of 14-50 ms. We made the stimulus presentation of each trial identical to that in the syntactic decision task, except that two verbs were presented as a choice stimulus.

determined by the subliminal verb and replicated by the target verb (see Fig. 3.1a). We thus analyzed the MEG signals to target verbs based on the distinction for sentence structures (OV/SV) and congruency, but not on the distinction for transitivity or grammaticality/anomaly.

In an SV sentence, the predicate cannot be uniquely specified, and thus the bottom-up determination of the transitivity from a presented stimulus had to be duplicated for both subliminal and target verbs. This interference would lead to longer RTs for the SV sentences than those for the OV sentences, independent from predictive effects, i.e., irrespective of the Cong and Incong conditions. As a control for the interference from a subliminal verb, we compared behavioral data for the SV and OV sentences when a subliminal NP was presented instead of a subliminal verb.

Previous fMRI studies of normal participants established that the left IFG and the left lateral premotor cortex play a crucial role in syntactic processes (Dapretto and Bookheimer, 1999; Embick *et al.*, 2000; Friederici *et al.*, 2003; Hashimoto and Sakai, 2002; Kinno *et al.*, 2008; Musso *et al.*, 2003; Stromswold *et al.*, 1996; Suzuki and Sakai, 2003); these regions have been proposed as putative grammar centers (Sakai, 2005). Other candidate regions, whose responses may be modulated under the OV-Cong condition, include the left SMG involved in lexical processing (Lee *et al.*, 2007; Ohta *et al.*, 2013; Pattamadilok *et al.*, 2010) and the midcingulate cortex (MCC) involved in task-set formations (Dosenbach *et al.*, 2006; Hyafil *et al.*, 2009). To examine the spatio-temporal properties of these multiple regions in an unbiased manner, we applied whole-brain analyses of MEG responses. We also tried to elucidate causal influences among these multiple regions with partial Granger causality analyses (Barrett *et al.*, 2010; Guo *et al.*, 2008). Under the OV-Cong condition, we expected that causal interactions between the left IFG and these other regions were enhanced. Our present study should help to elucidate the neural basis of syntactic processes that are both automatic and predictive.

3.2. Materials and methods

3.2.1. Participants

The participants in the MEG experiments were 16 native Japanese speakers. One participant, who reported that he was able to detect the subliminal verbs during the MEG experiments, was excluded from the behavioral and MEG data analyses, leaving a total of 15 participants (19-43 years; 4 females). All of them showed right-handedness (laterality quotients: 87-100) as determined by the Edinburgh inventory (Oldfield, 1971). In the pilot study for determining an appropriate interval of subliminal stimuli, 10 other native Japanese speakers (22-35 years; 1 female) participated. All participants were neurologically normal without any psychiatric symptoms. Written 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.

3.2.2. Stimuli

Generally in most languages, there are two types of intransitive verbs: unaccusative verbs and unergative verbs. The subjects of unaccusative verbs, as well as the objects of transitive verbs, have the semantic role of “theme” (the entity undergoing the effect of some action). In order to equate semantic factors among the conditions, we used unaccusative verbs alone for the intransitive verbs, so that the NPs of both OV and

SV sentences had the same semantic role. Moreover, we used the same set of nouns for both sentence structures. Note that in Japanese a null nominative-case pronoun is allowed as a subject, as well as in Spanish and Italian, and we omitted in SOV sentences a subject, whose semantic role is "agent" (the entity instigating some action). The following examples clarify the distinction between SVO and SV sentences in English, similar to the OV and SV distinction, respectively:

> a) *The coach* (= agent) *substituted* (= vt) *John* (= theme) *for Dave, and I* (= agent) *would have done so,*
> b) *John* (= theme) *substituted* (= vi) *for Dave, and I* (= theme) *would have done so,*

as "*done so*" substitutes for the VP "*substituted John for Dave*" or "*substituted for Dave*".

The distinction between vt and vi, i.e., verb transitivity, is one of the universal aspects of syntactic features among natural languages. In the Japanese language, there are a number of verb pairs, each of which consisted of morphologically and semantically related vt and vi (e.g., "*at-e-ru*" and "*at-ar-u*"; Table 3.1). The vt-vi pair relationships are determined by complex rules of morphosyntax (Shibatani, 1990), similar to the distinction of "*raise/rise, fell/fall, lay/lie, set/sit*" in English. There are some Japanese verbs, which lack such morphological distinction [e.g., "*hirak-u*" ("*open*") for both vt and vi], but we did not use them in the present study. Two vt-vi pairs were selected as stimuli for each noun, which was always inanimate and semantically related with the four verbs. For a single trial, a subliminal verb and a target verb were chosen from each of the two vt-vi pairs (e.g., "*at-e-ru*" and "*sor-as-u*"; see

Table 3.1), so that the subliminal and target verbs had neither direct semantic nor morphological/phonological relationships that may affect congruency.

Each word stimulus was either an NP (a noun and a case maker) or verb (Fig. 3.1b), which always consisted of three letters (three moras or syllables) spelled only in kana letters (Japanese phonograms) to ensure a consistent reading time. Using *Google* (http://www.google.co.jp/), we calculated a transitional probability from an NP to a verb within a sentence, and there was no significant difference between the normal OV and SV sentences [$t_{(35)} = -0.053$, $P > 0.9$ (paired *t*-test)]. In each trial starting from an NP for 300 ms, a mask was presented with a random interval of 100, 117, 134, 150, 167, 184, or 200 ms. This mask served as a *forward* mask for the next-coming subliminal verb, which was presented for 34 ms. A *backward* mask followed this subliminal stimulus with the same random intervals. A target verb was then presented for 300 ms. By varying the intervals of backward and forward masks, we separated the effects on the target verb from any responses to an NP or subliminal verb (Fig. 3.1b). The inter-trial interval was randomly varied within the range of 5 ± 0.5 s to reduce any periodical noises.

