博士論文

論文題目　Functional Anatomy of the Left Frontal Cortex
for Structure-dependent Sentence Processing
in Vocal and Sign Languages
(音声言語および手話言語の構造依存的文処理に対する
左前頭皮質の機能解剖学)

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Doctoral thesis

Functional Anatomy of the Left Frontal Cortex for Structure-dependent Sentence Processing in Vocal and Sign Languages

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List of Abbreviations

Abbreviations	Meanings
3D FSPGR	three-dimensional fast spoiled gradient-echo
a	anterior
Acc	accusative case
AC-PC line	anterior to posterior commissure line
AD order	accusative before dative order
AG	angular gyrus
AOA	age of acquisition
ASL	American Sign Language
BA	Brodmann’s area
C	canonical word order
CODA	children of Deaf adults
DA order	dative before accusative order
DARTEL	Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra
Dat	dative case
Disc task	discourse-level decision task
DOE	duration of exposure
EPI	echo-planar imaging
F3O	pars orbitalis of the inferior frontal gyrus
F3op/F3t	pars opercularis and triangularis of the inferior frontal gyrus
FA	flip angle
FDR	false discovery rate
(f)MRI	(functional) magnetic resonance imaging
FOV	field of view
(f)ROI	(functional) region of interest
FWHM	full width of half maximum
GM	gray matter
ICBM	International Consortium for Brain Mapping
ISI	inter-stimulus interval
ITG	inferior temporal gyrus
JPN	Japanese
JSL	Japanese Sign Language
Loc	locative case
LPMC	lateral premotor cortex
LQ	laterality quotients
MEG	magnetoencephalography
MNE	minimum norm estimate

Abbreviations	Meanings
MNI	Montreal Neurological Institute
MTG	middle temporal gyrus
N	noncanonical word order
Nom	nominative case
NP	noun phrase
Num	total number of probes or other stimuli in each task
p	posterior
P^+ sentence	sentence with a possessor
P^- sentence	sentence without a possessor
PreCG/PostCG	precentral gyrus and postcentral gyrus
pre-SMA	pre-supplementary motor area
R task	repetition task
rANOVA	repeated measures analysis of variance
RT	reaction time
SEM	standard error of the mean
Sent task	sentence-level decision task
SMG	supramarginal gyrus
STG	superior temporal gyrus
TE	echo time
TMS	transcranial magnetic stimulation
TR	repetition time
TRW	temporal receptive window
V	verb
V’	V-bar
VBM	voxel-based morphometry
VP	verb phrase
Word task	word-level decision task

CHAPTER 1.
General Introduction

Language is one of the essential human abilities, which forms a foundation of our communication and thinking. The most notable and unique characteristic of language is its combinatorial process of syntax, with which multiple words are combined into structurally complex constituents (Chomsky, 1965; Jackendoff, 2002). This process enables us to produce an infinite variety of expressions from our limited lexicon. The investigation of neuro-anatomical bases of structure-dependent sentence processing can thus contribute to deep understanding of the core property of the human mind. Accumulated evidence from recent lesion and neuroimaging studies has shown that the pars opercularis and triangularis of the left inferior frontal gyrus (F3op/F3t, Brodmann's areas (BAs) 44/45) are selectively involved in syntactic processing (Indefrey et al., 2001; Musso et al., 2003; Suzuki and Sakai, 2003; Kinno et al., 2009; Ohta et al., 2013). On the other hand, the neural relationships between syntax and other linguistic factors, such as semantic information of sentences and lexical/contextual information, still remain unclear. It is thus important to clarify how syntactic and other linguistic processes are temporally and spatially integrated in the left frontal cortex.

For this purpose, I investigated the functional anatomy of the left frontal cortex for structure-dependent sentence processing from two different directions of research. First, I examined temporal dynamics of the left Fop/F3t responses for syntactic processing, which was influenced by accompanying semantic processes of sentences (Inubushi et al., 2012). Using magnetoencephalography (MEG), I measured cortical responses during a syntactic decision task, and examined the effect of word orders in two semantically different types of sentences. The MEG methods have a high temporal resolution of 10 ~ 20 ms, suitable for temporal dynamics of cortical responses. Second, I investigated spatial localizations of functional and anatomical correlates of word-, sentence-, and discourse-level integration within the left frontal cortex (Inubushi and Sakai, 2013). Using functional magnetic resonance imaging (fMRI) and voxel-based morphometry (VBM), I investigated functional organization of the left frontal cortex for different levels of linguistic integration in a sign language, and I further examined correlations between the individual task performances and regional gray matter (GM) volumes. The MRI and fMRI methods have a high spatial resolution of 1 ~ 3 mm, suitable for spatial localization of the brain functions.

CHAPTER 2.

Left Inferior Frontal Activations Depending on the Canonicity Determined by the Argument Structures of Ditransitive Sentences: An MEG Study

2.1. Introduction

The ability to embed phrases within phrases and to construct hierarchical sentence structures has been proposed to be a fundamental property of language faculty that is unique to humans (Chomsky, 1965). This ability based on syntactic knowledge enables humans to utilize the expressive and creative power of language. Recent fMRI studies have shown that processing syntactic structures of sentences significantly elicits localized activation in the brain. To contrast sentences with canonical (i.e., typical) and noncanonical word orders has been one effective paradigm for further elucidating syntactic processes (Ben-Shachar et al., 2004; Bornkessel et al., 2005; Fiebach et al., 2005; Bahlmann et al., 2007; Kinno et al., 2008). Using sentences in German, Hebrew, and Japanese, larger responses to sentences with noncanonical word orders have been reported in some cortical regions including the left F3op/F3t, left lateral premotor cortex (LPMC, the lateral side of BAs 6/8), and left posterior middle/superior temporal gyrus (pMTG/STG, BAs 21/22). Recent lesion studies have also demonstrated that patients with a lesion in the left F3op/F3t showed profound deficits in the comprehension of noncanonical sentences (Kinno et al., 2009; Wilson et al., 2010). On the other hand, it has been reported that the change in word orders for the animacy of arguments affects the left F3op/F3t activation (Grewe et al., 2006). It should be then clarified how the syntactic processes of sentences are actually influenced by the animacy itself, together with any other semantic factors that may affect syntactic features (e.g., possessor/benefactive). To elucidate such underlying syntactic and semantic processes, we chose *ditransitive* sentences, each of which included a verb, as well as dative and accusative noun phrases (NPs). The syntactic structures of a ditransitive sentence can be partially determined by the argument structure of the verb, where two arguments correspond to different semantic roles of the NPs. Here we used MEG to examine more detailed temporal aspects of cortical activity.

It is interesting to note that English ditransitive sentences can be divided into two types: double object sentences (1a) and prepositional dative sentences (1b) (Bruening, 2010).