Mask stimuli, which should be unreadable while retaining some features of the kana stimuli, were made in the following procedures. We selected three verb stimuli, and rotated three kana letters of each verb stimulus in three different angles (±90º, 180º). By superimposing one of the resultant stimuli with two of six stimuli, each of which consisted of three pseudoletters, we made 27 different mask stimuli (see Fig. 3.1b). By presenting each mask stimulus alone for 200 ms in a pilot study, we tested whether any of the “letters” can be identified as one of 46 kana letters. In 243 trials, only two answers matched with original letters, indicating no significant difference from the chance (*P* > 0.6, *t*-test).

We prepared 36 verb pairs of vt and vi, and made 72 normal sentences (Table 3.1), each of which consisted of an NP and one of these verbs as a target verb (36 each for OV and SV sentences). We made 72 anomalous sentences from these normal sentences, exchanging vt and vi for the corresponding NPs (36 each for OV and SV sentences). For each of normal and anomalous sentences, we tested two different subliminal verbs, corresponding to either the Cong or Incong condition (see Fig. 3.1a). For each of four stimulus conditions (i.e., OV-Cong, SV-Cong, OV-Incong, and SV-Incong), there were thus 72 combinations for the set of an NP, a subliminal verb, and a target verb. As a control used for behavioral analyses alone, the same NP of a sentence was presented again for 34 ms, instead of a subliminal verb following the forward mask, as a *subliminal NP*. There were 144 possible combinations for the set of an NP, a masked subliminal NP, and a target verb (72 each for normal and anomalous sentences); we randomly chose 72 combinations for each participant. Each of these different combinations with subliminal stimuli (verb or NP) was tested only once for each participant.

Stimulus presentation and behavioral data collection were controlled using the Presentation software (Neurobehavioral Systems Inc., Albany, CA) and an NI-DAQ interface board (National Instruments, Austin, TX). Visual stimuli in gray against a dark background were projected with a refresh rate at 60 Hz (i.e., 16.67 ms for one video frame) from outside of the shield room onto the translucent screen within the visual angle of 5.7°, using a Digital Light Processing projector (TDP-EX20J; Toshiba, Tokyo, Japan) equipped with a projection lens (modified by NewOpto, Tokyo, Japan). For fixation to minimize eye movements, a red cross was always shown at the center of the screen, and the participants were instructed to refrain from blinking before the response.

3.2.3. Tasks

Native Japanese speakers judged the grammaticality of two-word sentences, i.e., an NP with a case marker and a target verb (Fig. 3.1b). The participants were instructed to respond to the target verb by pressing one of two buttons (right or left) as quickly as possible by using a right hand alone. Assignments of the two buttons for the judgment of sentences as normal or anomalous were counterbalanced across participants. This syntactic decision task, *per se*, was designed in the same way as in the experiment 1. The syntactic decision task could not be solved on the basis of the lexico-semantic relationship between a noun and a target verb, as it was always correct as explained above.

In each of four MEG runs tested in one day for a participant, there were 90 trials with either subliminal verb or NP. Each of the four stimulus conditions (i.e., OV-Cong, SV-Cong, OV-Incong, and SV-Incong) consisted of 72 trials for each of the 15 participants, resulting in 1080 observations per stimulus condition for an entire experiment. For all participants, the orders of sentence structures (OV or SV), congruency, and grammaticality were fully randomized and counterbalanced. Only trials with participants' correct responses were used for analyzing RTs and MEG data.

3.2.4. Pilot study for determining an appropriate interval of subliminal stimuli

In order to test whether the participants were actually unaware of a subliminal verb for 34 ms, we performed another pilot study with a forced-choice recognition task, thereby varying the interval of a masked verb (first verb) (Fig. 3.1c). We made the stimulus presentation of each trial identical to that in the syntactic decision task, using the same set of 288 combinations for the set of an NP, a masked first verb, and a second verb, except that two verbs were presented as a choice stimulus, which remained on the screen until the participant responded. In each trial, participants chose which of the two verbs had actually appeared as the first verb, simply neglecting the NP or second verb. The participants were explicitly informed of the presence of a first verb even when it was too short to recognize. For each choice stimulus, a distractor was taken from the particular vt-vi pair of the first verb (Table 3.1). There were two runs, in which we used a fixed refresh rate of the Digital Light Processing projector (one with 60 Hz, and the other with 75 Hz). For the refresh rate at 60 Hz (i.e., 16.67 ms for one video frame), we randomly tested three intervals of the first verb (17, 34, or 50 ms set with the Presentation software); for the refresh rate at 75 Hz (i.e., 13.33 ms for one video frame), we also randomly tested three intervals of the first verb (14, 27, or 40 ms). We calculated *d*', i.e., the discriminability of stimuli, from each participant's hit and false-alarm rates.

3.2.5. MEG and MRI data acquisition

The 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. This bandwidth was set according to the Nyquist sampling theorem. At the time of setting up the MEG system, there was no salient noise just below 2000 Hz that might cause aliasing in our target frequency of 2-30 Hz. We basically followed the same procedures described in our previous studies (Iijima *et al.*, 2009; Inubushi *et al.*, 2012). Using the BESA 5.2 software (BESA, Gräfelfing, Germany), the MEG signals evoked by a target verb from –100 to +400 ms were analyzed. The signals from –100 to 0 ms were used as a baseline, which was within the period of presenting the backward mask (see Fig. 3.1b). Only artifact-free trials (peak-to-peak amplitude < 2500 fT) with participants' correct responses were averaged under each condition, and the averaged MEG signals were band-pass filtered from 2 to 30 Hz to eliminate large eye movement noises. Artifact-free trials with participants' correct responses were about 85% of observations, which were not significantly different across conditions ($P > 0.9$).

For mapping with the individual brain, high resolution T1-weighted MR images (repetition time, 8.4 ms; echo time, 2.6 ms; flip angle, 25°; field of view, 256×256 mm^2; resolution, $1 \times 1 \times 1$ mm^3) were acquired using a 3.0-T Scanner (Signa HDxt; GE Healthcare, Milwaukee, WI). The sensor positions for each of four runs were realigned with five fiducial markers (small coils) on the head surface, and coregistered with a least-squares fit algorithm to the MR images (MEG Laboratory; Yokogawa Electric Corporation, Kanazawa-city, Japan); we attached MR markers (alfacalcidol beads; diameter: 3 mm) at the same positions as the fiducial markers. Using BrainVoyager QX 1.8 software (Brain Innovation, Maastricht, Netherlands), each individual brain was normalized to the image of the Montreal Neurological Institute 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 partitioned into 3445 cortical patches with a mean distance of 5.6 mm (Kriegeskorte and Goebel, 2001). We confirmed that cortical patches were appropriately created in both lateral and medial regions. Using the transformation matrix for normalization, the cortical patches on the standard brain were inversely transformed into the individual space for each participant, and were used for the cortex-based data analysis.

3.2.6. MEG data analyses

An overview of MEG data analyses is as follows; we first estimated current dipoles in the individual space, and then compared cortical currents between two specified conditions. For each of temporal bins, we used a cluster permutation test (Maris and Oostenveld, 2007) to calculate each cluster's *P*-values among the spatially distributed clusters. Across temporal bins, we further corrected each cluster's *P*-values using the false discovery rate (Benjamini and Hochberg, 1995).

For each participant, the distribution of cortical activation underlying the MEG signals, which were averaged among all correct trials under each condition, was modeled with the minimum norm estimates of currents using BESA 5.2. A current dipole was perpendicularly placed at each center of the 3445 transformed cortical patches, approximating any spatial distributions of currents on the cortex, but assuming neither the number of dipoles nor starting positions for the dipole fitting (Dale and Sereno, 1993; Hämäläinen *et al.*, 1993). The locations of current dipoles of each participant were then transformed back to the Talairach space, enabling averaging across participants. After the estimation of current dipoles, the following analyses were performed on MATLAB (http://www.mathworks.com/products/matlab). The current density at each cortical patch was obtained by dividing the strength of each current dipole by the mean area of the cortical patches. The current density at each cortical patch was averaged for a bin of 20 ms; the temporal bin was slid in 10 ms steps over the

0-400 ms period after the onset of a target verb, resulting in 39 temporal bins. We have adopted the same procedures for temporal bins in our previous studies (Iijima *et al.*, 2009; Inubushi *et al.*, 2012).

We first reduced search spaces by excluding noisy cortical patches with a universal, no-biased mask, consisting of a set of patches, in which the current density averaged across temporal bins was larger than the mean baseline under all of the four conditions (paired t-tests; uncorrected $P < 0.001$). For each of temporal bins, we then compared cortical currents between two specified conditions, using the cluster permutation test (Maris and Oostenveld, 2007). For the current density of each cortical patch, we performed a paired t-test between two specified conditions, and selected all patches whose absolute t-values were larger than the threshold of $t = 3.8$ ($Z = 3.3$, uncorrected $P = 0.001$). We clustered the selected patches into multiple sets on the basis of spatial adjacency (7 mm), and took the sum of t-values (absolute values) as a representative index for each cluster. The statistical significance of observing a cluster was first corrected for multiple comparisons across the whole brain. For all cortical patches, the current density was exchanged between the two conditions in some of the 15 participants, and the t-values were recalculated, followed by clustering patches again. The largest sum of the t-values was then determined among the clusters for each new permutation. There were $2^{15} = 32{,}768$ permutations, which produced a reference distribution of the sum of t-values for determining each cluster's P-values.

Next, each cluster's P-values were further corrected for multiple comparisons across temporal bins using the false discovery rate based on the Benjamini-Hochberg procedure (Benjamini and Hochberg, 1995). Through these two steps, we corrected each cluster's P-values across both spatial and temporal domains ($P_{\mathrm{corr}} \leq 0.05$); this method is similar to that in a previous MEG study (Brennan and Pylkkänen, 2012). In the present study, we defined regions of interest (ROIs) as the resultant significant clusters, in which the magnitude of the current density for each temporal bin was averaged, as shown in line graphs and histograms. To visualize a cluster with significant *P*-values, color spheres (7 mm in diameter) were placed on cortical patches. Using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8) on MATLAB, these spheres were spatially filtered with a Gaussian (full width at half maximum, 7 mm) and superimposed onto the transformed standard brain with MRIcron (http://www.cabiatl.com/mricro/mricron/index.html).

3.2.7. Partial Granger causality analyses

By using Granger causality analyses (Geweke, 1982; Granger, 1969), we further examined which pairs of two ROIs had significant causality for a specified time window. Among the four ROIs that we selected, there were 12 possible *causal influences*, e.g., from a ROI *X* to a ROI *Y*. According to the standard Granger causality, a variable *x* (a time series of the ROI *X*) “Granger-causes” a variable *y* (a time series of the ROI *Y*), if information in the past of *x* (with specified time-lags) helps predict the future of *y* with better accuracy than is possible when considering only information in the past of *y* itself. Partial Granger causality is a superior extension of the standard Granger causality, in that it takes into account causal influences of any exogenous inputs and latent variables (Barrett *et al.*, 2010; Guo *et al.*, 2008). This method is suitable for our present study, because it can adequately examine multiple ROIs that may receive exogenous common inputs under all conditions. Under each condition, the time series data of the current density without binning were averaged within each ROI for every participant, and the results were divided into three periods of 100 ms, starting from the first significant responses (70 ms) after the target verb onsets. For this averaging, we considered only the magnitude of the current density at each cortical patch, since the orientation of a dipole was fixed perpendicularly in a similar direction for adjacent patches in a ROI. The use of 100-ms periods would be suitable for examining cortico-cortical interactions, since these periods have been used for Granger causality analyses in various human systems (Lou *et al.*, 2011; Ploner *et al.*, 2009).

Using a MATLAB Toolbox called GCCA (Granger Causality Connectivity Analysis) (Seth, 2010), we removed the linear trends from the time series data by the function cca_detrend. Non-stationarities due to variation of the mean during each period were further removed by subtracting the ensemble mean for each period and across participants. The variation among the participants was further removed by dividing each standard deviation by the ensemble standard deviation. These steps were performed by the function cca_rm_ensemblemean. The non-stationarities of the resultant data were not statistically significant ($P > 0.05$) in the previously proposed test (Kwiatkowski *et al.*, 1992), implemented by the function cca_kpss_mtrial.