(1a) *I threw John the ball*
(1b) *I threw the ball to John*

These two types of sentences have different argument structures of the verb (*threw* in this example), which result in different sentence meanings (Green, 1974; Pinker, 1991). The argument structure of a double object sentence is [agent, possessive goal, theme], representing "*X* (agent) causes *Y* (possessive goal) to have *Z* (theme)". *Y* is the goal to which *Z* goes as the result of its movement or transfer, and at the same time *Y* should become the possessor of *Z*; *Y* is thus defined as a possessive goal. On the other hand, the argument structure of a prepositional dative sentence is [agent, locative goal, theme], representing "*X* (agent) causes *Z* (theme) to go to *Y* (locative goal)". Here, *Y* is simply the goal to which *Z* goes as the result of its movement or transfer; *Y* is thus called a locative goal. With such a different semantic role, a possessive goal has an additional privilege to have the property of the *possessor*. In summary, a possessive goal defines a sentence with a possessor (P^+) like (1a), whereas a locative goal defines a sentence without a possessor (P^-) like (1b). This point becomes clearer in the following examples.

(2a) **I threw the target the ball*

(2b) *I threw the ball to the target*

As shown in (2a, b), the inanimate noun (*the target* in this example) that cannot be a possessor makes the sentence ungrammatical in double object sentences, whereas it is allowed in prepositional dative sentences.

Another critical factor regarding the argument structures of ditransitive sentences is the order of two NPs.

(3a) **I threw the ball John*

(3b) **I threw to John the ball*

As shown in (3a, b) where (3b) has no heavy NP (Larson, 1988), scrambling the word order is not allowed in English, even if these sentences preserve the argument structures in (1a, b). One relevant hypothesis on the preference of word orders in general is the linearization of a grammatical feature or order-related factors. For example, a hierarchy of subject > direct object > indirect object > oblique (other) object (from highest to lowest), that of nominative > dative > accusative, and that of animate > inanimate have been proposed in cross-linguistic studies (Comrie, 1989). Previous fMRI studies contrasting canonical and noncanonical sentences have interpreted that an activation increase at the left F3op/F3t was due to the violation of these linearization rules (Bornkessel et al., 2005; Grewe et al., 2006). However, any theories based on such linearization alone fail to explain the word orders of (1a, b), because in (1a), an indirect object (*John*) precedes a direct object (*the ball*), while in (1b), an accusative and inanimate object (*the ball*) precedes a dative and animate object (*to John*). An alternative approach is a structural model that focuses on the syntactic structures of sentences. This model predicts that the examples of (1a, b) actually have different syntactic structures, such that the possessor/benefactive (*John*) in (1a) takes the higher position than the theme (*the ball*), while the theme (*the ball*) in (1b) is higher than the prepositional phrase (*to John*) (Larson, 1988; Marantz, 1993). Therefore, we may naturally assume that the basic structures of P^+ and P^- sentences are also different in languages other than English.

One notable difficulty here is to separate the factor of word order from the grammaticality of sentences. This problem can be resolved by using other natural languages, in which the basic features of the argument structures are universal, but scrambling is allowed. Indeed, the argument structures of Japanese ditransitive verbs are either [agent, possessive goal, theme] or [agent, locative goal, theme], where each argument is marked by nominative (Nom), dative (Dat), or accusative (Acc) case marker. Note that the dative case particle '-*ni*' is used for both sentence types (Sadakane and Koizumi, 1995), and that an agent can be a phonetically null subject (pro-drop) in Japanese, as well as in Spanish and Italian (Jaeggli, 1981).

(4a) '*yuujin-ni kagu-o ageta*'
(a word-by-word translation in English: *friend*-Dat *furniture*-Acc *gave*)
Someone gave his friend furniture
(4b) '*kagu-o nikai-ni ageta*'
(*furniture*-Acc *upper floor*-Dat *lifted*)
Someone lifted furniture to the upper floor

These two sentences are actually paired, sharing the same accusative NP (theme) and phonologically same verb ('*ageta*'), but having different meanings and argument structures. Such ditransitive verb pairs actually form a general class of verbs,

Table 1. Examples of ditransitive sentences used in the present study.

Sentence with a possessor (P^+)	Sentence without a possessor (P^-)
'*yuujin-ni kagu-o ageta*' *Someone gave his friend furniture*	'*kagu-o nikai-ni ageta*' *Someone lifted furniture to the upper floor*
'*jouren-ni sushi-o dashita*' *Someone served a regular customer sushi*	'*sushi-o syokutaku-ni dashita*'† *Someone placed sushi on the table*
'*ooya-ni yachin-o ireta*' *Someone paid the owner the house rent*	'*yachin-o kinko-ni ireta*' *Someone put the house rent into the safe*
'*chijin-ni shinsya-o kaeshita*' *Someone returned an acquaintance his new car*	'*shinsya-o syako-ni kaeshita*' *Someone returned his new car to the garage*
'*joukyaku-ni kippu-o modoshita*' *Someone returned the passenger the ticket*	'*kippu-o saifu-ni modoshita*' *Someone returned the ticket to the wallet*
'*gyousya-ni kinzoku-o nagashita*' *Someone sent the trader the metal*	'*kinzoku-o igata-ni nagashita*' *Someone poured metal into the mold*
'*shinseki-ni kozutsumi-o okutta*' *Someone sent his relative the gift*	'*kozutsumi-o yashiki-ni okutta*' *Someone sent the gift to the residence*
'*kanja-ni yakuhin-o todoketa*' *Someone sent the patient the drugs*	'*yakuhin-o byouin-ni todoketa*' *Someone delivered the drugs to the hospital*
'*zen'in-ni soubi-o tsuketa*' *Someone gave everyone the equipment*	'*soubi-o kabegiwa-ni tsuketa*' *Someone attached the equipment to the wall*
'*shinzoku-ni zaisan-o utsushita*' *Someone sent his relative property*	'*zaisan-o chika-ni utsushita*' *Someone delivered property to the basement*
'*suifu-ni kobune-o watashita*' *Someone gave the sailor a boat*	'*kobune-o taigan-ni watashita*' *Someone moved a boat to the opposite shore*
'*kouhai-ni furuhon-o yatta*' *Someone gave the junior fellow a used book*	'*furuhon-o katasumi-ni yatta*' *Someone put a used book in the corner*
'*sakusya-ni tegami-o yoseta*' *Someone sent the author letters*	'*tegami-o madogiwa-ni yoseta*' *Someone put letters near the window*

The argument structures of the verbs in the P^+ and P^- sentences are [agent, possessive goal, theme] and [agent, locative goal, theme], respectively. We omitted an agent from the stimuli, as a phonetically null subject (pro-drop) is allowed in Japanese. For each pair of P^+ and P^- sentences, as shown in each line of the Table, the same accusative NP and phonologically same verb were used. All used verbs, 26 of 100 dative NPs (always animate for P^+ and inanimate for P^-), and 13 of 50 accusative NPs (always inanimate), are shown here in the alphabetical order of Japanese verbs. †Some P^- sentences might imply the presence of a recipient, but an inanimate dative NP itself cannot become a possessor for all examples.

just like the English verb *threw* in (1a, b). We used a set of sentence stimuli (Table 1), in which each of the animate dative NPs is naturally interpreted as a possessive goal that defines a P^+ sentence like (4a), whereas each of the inanimate dative NPs is naturally interpreted as a locative goal that defines a P^- sentence like (4b). This is substantiated by the fact that English P^+ sentences become odd in meaning with addition of a sentence that implies failure of transfer: e.g., **My aunt gave my brother some money for new skis, but he never got it* (Rappaport Hovav and Levin, 2008), which is also true for Japanese P^+ sentences: e.g., '**yuujin-ni kagu-o ageta-ga, sono yuujin-wa moratte inakatta*' (**Someone gave his friend furniture, but his friend never got it*). Therefore, native

Table 2. Examples of ditransitive sentences under the four conditions.