Using the time series data of 15 participants, regarded as 15 repetitions, a partial Granger causality for each causal influence was calculated by the function cca_partialgc_doi_permute. A model order, i.e., the number of time-lags used in a multivariate autoregressive model, was specified by the function cca_find_model_order_mtrial, using Akaike information criterion (Akaike, 1974). The range of a model order was first set between 10-20 ms as used previously (Gaillard *et al.*, 2009; Gow, Jr. *et al.*, 2008), and the resultant optimal model order was between 10 and 14.5 ms. This time range is consistent with the latency of cortico-cortical evoked potentials from the parietal regions to the frontal regions (Matsumoto *et al.*, 2012). The significance level or P-value of a partial Granger causality was then determined with a permutation test for each window and stimulus condition. The time series data were divided into bins of 20 ms, which should be longer than the optimal model order, and these bins from multiple participants were permutated randomly and independently for each ROI. For each of 2000 new permutations, a partial Granger causality was then recalculated to produce a reference distribution of partial Granger causalities. Next, the P-values of partial Granger causalities were further corrected for multiple comparisons across 12 causal influences using the false discovery rate based on the Benjamini-Hochberg procedure ($P_{\mathrm{corr}} \leq 0.05$). Because the statistical thresholds of partial Granger causalities were different for windows and stimulus conditions, we presented each normalized partial Granger causality with the division of its own threshold (i.e., significant if normalized partial Granger causality ≥ 1.0). For the 12 causal influences, we further examined the differences in causalities between two specified stimulus conditions, where the P-value of a difference was determined with the permutation tests as explained above. For each pair of i-th permutations ($i = 1, 2, ..., 2000$) for the two conditions, a *difference* in causalities was calculated to produce a reference distribution of differences in causalities. These P-values were also corrected for multiple comparisons across 12 causal influences ($P_{\mathrm{corr}} \leq 0.05$).

3.3. Results

3.3.1. Assessment of the visibility of masked stimuli

In the pilot study with the forced-choice recognition task, we assessed the visibility of a first verb by varying the interval of this masked stimulus itself (Fig. 3.1c). Among the intervals of 50, 40, 34, 27, 17, and 14 ms, the mean d' data for the 50 and 40 ms intervals were significantly different from zero (Bonferroni-corrected) [50 ms: d' (mean ± SEM) = 0.78 ± 0.12, $t_{(9)} = 6.4$, $P_{\mathrm{corr}} = 0.0008$; 40 ms: $d' = 0.40 \pm 0.10$, $t_{(9)} = 4.0$, $P_{\mathrm{corr}} = 0.02$] (Fig. 3.2a), indicating that the first verb was clearly visible to the participants. In contrast, the mean d' data for the other intervals were not significantly

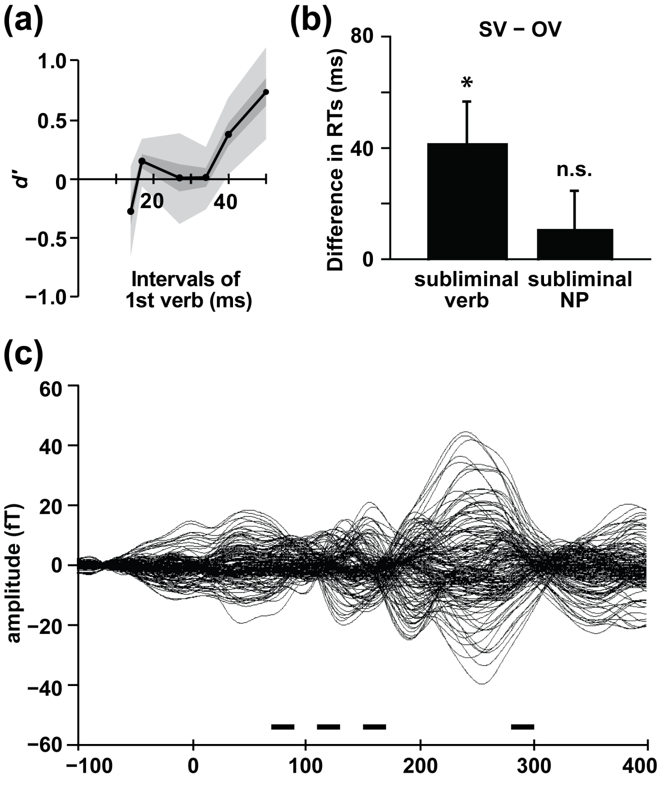


Fig. 3.2. Behavioral results and MEG signals. **(a)** Results of the forced-choice recognition task. The discriminability of stimuli (*d*’) is shown against various intervals of the first verb. The SEMs and 95% confidence intervals (Bonferroni-corrected) are shown in the lighter and lightest shades, respectively (n = 10). The results showed that subliminal verbs of 34 ms were too short to be seen. **(b)** Interference from a subliminal verb for the SV sentences in the syntactic decision task. The histograms show the differences in RTs obtained by subtracting RTs for the OV sentences from those for the SV sentences (mean ± SEM, n = 15). A significantly larger difference in RTs for a subliminal verb, but not for a subliminal NP, was observed. An asterisk denotes a significant difference ($P \leq 0.05$, paired *t*-test). **(c)** The averaged MEG signals for all artifact-free and correct trials from 15 participants, shown for each sensor. The black bars below the waveforms indicate the temporal bins, where significant responses were observed in the contrasts shown in Figure 3.

different [34 ms: $d' = 0.020 \pm 0.083$, $t_{(9)} = 0.24$, $P_{\text{corr}} > 0.9$; 27 ms: $d' = 0.016 \pm 0.12$, $t_{(9)} = 0.13$, $P_{\text{corr}} > 0.9$; 17 ms: $d' = 0.16 \pm 0.062$, $t_{(9)} = 2.6$, $P_{\text{corr}} = 0.2$; 14 ms: $d' = -0.28 \pm 0.12$, $t_{(9)} = 2.4$, $P_{\text{corr}} = 0.3$]. For the MEG experiments, we thus chose the longest interval of 34 ms for subliminal stimuli (verb or NP) of which the participants were unaware, so that the presence of a subliminal verb was long enough to affect syntactic decisions.

In order to confirm that the participants were indeed unaware of the subliminal verbs, two additional examinations were performed *after* the MEG recordings. First, the participants were notified that a subliminal verb actually appeared between an NP and a target verb, and asked if they were aware of any subliminal verbs or not. Only one participant reported that he was aware of the existence of subliminal verbs at all during the MEG experiments; this participant was thus excluded from the behavioral and MEG data analyses. Secondly, we assessed the visibility of a first verb once more with the same forced-choice recognition task in one hundred trials, but with a fixed interval of 34 ms. Consistent with the other participants' reports, the mean d' for the first verb was not significantly different from zero [$d' = 0.20 \pm 0.12$, $t_{(14)} = 1.6$, $P = 0.1$]. These results confirmed that the participants remained unconscious to subliminal verbs even after repeated exposure during the MEG experiments.

3.3.2. Behavioral results

The behavioral data are shown in Table 3.2. As regards the accuracy, there were neither significant main effects nor an interaction in a two-way rANOVA [sentence structures (OV, SV) × subliminal stimuli (verb, NP)] ($P > 0.09$). As regards RTs for the target verbs, an rANOVA showed a significant main effect of sentence

Table 3.2. Behavioral data of the syntactic decision task.

		Subliminal stimuli		Congruency for subliminal verb	
		verb	NP	Cong	Incong
OV	Accuracy (%)	89 ± 1.7	87 ± 2.1	89 ± 1.4	90 ± 2.3
	RTs (ms)	1041 ± 38	1052 ± 35	1044 ± 37	1037 ± 39
SV	Accuracy (%)	90 ± 1.8	91 ± 2.1	90 ± 1.8	90 ± 2.0
	RTs (ms)	1082 ± 47	1062 ± 35	1082 ± 44	1083 ± 51

Behavioral data (mean ± SEM) of the accuracy and reaction times (RTs) are shown for each condition performed by the 15 participants. Only correct trials were included for RTs, which were measured after the onset of target verbs.

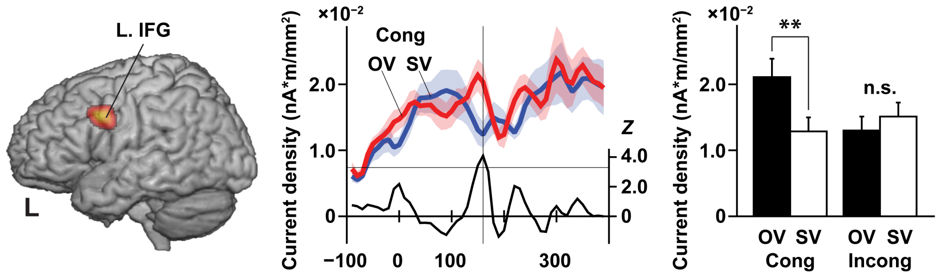
structures [$F_{(1,14)} = 5.2$, $P = 0.04$] with neither main effect of subliminal stimuli [$F_{(1,14)} = 0.073$, $P = 0.8$] nor interaction [$F_{(1,14)} = 2.7$, $P = 0.1$]. A post-hoc *t*-test revealed that subliminal verbs significantly increased the RTs for the SV sentences than those for the OV sentences [mean difference ± SEM: 41 ± 14 ms; $t(14) = 2.7$, $P = 0.02$] (Fig. 3.2b), while there was no such a difference for subliminal NPs [11 ± 14 ms: $t(14) = 0.76$, $P = 0.5$]. As regards RTs under the conditions where subliminal verbs were used, a further rANOVA [sentence structures (OV, SV) × congruency (Cong, Incong)] showed a significant main effect of sentence structures [$F(1,14) = 7.2$, $P = 0.02$] with neither main effect of congruency [$F(1,14) = 0.25$, $P = 0.6$] nor interaction [$F(1,14) = 0.19$, $P = 0.7$], confirming the interference from a subliminal verb for the SV sentences irrespective of the Cong and Incong conditions.

3.3.3. *Selectively enhanced or reduced cortical responses under the OV-Cong condition*

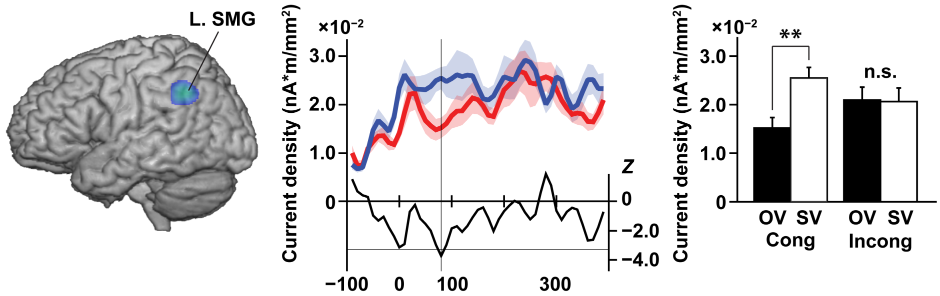
We obtained MEG signals to target verbs for 400 ms after the onsets (Fig. 3.2c), and estimated the current density of whole cortical patches under each of the four stimulus conditions. We examined the effects of sentence structures by directly comparing the OV and SV sentences. When corrected across both spatial and temporal domains, there was no significant difference between the OV and SV sentences under the Incong condition ($P_{\text{corr}} > 0.05$). Under the Cong condition, significantly enhanced responses to the OV sentences (i.e., OV > SV) were found in the left IFG [Talairach coordinates of peak voxels, $(x, y, z) = (–50, 5, 29)$; Brodmann’s areas (BAs) 44/45/6; $P_{\text{corr}} = 0.04$] at 150-170 ms (Fig. 3.3a, left panel). The temporal changes of Z-values of this comparison (positive for OV > SV) confirmed that this temporal bin and an immediately earlier temporal bin (140-160 ms) alone satisfied the selection criteria of patches ($Z > 3.3$) (Fig. 3.3a, middle panel), and that the difference of OV > SV started to appear as early as 120 ms. Under the Incong condition, in contrast, there was no significant difference between the OV and SV sentences in this temporal bin ($t_{(14)} = –0.73$, $P = 0.5$) (Fig. 3.3a, right panel).