Possessivity	Canonicity	Example
P^+ sentences	Canonical	'*yuujin-ni kagu-o ageta*' (*friend*-Dat *furniture*-Acc *gave*) *Someone gave his friend furniture*
	Noncanonical	'*kagu-o yuujin-ni ageta*' (*furniture*-Acc *friend*-Dat *gave*) *Someone gave his friend furniture*
P^- sentences	Canonical	'*kagu-o nikai-ni ageta*' (*furniture*-Acc *upper floor*-Dat *lifted*) *Someone lifted furniture to the upper floor*
	Noncanonical	'*nikai-ni kagu-o ageta*' (*upper floor*-Dat *furniture*-Acc *lifted*) *Someone lifted furniture to the upper floor*

Dat, dative case marker; Acc, accusative case marker. A word-by-word translation in English is shown after each example. In Japanese, the sentences with dative before accusative (DA) order and those with accusative before dative (AD) order are all grammatical and commonly used. We hypothesize that "the P^+ sentences with the DA order" and "the P^- sentences with the AD order" are canonical in word order; the canonicity depends on the semantic contrasts between P^+ and P^- sentences (see **2.1. Introduction**).

speakers of Japanese can correctly differentiate two meanings of the phonologically same verb. The argument structure of a verb in a grammatical sentence can be thus determined from the animacy of the dative NP with '*-ni*' and the presence of the accusative NP with '*-o*' (theme) in each sentence, which are all given before the verb presentation. Because scrambling is allowed in Japanese, the sentences with dative before accusative (DA) order and those with accusative before dative (AD) order are all grammatical with same meanings (Table 2). By using these four separate conditions, we can examine the effect of *possessivity* (P^+ or P^-) and that of word orders without changing the grammaticality of the sentences.

There are two possible syntactic structures for each of Japanese ditransitive sentences: either canonical (C) or noncanonical (N) in word order (Figure 1). We regard *canonicity* (canonical or noncanonical word orders) as another key concept in our present study. Canonicity involves structural computation, in that a long-distance dependency (e.g., an NP-movement) is necessary to yield the surface word order of noncanonical sentences. According to current linguistic theories (Chomsky, 1995; Radford, 1997), the second NP and verb in a canonical sentence are merged to form a V-bar (V') with a minimum *structural distance* (the upper panels in Figure 1). The first NP and V' are then merged to form a verb phrase (VP). On the other hand, in a noncanonical sentence, the second NP and lower V' are merged to form a higher V' (the lower panels in Figure 1). The first NP and higher V' are then merged to form a verb phrase (VP), making a longer structural distance between the verb and each of the first and second NPs. According to linguistic theories on the Japanese language (Hoji, 1986; Saito, 1992; Fukui, 1993; Takano, 1998; Yatsushiro, 2003; Kishimoto, 2008), the canonical word order of P^+ sentences is DA. Although it has been controversial whether the canonical word order of P^{-} sentences is AD or DA (Miyagawa and Tsujioka, 2004; Kishimoto, 2008), a recent behavioral study has indicated that the P^{-} sentences with the AD order were produced more often than the P^{+} sentences with the AD order