We observed significantly *reduced* responses to the OV sentences (i.e., OV < SV) in the left SMG [(–45, –55, 35); BAs 39/40; $P_{\text{corr}} = 0.05$] at 70-90 ms (Fig. 3.3b, left panel), as well as in the MCC [(–6, –3, 39); BA 24; $P_{\text{corr}} = 0.04$] at 280-300 ms (Fig. 3.3c, left panel). The temporal change in the MCC for an immediately earlier temporal bin (270-290 ms) also satisfied the selection criteria of patches ($Z < –3.3$), and the difference of OV < SV started to appear as early as 250 ms (Fig. 3.3c, middle panel), indicating that this later response is reliable. Under the Incong condition, in contrast,

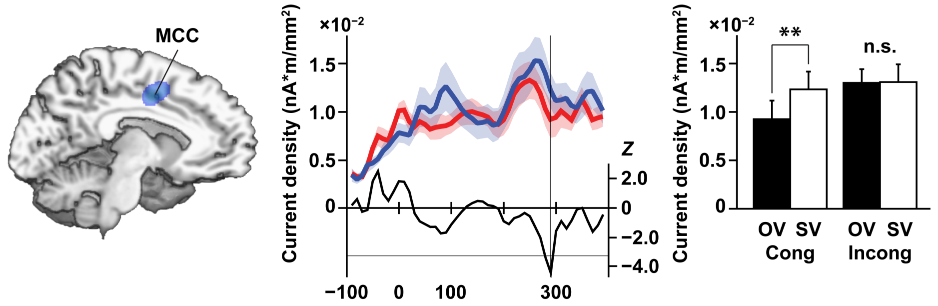
(a) OV > SV, Cong (150-170 ms)



(b) OV < SV, Cong (70-90 ms)



(c) OV < SV, Cong (280-300 ms)



(d) SV > OV, Cong (110-130 ms)

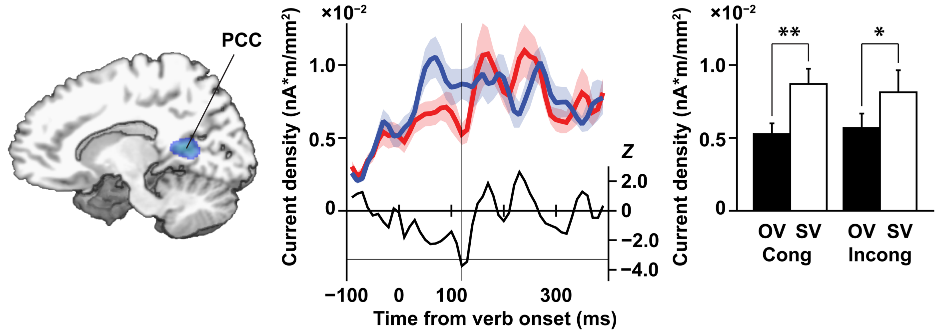


Fig. 3.3 Cortical responses with significant differences between the OV and SV sentences under the Cong condition. The left panels show *t*-maps on the transformed standard brain ($P_{\mathrm{corr}} \leq 0.05$). The middle panels show temporal changes of the current density under the Cong condition, averaged within each significant cluster. The red and blue line graphs show the current density for OV and SV sentences, respectively (mean ± SEM, $n = 15$). The black line graphs plotted for each temporal bin show temporal changes of Z values of this comparison (positive for OV > SV). The horizontal black lines at $Z = \pm 3.3$ denote the selection criteria of patches (uncorrected $P = 0.001$, paired *t*-test), and the vertical black lines denote temporal bins, when significant responses were observed. The right panels show histograms for the current density under each of four stimulus conditions (i.e., OV-Cong, SV-Cong, OV-Incong, and SV-Incong). **(a)** Significantly enhanced responses to the OV sentences observed in the left inferior frontal gyrus (L. IFG) at 150-170 ms. **(b, c)** Significantly reduced responses to the OV sentences observed in other regions: the left supramarginal gyrus (L. SMG) at 70-90 ms (b), midcingulate cortex (MCC) ($x = -6$) at 280-300 ms (c). **(d)** Significantly enhanced responses to the SV sentences observed in the posterior cingulate cortex (PCC) ($x = 11$) at 110-130 ms under both the Cong and Incong conditions. A double asterisk (**) indicates a significant difference corrected across both spatial and temporal domains ($P_{\mathrm{corr}} \leq 0.05$). A single asterisk (*) indicates a significant difference in each region by paired *t*-test ($P \leq 0.05$).

there was no significant difference between the OV and SV sentences in these temporal bins (left SMG: $t_{(14)} = 0.093$, $P = 0.9$; MCC: $t_{(14)} = –0.055$, $P > 0.9$) (Fig. 3.3b-c, right panels).

Consistent with the longer RTs for the SV sentences, enhanced responses to the SV sentences (i.e., SV > OV) were observed in the posterior cingulate cortex (PCC) [(11, –49, 9); BAs 29/30; $P_{\mathrm{corr}} = 0.05$] at 110-130 ms (Fig. 3.3d, left panel), which was significant under the Cong condition, as well as under the Incong condition ($t_{(14)} = –2.1$, $P = 0.05$) (Fig. 3.3d, right panel). The temporal changes of Z-values in this region confirmed that this temporal bin and an immediately later temporal bin (120-140 ms) alone satisfied the selection criteria of patches ($Z < –3.3$) (Fig. 3.3d, middle panel). These results indicate differential roles between the left IFG and the multiple regions of the left SMG, MCC, and PCC.

3.3.4. Selectively increased partial Granger causalities under the OV-Cong condition

By using the partial Granger causality analyses, we examined which causal influences among these four regions were significantly enhanced under the OV-Cong condition. For the pair of the left IFG and MCC, we found significant differences in causalities for the OV > SV contrast at 70-170 ms (from the MCC to the left IFG: $P_{\mathrm{corr}} = 0.02$; from the left IFG to the MCC: $P_{\mathrm{corr}} = 0.04$) (Fig. 3.4a). Under the OV-Cong condition, the normalized partial Granger causality was significant from the MCC to the left IFG (normalized partial Granger causality = 4.6, $P_{\mathrm{corr}} = 0.02$), as well as from the left IFG to the MCC (normalized partial Granger causality = 2.3, $P_{\mathrm{corr}} = 0.02$) (Fig. 3.4b). At 170-270 ms, in contrast, we found a significant difference in causalities for the OV > SV contrast from the left IFG to the left SMG ($P_{\mathrm{corr}} = 0.002$) (Fig. 3.4c). Under

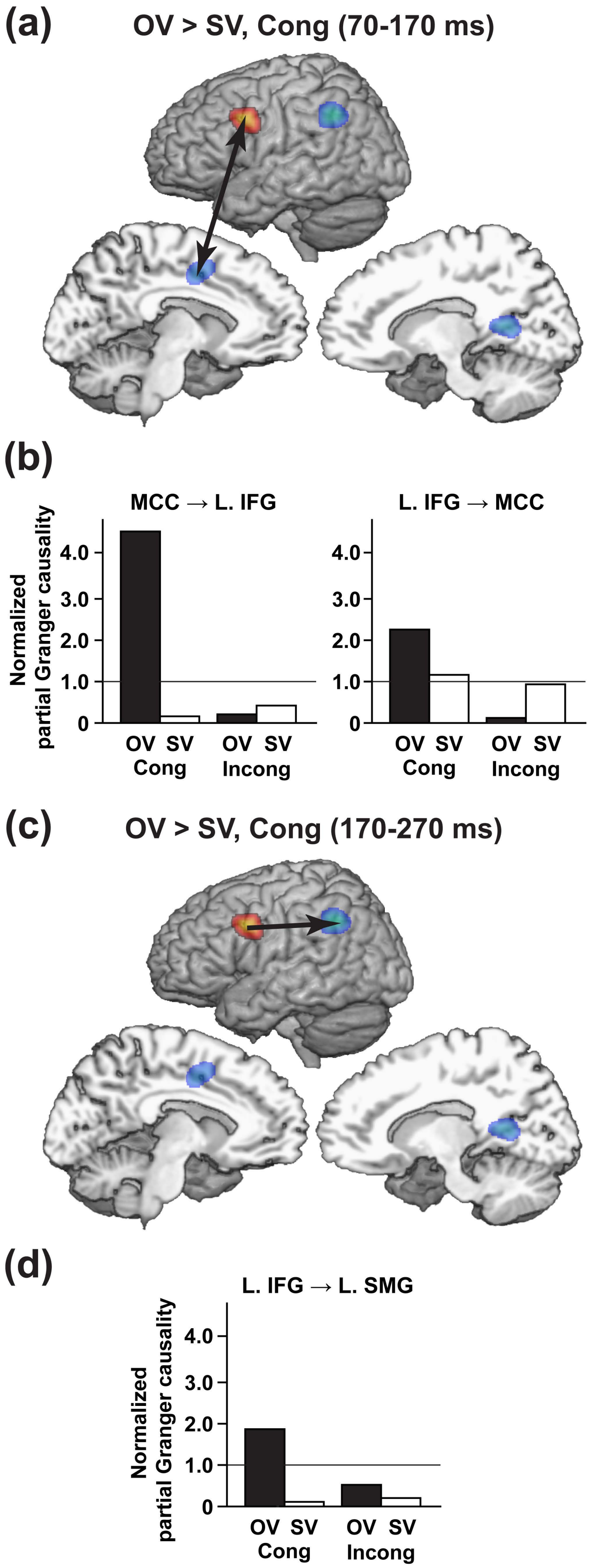


Fig. 3.4. Increased partial Granger causalities under the OV-Cong condition. For the OV > SV contrast under the Cong condition, significant differences in causalities ($P_{corr} \leq 0.05$, false discovery rate) are schematically shown with arrows on the standard brain with ROIs, which were selected from the results of Figure 3.3. **(a)** Causal influences between the L. IFG and MCC at 70-170 ms. **(b)** Histograms for the normalized partial Granger causalities of both directions shown in (a). **(c)** Causal influence from the L. IFG to the L. SMG at 170-270 ms. **(d)** Histograms for the normalized partial Granger causalities of the direction shown in (c). Horizontal lines at 1.0 in the histograms denote the significance level for normalized partial Granger causalities ($P_{corr} = 0.05$, false discovery rate).

the OV-Cong condition, the normalized partial Granger causality was significant from the left IFG to the left SMG (normalized partial Granger causality = 1.9, $P_{\mathrm{corr}} = 0.002$) (Fig. 3.4d). At 270-370 ms, there was no significant difference in causalities between OV and SV. The bidirectional interactions between the left IFG and MCC, as well as a top-down effect from the left IFG to the left SMG, indicate information flows during the syntactic decision task at their specific timings.

3.4. Discussion

In the present study, we obtained the following results. In the contrast between OV and SV sentences under the Cong condition, we observed significantly enhanced left IFG responses at 150-170 ms after the target verb onset (Fig. 3.3a). In contrast, cortical responses in the left SMG at 70-90 ms and those in the MCC at 280-300 ms were significantly *reduced* under the OV-Cong condition (Fig. 3.3b, c). Moreover, the PCC responses at 110-130 ms were significantly enhanced under both the SV-Cong and SV-Incong conditions (Fig. 3.3d), consistent with the behavioral results (Fig. 3.2b). Finally, by using the partial Granger causality analyses, we revealed a bidirectional interaction between the left IFG and MCC at 70-170 ms (Fig. 3.4a, b), as well as a top-down effect from the left IFG to the left SMG at 170-270 ms (Fig. 3.4c, d). These results suggest a pivotal role of the left IFG among these multiple regions during syntactic decisions.