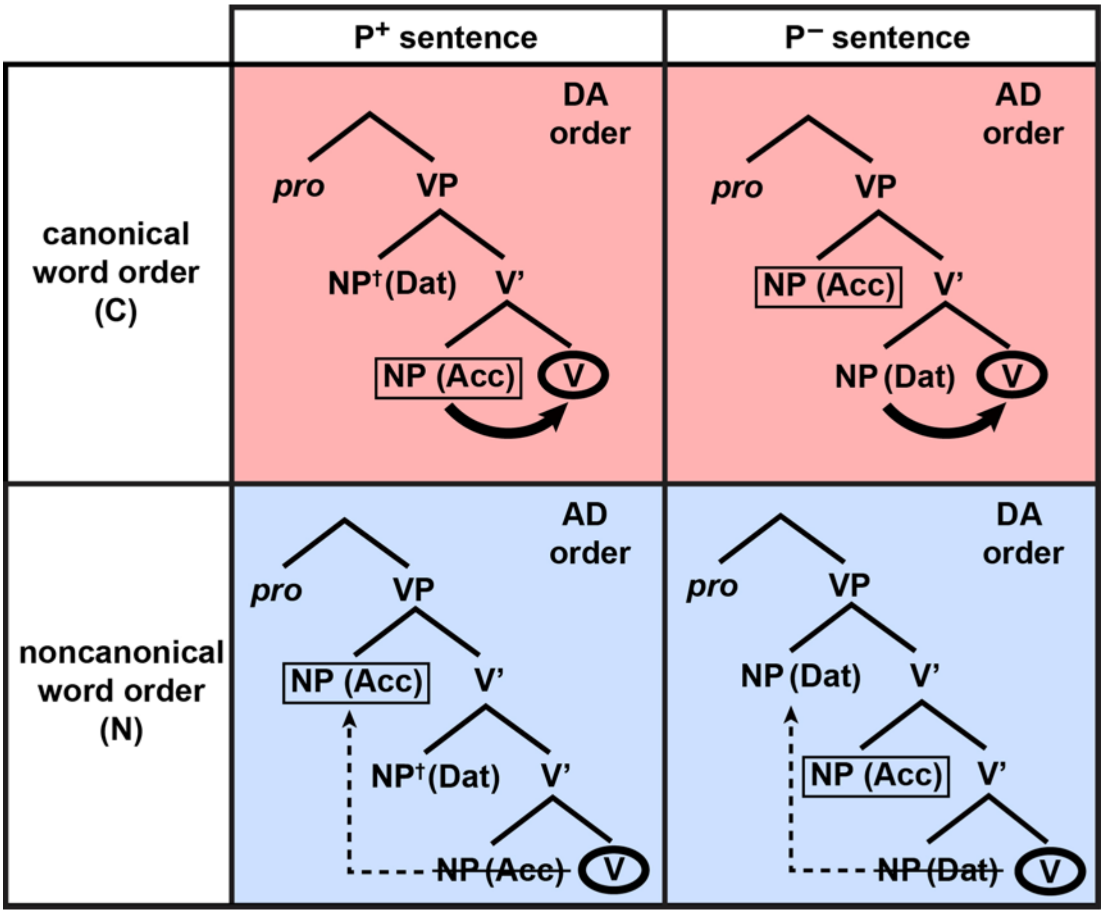

Figure 1. Structures of ditransitive sentences. A succinct version of linguistic tree structures representing the syntactic structures of ditransitive sentences. P^{+} and P^{-} sentences are in columns, while canonical (C, shown in red) and noncanonical (N, shown in blue) word orders, i.e., the canonicity of sentences, are in rows. Dat, dative case marker; Acc, accusative case marker; pro, pronoun, which is a phonetically null subject. For the syntactic structures of noncanonical sentences (lower row), a noun phrase (NP) closest to a verb (V) is moved to the front of another NP (dashed arrow), and merged with the higher V-bar (V') to form a verb phrase (VP). The moved NP then leaves a *trace* in its original or canonical position, producing a gap with a longer structural distance between the second NP and V. In our paradigm, each pair of P^{+} and P^{-} sentences had the same accusative NP (boxed) and phonologically same verb (circled) (see Table 1). We examined the predictive effects of precedent NPs on the verb, which were expected to be larger for the *canonical* sentences with shorter structural distances (curved arrows) than the noncanonical sentences. Among the four conditions, an animate NP (with a dagger) appeared only as the dative NP of the P^{+} sentences.

(Nakamoto et al., 2006). We hypothesize that the P^{-} sentences with the AD order, as well as the P^{+} sentences with the DA order, are canonical in word order. The differential *canonical* word orders in Japanese ditransitive sentences (sentence examples 4a, 4b), depending on the semantic contrasts between P^{+} and P^{-} sentences, are also consistent with the *grammatical* word orders in English ditransitive sentences (sentence examples 1a, 2b), suggesting the universal property of syntactic processes, which are indeed influenced by the accompanying semantic processes. In the analyses of behavioral and MEG data, we performed two-way repeated measures analysis of variance (rANOVA) (factors: possessivity × canonicity), and particularly focused on the main effect of canonicity, rather than on a single condition out of the four conditions, because the linearization of order related-factors (e.g., direct object > indirect object, dative > accusative, and animate > inanimate) can be canceled out between P^{+} and P^{-} sentences, leaving out the canonicity effects alone. Here we mainly analyzed the cortical responses to ditransitive verbs.

Some previous fMRI studies have examined the effects of verb argument structures or those of verb groups with different syntactic phrase types, and have reported activation in the left F3op/F3t, as well as in the temporo-parietal regions (Shetreet et al., 2007; Thompson et al., 2007). However, these previous studies have used a lexical decision or semantic decision task that involves syntactic factors only implicitly, and it has been already known that the cortical activation depends on the choice of linguistic tasks, even if target stimuli are kept identical (Wildgruber et al., 2004; Sahin et al., 2009). In previous fMRI and MEG studies, we have clearly shown that selective activations are observed in the left F3op/F3t during explicit syntactic processing (in a syntactic decision task), when compared with implicit syntactic processing (in semantic decision and other tasks) (Suzuki and Sakai, 2003; Iijima et al., 2009). It was thus necessary to use an explicit syntactic decision task in the present study (Figure 2), together with well-controlled stimuli as shown in Table 1. It is thus expected that such an explicit grammaticality judgment selectively activates the left F3op/F3t.

There are at least two factors that can differentiate processing of canonical vs. noncanonical sentences. One factor is certain processing loads, which become larger for *noncanonical* sentences (i.e., N > C) as indicated by behavioral studies (Stowe, 1986; Frazier and d'Arcais, 1989; Tamaoka et al., 2005; Koizumi and Tamaoka, 2010). Previous neuroimaging studies have also suggested that the activation of the left F3op/F3t, as well as that of the left temporo-parietal regions, may reflect the load of the

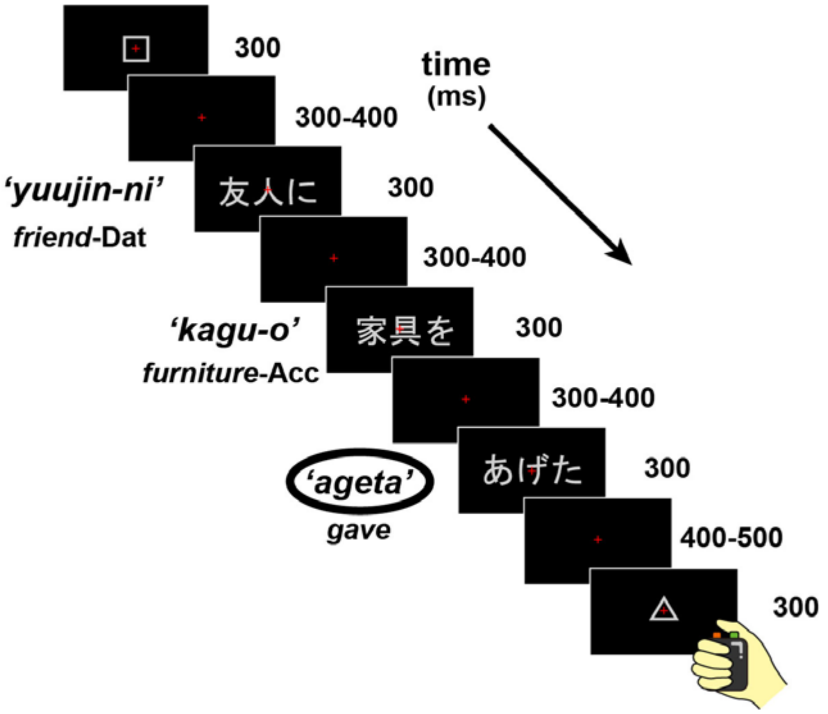

Figure 2. Serial presentation of each sentence. First, a grey square was presented to inform the participant that the trial had begun. Next, a sentence, consisting of two NPs and a verb, was presented in a serial, phrase-by-phrase manner. A grey triangle was shown after a verb to inform participants to initiate a button press. Inter-stimulus intervals were randomly varied so that the responses to verbs were not confounded with those to precedent NPs. We mainly analyzed the cortical responses to ditransitive verbs.

short-term memory (Fiebach et al., 2005), the computation of movement (i.e., the displacement of words) (Grodzinsky and Santi, 2008), or the syntactic processing associated with noncanonical word orders (Kinno et al., 2008; Wilson et al., 2010). The other factor is the predictive effect, which would become larger for *canonical* sentences (i.e., C > N). Recently, some neuroimaging studies have shown that the left F3op/F3t activation reflects predictive effects associated with syntactic processing (Iijima et al., 2009; Santi and Grodzinsky, 2012). For example, in our previous MEG study, we showed that the left F3op/F3t responses to a transitive verb in an object-verb sentence were enhanced, selectively for syntactic judgments on minimum sentences consisting of an NP and a verb (Iijima et al., 2009). Because this enhancement was observed irrespective of syntactic anomaly itself, it cannot be explained by computations of matching or error detection/correction alone. The left F3op/F3t responses may reflect more specific computations or predictive effects, such that an accusative NP predicts a next-coming verb as *transitive* verb, which is the only possible verb type for minimum sentences. Moreover, this previous result cannot be explained by associative memory or transition probability, and it provides an explicit hypothesis, such that a precedent NP *facilitates* syntactic processing when the NP and verb are merged with a minimum structural distance. Indeed, modern linguistics has elucidated the importance of minimizing structural distance (Chomsky, 2011), and we hypothesize that the predictive processing can be regarded as a function of structural distance. In terms of on-line computations, canonicity and predictability are closely related in syntactic processing, because a structural distance becomes minimum for canonical sentences. If the syntactic structure of a canonical sentence is readily predicted in an incremental manner (see Figure 1), it is likely that the sentence becomes easier to comprehend for the participants. Therefore, we expected to observe any predictive effects on a ditransitive verb for *canonical* sentences. To detect activation changes in an unbiased manner, we adopted whole-brain analyses. We had focused on an earlier period of 100 ~ 300 ms for a minimum sentence in the previous MEG study, but it is expected that the predictive effect becomes delayed when the two NPs and verb are merged in more complex ditransitive sentences. We thus extended the time window as late as 700 ms, which was the stimulus interval plus the following shortest inter-stimulus interval (ISI) (Figure 2), to search for any C > N or N > C effects in the present study.

2.2. Materials and Methods

2.2.1. Participants

The participants in the present study were 11 native Japanese speakers. One participant, whose data contained a large amount of noise due to eye movement or blinking, was discarded from the analysis (the ratio of trials with a noise > 2500 fT over the period of –100 ~ 700 ms after the verb onset: 62.2% for the excluded participant and 9.7 ~ 27.0% for the others), leaving a total of 10 participants (21 ~ 32 years; 1 female). The 10 participants showed right-handedness (laterality quotients (LQ): 50 ~ 100) as determined by the Japanese translation of the Edinburgh inventory (Oldfield, 1971) (Appendix 1). Prior to participation in the study, written informed consent was obtained from all participants 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

In our paradigm, we prepared 50 grammatical sentences under each of four conditions (Table 2). Each sentence consisted of a dative NP (always animate for P^+ and inanimate for P^-), an accusative NP (always inanimate), and a verb. Although many ditransitive verbs take either P^+ or P^- alone, we used here such verbs that can take both P^+ and P^-. There has been no assessment of whether Japanese ditransitive verbs were preferentially associated with P^+ or P^- structures, but some English ditransitive verbs have been assessed whether they were preferentially associated with double object sentences or prepositional dative sentences (Bresnan and Ford, 2010). For each pair of P^+ and P^- sentences, as shown in each line of Table 1, the same verb and same accusative NP were used to control the stimuli among different conditions. All verbs and NPs always consisted of three letters of kana (or katakana) and kanji to ensure a consistent reading time. We prepared 200 original sentences (50 × 4) that were all grammatical. Each sentence stimulus appeared only twice for each participant.

To examine transition probabilities between words, all of our ditransitive sentences used in the present study were checked against actual examples of Japanese sentences on the internet, searched with *Google* (http://www.google.co.jp/) and *Yahoo* (http://www.yahoo.co.jp/). Regarding the transition probabilities from the second NP to the verb, a one-way rANOVA showed no significant difference among animate dative NPs, inanimate dative NPs, and accusative NPs used as second NPs [F (2, 98) = 0.15, p = 0.85]. We also compared the transition probabilities from the two NPs to the verb among the four conditions; two-way ANOVAs (possessivity × canonicity) showed no significant main effects of possessivity [F (1, 155) = 0.88, p = 0.35] and canonicity [F (1, 155) = 0.85, p = 0.36], with no significant interaction ([F (1, 155) = 0.40, p = 0.53].

For a syntactic decision task, we added grammatical and ungrammatical modified sentences (120 each) to the grammatical ditransitive sentences. To ensure that the participants paid attention to the relationships between both NPs and a verb, two sets of modified sentences were prepared by changing the ditransitive verbs of the subset of original sentences into either monotransitive verbs (compatible with an accusative NP) or intransitive verbs (compatible with a dative NP) (see Table 3). One set of modified sentences (60 each for grammatical and ungrammatical modified sentences) had *monotransitive* verbs that cannot take a dative NP. The grammaticality was thus dependent on the presence of a dative NP. For example, '*yuujin-ni kagu-o ageta*' and '*nikai-ni kagu-o ageta*' (see sentence examples 4a, 4b) were changed to '**yuujin-ni*

Table 3. Examples of grammatical modified sentences with either monotransitive or intransitive verbs.

Verb type	Example
Monotransitive	'*yuujin-ga kagu-o migaita*' (*friend*†-Nom *furniture*-Acc *polished*) *His friend polished furniture*
	'*nikai-de kagu-o migaita*' (*upper floor*-Loc *furniture*-Acc *polished*) *Someone polished furniture at the upper floor*
Intransitive	'*kagu-ga yuujin-ni tsuita*' (*furniture*-Nom *friend*†-Dat *arrived*) *A piece of furniture arrived at his friend*
	'*kagu-ga nikai-ni tsuita*' (*furniture*-Nom *upper floor*-Dat *arrived*) *A piece of furniture arrived at the upper floor*

Nom, nominative case marker; Loc, locative postposition. Canonical sentences are shown here. Noncanonical sentences were made by scrambling two NPs in each sentence. Among these conditions, an animate NP (with a dagger) appeared either as the nominative NP or as the dative NP.

kagu-o migaita’ (*friend*-Dat *furniture*-Acc *polished*) and ‘**nikai-ni kagu-o migaita*’ (*upper floor*-Dat *furniture*-Acc *polished*), respectively. From the ungrammatical sentences with the animate dative NPs, grammatical sentences were made by changing the dative case particle (‘-*ni*’) to the nominative case particle (‘-*ga*’) (Table 3). From the ungrammatical sentences with the inanimate dative NPs, grammatical sentences were made by changing the dative case particle (‘-*ni*’) to the locative postposition (‘-*de*’).

Another set of modified sentences (60 each for grammatical and ungrammatical modified sentences) had *intransitive* verbs that cannot take an accusative NP. The grammaticality was thus dependent on the presence of an accusative NP. For example, we prepared ‘**kagu-o yuujin-ni tsuita*’ (*furniture*-Acc *friend*-Dat *arrived*) and ‘**kagu-o nikai-ni tsuita*’ (*furniture*-Acc *upper floor*-Dat *arrived*). Grammatical modified sentences were made by changing the accusative case particle (‘-*o*’) to the nominative case particle (‘-*ga*’).