The left SMG has been implicated in lexical processing (Lee *et al.*, 2007; Ohta *et al.*, 2013; Pattamadilok *et al.*, 2010). In the present study, we observed reduced left SMG responses under the OV-Cong condition at 70-90 ms, together with a top-down effect from the left IFG to the left SMG at 170-270 ms. Since the transitivity of target verbs matched that of the subliminal verbs under the Cong condition, early bottom-up processing of verb types, but not that of the exact words, would be reduced, leading to the reduced left SMG responses at 70-90 ms. Using MEG, it has been shown that the left SMG responses, as well as the left IFG responses, were observed around 100 ms after the visual word onset during a word detection task (Pammer *et al.*, 2004). Moreover, event-related TMS pulses selectively inhibited homophone judgments, when the TMS pulses to the left SMG were administrated as early as 80 ms after the visual word onset (Sliwinska *et al.*, 2012). These previous studies are consistent with the present study regarding early reduction in the left SMG, supporting the interactive model of the visual word processing with the higher-order regions (Carreiras *et al.*, 2014). After the enhancement of predictive effects in the left IFG at 150-170 ms, lexical processing would be resumed in the left SMG at 170-270 ms by checking the transitivity of target verbs against associated argument structures in a top-down manner. Such a top-down information flow is consistent with our recent fMRI study, which showed the top-down connection from the left IFG to the left SMG by dynamic causal modeling (Ohta *et al.*, 2013). Our present results further suggest that lexical processing has two stages, one occurring before and the other after syntactic processing. On the other hand, in the present study, we observed no response in the middle temporal gyrus (MTG), which might be involved in lexical processing. Our previous fMRI study suggested that the left MTG was involved in either syntactic or lexico-semantic anomaly (Suzuki and Sakai, 2003).

In the MCC, we observed the bidirectional interaction with the left IFG at 70-170 ms, together with the reduced responses under the OV-Cong condition at 280-300 ms. Previous studies have suggested that the medial prefrontal regions, including the

MCC and the adjacent dorsal anterior cingulate cortex, are involved in task-set formations (Dosenbach *et al.*, 2006; Hyafil *et al.*, 2009). In these studies, task sets were defined as “context-appropriate stimulus-responses relationships.” In the present study, the task sets for syntactic decisions were the relationships between the transitivity of the target verb and the grammaticality of the sentence. Under the OV-Cong condition, task-set formations would be facilitated, since the transitivity of subliminal verbs could already specify the task sets for final responses. Such facilitation would be realized by the bidirectional interaction between the left IFG and MCC. This time window includes that of the enhanced left IFG responses at 150-170 ms, consistent with the involvement of the left IFG. As a result of this task-set formation for syntactic decisions, the later MCC responses at 280-300 ms would thus be reduced. While band-pass filtering in the present study removed information of the gamma band (above 30 Hz), some recent studies revealed the important role of the beta band (13-30 Hz) in language processing (Weiss and Mueller, 2012). Another potential concern is that any spatial spread of the MEG field might produce spurious causal influences among multiple regions. Based on simulated data, it has been recommended to perform causality analyses on estimated cortical currents, but not on signals of MEG sensors, and to contrast two conditions to cancel out general effects of field spread (Schoffelen and Gross, 2009; Gross *et al.*, 2013); our procedures followed this recommendation.

In contrast to the left SMG and MCC, the PCC showed significantly enhanced responses to the SV sentences under the Cong and Incong conditions. This enhancement is consistent with the longer RTs under the SV sentence conditions where subliminal verbs were used (Fig. 3.2b). It has been proposed that the PCC is recruited in decision making under uncertainty (Pearson *et al.*, 2011). Moreover, it has been recently reported that perceptual guessing under uncertainty enhanced activations in the PCC and adjacent precuneus (Bode *et al.*, 2013). In the present study with the SV sentences, the interference due to the duplicated determination of the transitivity from a presented stimulus may cause decision conflicts, leading to the PCC enhancement and then the longer RTs. The PCC responses, as well as the MCC responses, were optimal solutions and located in the medial wall of the brain. Based on simulated data with minimum norm estimates, the peak of estimated currents was shown to be the true deep source in the medial plane, even when the deep sources tended to be estimated in widespread regions (Hauk, 2004).

4. General Discussion

In the experiment 1, using MEG with the minimal-pair paradigm to compare the syntactic and semantic tasks, we found that the responses to the normal OV sentences in the left IFG at 120-140 ms were selective for explicit syntactic processing. The earliest left IFG 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, it was revealed that 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 processing of each next-coming word, which is crucial during on-line sentence processing.

The experiment 1 revealed enhanced left IFG responses at 120-140 ms after the verb onset of the OV sentences, indicating predictive effects during syntactic processing (Iijima *et al.*, 2009). In the experiment 2, we observed the enhanced left IFG responses (more dorsoposterior) at 150-170 ms after the target verb onset of the OV sentences, which would be regarded as predictive effects if certain spatial and temporal variations are considered. The results of the experiment 2 further showed that subliminal verbs under the Cong condition indeed enhanced the left IFG responses to the OV sentences. The predictive effects can be regarded as fast, because these effects were observed in the left IFG responses as soon as a target verb appeared. The effects are also unconscious, because a subliminal verb under the OV-Cong condition indeed enhanced the left IFG responses (see Fig. 3.3a). The effects would be regarded as obligatory, because these effects were caused by a preceding object, i.e., in a stimulus-driven manner, if only a target verb was congruent with the subliminal verb. Moreover, these effects were independent both from the transitivity of target verbs and from the grammaticality of sentences (normal or anomalous), i.e., in a goal-independent manner. These fast, unconscious, and obligatory features support the automaticity of the predictive effects observed here (Moors and De Houwer, 2006).

Our previous TMS study showed that event-related TMS pulses selectively facilitated syntactic decisions for OV sentences, only when the TMS pulses to the left IFG were administrated at 150 ms after the verb onset, i.e., also at 150 ms after the *offset* of the preceding NP in that study (Sakai *et al.*, 2002). It is possible that the TMS pulses temporarily raised the overall excitability of neurons, thereby creating a “stand-by” state in the left IFG, which leads to more effective activation when specific responses of those cells are required for syntactic decisions (Sakai *et al.*, 2003). This timing is consistent with that of our present study, in which subliminal verbs were presented at more than 100 ms after the offset of the preceding NP (see Fig. 3.1b). These results suggest that the automatic predictive effects in the left IFG were closely related to the prior state of this region.

The results of the partial Granger causality analyses in the experiment 2 indicate that subliminal enhancement of predictive effects is related to at least two steps: (1) making task sets for syntactic decisions, and (2) integrating syntactic information with lexical information. The elucidation of this two-step process highlights the dynamic interactions among these identified regions, in which the left IFG acts to relay the information necessary for its automatic and predictive processes, and extends our knowledge of sentence processing.

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