Each modified sentence appeared only twice for each participant. Moreover, the same number of modified sentences were created for each pair of P^+ and P^- sentences, and thus the use of words was perfectly counterbalanced across the four conditions of the original sentences. We were targeting the sentences and associated *structures*, not the words themselves in the present study; the repeated use of the same words would habituate any word-level processes, leaving out sentence-level processes under the conditions with the original sentences.

2.2.3. Task

A syntactic decision task was performed, in which the participants decided whether the presented sentence was grammatically correct or not. This task was necessary to ensure the participants' syntactic judgment based on the argument structure of each verb. In each trial, visual stimuli were presented in grey against a dark background (Figure 2); the stimuli were projected from outside of the shield room onto a translucent screen (within a visual angle of 5.7°). For fixation, a red cross was always shown at the center of the screen. To inform the participants that the trial was beginning, a grey square was presented. Next, the stimuli of a sentence were presented in a serial, phrase-by-phrase manner. Each stimulus was presented for 300 ms, and the ISI was randomly varied from 300 to 400 ms. Lastly, a grey triangle was presented 700 ~ 800 ms after the verb onset to inform participants to start pushing one of two buttons according to the grammaticality of the sentence. The participants were required to respond within 1800 ms after the onset of the grey triangle. The task was performed in 10 separate MEG runs, each with 88 trials. The inter-trial interval was randomly varied from 4700 to 5300 ms to reduce any periodical noises. The possessivity and canonicity of the sentences in each run were fully randomized and balanced. The stimulus presentation and behavioral data collection were controlled using the Lab-VIEW software package and interface (National Instruments, Austin, TX). Only trials with participants' correct responses were used for analyzing reaction times (RTs) and MEG data.

2.2.4. MEG Data Acquisition

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. We basically followed the same procedures described in our previous study (Iijima et al., 2009). Using the BESA 5.2 software package (BESA GmbH, Munich, Germany), the MEG signals during the stimulus interval and the following shortest ISI (i.e., –100 ~ 700 ms for a verb, and –100 ~ 600 ms for a second NP; see Figure 2) were analyzed, where the signals from –100 to 0 ms were used as a baseline. 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 1 to 30 Hz to eliminate large eye movement noises. For mapping with the individual brain, high resolution T1-weighted MR images (repetition time (TR), 30 ms; echo time (TE), 8.0 ms; flip angle (FA), 60°; field of view (FOV), 256×256 mm^2; resolution, $1 \times 1 \times 1$ mm^3) were acquired using a 1.5-T Scanner (Stratis II, Premium; Hitachi Medical Corporation, Tokyo, Japan). The sensor positions for each of ten runs were realigned with five fiducial markers (small coils) on the head surface, and then coregistered with a least-squares fit algorithm to the MR images by attaching MR markers (alfacalcidol beads; diameter: 3 mm) at the same positions of fiducial markers (MEG Laboratory, Yokogawa Electric Corporation, Kanazawa-city, Japan). Using BrainVoyager QX 1.8 software (Brain Innovation, Maastricht, Netherlands), each individual brain was normalized to the image of the Montreal Neurological Institute (MNI) standard brain, which was already transformed into the Talairach space

(Talairach and Tournoux, 1988). In order to perform a cortex-based data analysis, the GM 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).

2.2.5. MEG Analyses

The distribution of cortical activation underlying the MEG signals was modeled with the minimum norm estimates (MNEs) of currents using BESA 5.2. A current dipole was perpendicularly placed at each center of the 3445 cortical patches, approximating any spatial distributions of currents on the cortex (Dale and Sereno, 1993; Hämäläinen et al., 1993). The current density at each cortical patch was then obtained by dividing the strength of each current dipole by the mean area of the cortical patches. For each participant, the current densities at each cortical patch were averaged for a bin of 20 ms; this time bin was moved in 10 ms steps over the 100 ~ 700 ms period after the verb onset or the 100 ~ 600 ms period after the second NP onset. According to the sampling theorem, this sampling time of 20 ms corresponded to the highest frequency of 25 Hz, which was within the band-pass filter. We have successfully used the same time bin in our previous study (Iijima et al., 2009).

We adopted whole-brain analyses that did not rely on any particular regions *a priori,* which is equivalent to performing all possible “functional region of interest (fROI)” analyses (Friston and Henson, 2006). We compared the cortical responses under the four conditions with a cluster-based nonparametric test (Maris and Oostenveld, 2007) as follows. First, we performed a two-way rANOVA (possessivity × canonicity) for the current density of each cortical patch, and selected all patches whose *F*-values were larger than the clustering threshold at $p < 0.0005$. Next, we clustered the selected patches into connected sets on the basis of spatial adjacency (7 mm), and calculated cluster-level statistics by taking the sum of the *F*-values within a cluster as a representative index. The statistical results for each cluster were then spatially corrected for multiple comparisons across the whole brain (corrected $p < 0.05$), using a permutation test for the current density of each condition (Karniski et al., 1994; Pantazis et al., 2005). For example, in the comparison between the P^+ and P^- sentences, the data for all cortical patches were exchanged between these two conditions in some of the 10 participants. For each permutation, the largest of the cluster-level statistics was determined among the clusters. There were $2^{10} = 1024$ permutations, which produced a reference distribution of the cluster-level statistics for determining the corrected *P*-values. Correction for multiple comparisons using *F*-values 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 (Karniski et al., 1994). On each cortical patch in a cluster with significance, a 7-mm-diameter sphere was placed. Using statistical parametric mapping software (SPM8; Wellcome Trust Center for Neuroimaging, London, UK) run on MATLAB software (MathWorks, Natick, MA), these spheres were spatially filtered with a Gaussian (full width of half maximum (FWHM), 8 mm) and superimposed onto the standard brain with MRIcroN (http://www.cabiatl.com/mricro/mricron/index.html).

2.3. Results

2.3.1. Behavioral Data

Behavioral data on the accuracy and RTs for each condition of the original ditransitive sentences are shown in Table 4. A two-way rANOVA (possessivity × canonicity) for the accuracy and RTs showed no significant main effect of possessivity [accuracy: $F(1, 9) = 0.01$, $p = 0.90$; RTs: $F(1, 9) = 0.61$, $p = 0.45$] or canonicity [accuracy: $F(1, 9) = 2.4$, $p = 0.16$; RTs: $F(1, 9) = 0.30$, $p = 0.60$], with no significant interaction between these two factors [accuracy: $F(1, 9) = 0.13$, $p = 0.73$; RTs: $F(1, 9) = 1.5$, $p = 0.25$]. These behavioral results indicate that all of the four conditions were performed equally well by the participants. Therefore, selective responses among these conditions, if any, cannot be explained by performances alone.

We also compared the original sentences with the grammatical modified sentences (the mean ± SEM; accuracy: 89.9 ± 3.2%; RTs: 481 ± 72 ms) and the ungrammatical modified sentences (accuracy: 91.9 ± 2.8%; RTs: 510 ± 69 ms). A one-

Table 4. Behavioral data for ditransitive sentences under each condition.

Possessivity	Canonicity	Accuracy (%)	RTs (ms)
P^+ sentences	Canonical	92.6 ± 2.0	449 ± 72
	Noncanonical	93.7 ± 2.7	460 ± 72
P^- sentences	Canonical	92.7 ± 1.9	462 ± 68
	Noncanonical	93.4 ± 2.2	459 ± 73
Mean		93.1 ± 2.2	458 ± 71

Data are shown as the mean ± SEM. Reaction times (RTs) were obtained from trials with correct responses.

way rANOVA for the accuracy and RTs of these three types of sentences showed a significant main effect only for RTs [accuracy: $F(2, 18) = 0.72$, $p = 0.50$; RTs: $F(2, 18) = 4.3$, $p = 0.03$]. According to paired *t*-tests, the RTs of the original sentences were shorter than those of the grammatical and ungrammatical modified sentences [grammatical: $t(9) = 2.4$, $p = 0.042$; ungrammatical: $t(9) = 2.4$, $p = 0.041$]. It is possible that this difference was due to the higher frequency of the original sentences (400 per participant) than the grammatical and ungrammatical modified sentences (240 each). For the grammatical modified sentences, we also compared the canonical (accuracy: 90.0 ± 3.3%; RTs: 473 ± 68 ms) and noncanonical (accuracy: 89.7 ± 3.2%; RTs: 489 ± 78 ms) sentences, and there was no significant difference [accuracy: $t(9) = 0.46$, $p = 0.66$; RTs: $t(9) = 0.72$, $p = 0.49$], indicating that both conditions were also performed well by the participants.

2.3.2. MEG Data: Canonicity Effects on Ditransitive Verbs

In the analyses of cortical responses (current density) to ditransitive verbs, we compared the activities of the whole brain under the four conditions, in which *phonologically same* verbs were presented (Table 2), using a statistical parametric map with a two-way rANOVA (possessivity × canonicity). At 530 ~ 550 ms after the verb onset, we found a significant main effect of canonicity at only one cluster of three adjacent cortical patches in the left F3op/F3t (corrected $p = 0.048$) [Talairach coordinates, $(x, y, z) = (-43, 13, 16), (-48, 10, 18)$, and $(-53, 10, 23)$] (Figure 3A), which was confirmed to be C > N. In our paradigm (Figure 1), both canonical P^+ and noncanonical P^- sentences were with the DA order, and the accusative NP, i.e., the *second* NP, was physically identical (see Table 2). Even when the same NP preceded a verb, we found a significant C > N effect in the left F3op/F3t responses to the verb at 530 ~ 550 ms [*t* (9) = 3.4, *p* = 0.008] (Figure 3B). This predictive effect thus depended on *both* NPs that actually determined the canonicity of sentences. Indeed, the animacy of the first dative NP alone was not sufficient to determine the canonicity of sentences, because an animate NP could appear as a first NP in the *noncanonical* modified sentences (see Table 3). On the other hand, neither C > N effects at other time windows nor N > C effects over the 100 ~ 700 ms period were significant (corrected *p* > 0.05). Moreover, neither a main effect of possessivity nor an interaction of the two factors was significant in the whole brain over the entire period.

We also performed an independent ROI analysis based on the left F3op/F3t activation at (–54, 9, 18) in MNI coordinates, which was previously identified with a

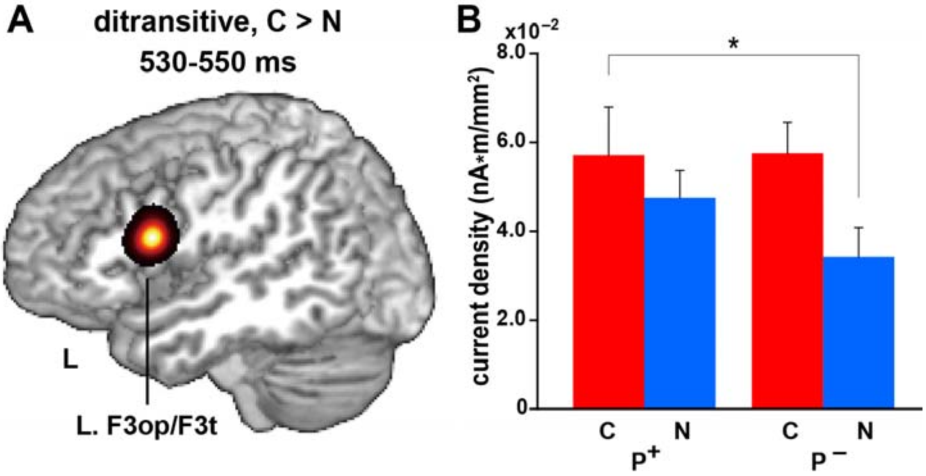

Figure 3. Significant activation with canonicity effects on ditransitive verbs. (A) Cortical activation showing a significant main effect of canonicity at 530 ~ 550 ms. A significant C > N effect (corrected $p < 0.05$) was observed at a single cluster in the left (L.) F3op/F3t (shown in yellow to black), which was superimposed on a sagittal section of the standard brain at the peak [Talairach coordinates, (x, y, z) = (–48, 10, 18)]. **(B)** The current density in the left F3op/F3t cluster for each of the four conditions. Error bars indicate the SEM of participants, and an asterisk denotes the significant difference ($p < 0.05$, paired *t*-test) between the two conditions, under which the same NP preceded a verb (see Table 2).

past tense task using Japanese verbs (Sakai et al., 2004). This focus corresponded to (–51, 7, 18) in Talairach coordinates, and we defined a 7-mm-radius sphere at this voxel as a ROI (five patches). To *temporally* correct multiple comparisons across the whole time windows (100 ~ 700 ms after the verb onset with a bin of 20 ms), a permutation test was performed for the current density (clustering threshold at $p < 0.005$). This additional analysis showed the significant main effect of canonicity at 530 ~ 560 ms (corrected $p = 0.018$), which was also C > N. Therefore, both whole-brain and ROI analyses suggest that the canonicity indeed modifies the brain activity in the left F3op/F3t.

Regarding the identical accusative NPs of the sentences with the DA order, i.e., the *second* NPs, there was no significant difference in the whole brain between canonical P^+ and noncanonical P^- sentences over the 100 ~ 600 ms period after the second NP onset (corrected $p > 0.05$). The canonicity effects shown above were thus selective to verbs. The activation patterns of the left F3op/F3t clearly established that the selective activations were due to the canonicity of ditransitive sentences, which was predictive in nature.

2.3.3. MEG Data: Canonicity Effects on Monotransitive and Intransitive Verbs

We further examined any canonicity effects for grammatical modified sentences with *monotransitive* or *intransitive* verbs. As a prerequisite of canonicity effects, only cortical patches with a weak main effect of canonicity for *ditransitive* sentences at least in one time window at 100 ~ 700 ms (uncorrected $p < 0.05$) were analyzed. We used paired *t*-tests (factor: canonicity alone) with the same spatial correction procedure described above (corrected $p < 0.05$). We observed a significant N > C effect on activations in the left supramarginal gyrus (SMG, BA 40) at 480 ~ 510 ms (Figure 4A), as well as at 570 ~ 590 ms (Figure 4B). A significant N > C effect was also observed in the left pSTG at 600 ~ 650 ms (Figure 4C), as well as in the right anterior middle and inferior temporal gyrus (aMTG/ITG, BAs 38/20) at 650 ~ 670 ms (Figure 4D). There was no significant C > N effect in any cortical regions for the monotransitive and intransitive verbs, indicating that the C > N effect was more sensitive to ditransitive verbs.

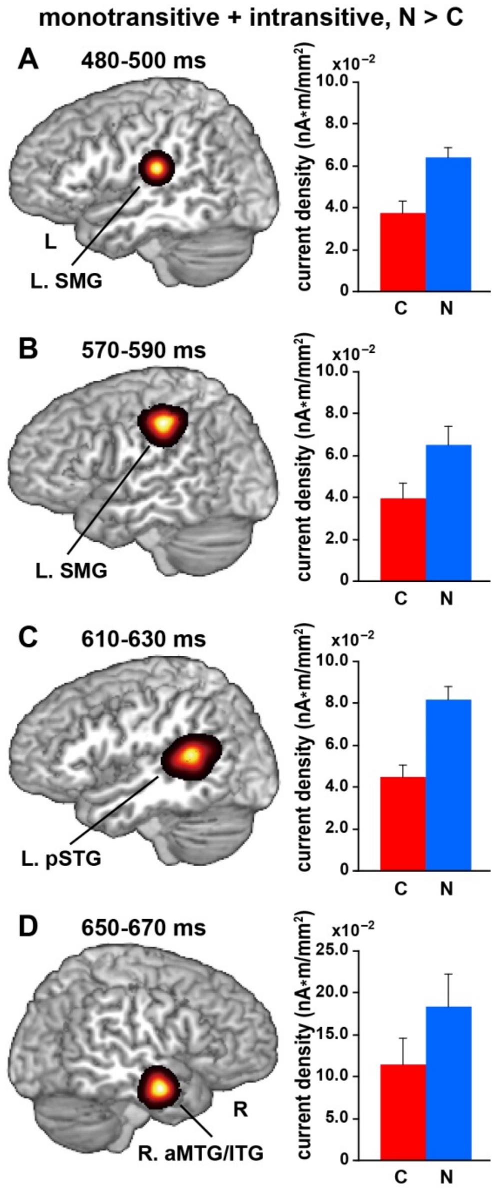

Figure 4. Significant activation with canonicity effects on monotransitive and intransitive verbs. We examined any canonicity effects for grammatical modified sentences with *monotransitive* or *intransitive* verbs. Each activation cluster was shown for a representative (i.e., with more activation) time bin of 20 ms, superimposed on a sagittal section of the standard brain at the peak. Paired *t*-tests resulted in a significant N > C effect (corrected $p < 0.05$) in the following activated regions. The current density for canonical and noncanonical conditions is also shown for each cluster. **(A)** The left SMG activation [pea k: (–50, –24, 7)] at 480 ~ 500 ms. **(B)** The left SMG activation [peak: (–57, –27, 11)] at 570 ~ 590 ms. **(C)** The left pSTG activation [peak: (–48, –45, 13)] at 610 ~ 630 ms. **(D)** The right (R.) aMTG/ITG activation [peak: (54, –3, –18)] at 650 ~ 670 ms.

2.4. Discussion

In the present study, we found a significant main effect of canonicity on the current density in the left F3op/F3t at 530 ~ 550 ms (Figure 3). This effect was selective to canonical sentences with ditransitive verbs, i.e., C > N, and significant even when the precedent NP was physically identical. In addition, we observed a significant N > C effect for the modified sentences with monotransitive and intransitive verbs in the temporo-parietal regions (Figure 4). These results demonstrate that the left F3op/F3t responses were selectively modulated by the canonicity of ditransitive sentences, in which the syntactic structures were different depending on the semantic contrasts between P^+ and P^- sentences (Figure 1).

In our paradigm, possessivity and word orders were varied among the four conditions (Table 2), and thus at least two major factors other than the argument structures of the verb might have been involved. First, the sentence meanings were different between each pair of P^+ and P^- sentences (Table 1), because different dative NPs were used and the verbs had different meanings. However, the main effect of possessivity was not significant in any regions or time windows. Second, the case particle of an NP just before the verb was different between DA and AD orders. However, the interaction between possessivity and canonicity, i.e., the effect of DA and AD orders (see Figure 1), was not significant. Furthermore, our results cannot be explained by general cognitive factors, such as task difficulty, because there was no main effect of canonicity on the behavioral data. Linear order models for word sequences might be able to predict the upcoming word based on lexico-semantic association or statistics, i.e., transition probabilities between single words in a sentence

(Cleeremans and McClelland, 1991; Elman, 1991). In the present experiment, however, we controlled statistical factors, such that the transition probabilities from the second NP, as well as from the two NPs, to the verb in ditransitive sentences (see **2.2.2. Stimuli**). Therefore, any cortical responses modulated by the argument structures of a ditransitive verb depend on computations of syntactic structures that do not entirely reduce to linear orders or statistical effects.

As many previous studies have suggested that the left F3op/F3t has a pivotal role in syntax (Sakai, 2005), it is probable that the C > N effect observed in the present study was due to syntactic processes associated with the structural distance between the verb and NPs. More specifically, the shorter the structural distance between the verb and each NP was, the more influential the predictive effect of the two NPs became. During the syntactic decision task, the syntactic structure of each sentence would be constructed in an incremental manner based on the predicted argument structure of the ditransitive verb. We hypothesize that the argument structure predicted from both dative and accusative NPs was readily verified and processed further in a *canonical* sentence, where the NPs and verb were merged with a minimum structural distance, thus leading to the larger activations in the left F3op/F3t when the verb was presented. This hypothesis is consistent with the C > N effect in the left F3op/F3t responses, even when the same NP preceded a verb (Figure 3B). These results demonstrate that the left F3op/F3t plays a predictive role in syntactic processing, which depends on the canonicity determined by argument structures.

In the analyses of the responses to monotransitive and intransitive verbs, we found significant N > C effects in the temporo-parietal regions (Figure 4). Structural computation of the modified sentences was simpler than that of ditransitive sentences, because there was no such a distinction as P^+ or P^- sentences that affected the canonicity of sentences. It is thus more likely that the canonicity effects on monotransitive and intransitive verbs reflect non-syntactic (probably semantic) factors from the two NPs associated with the canonicity. At 480 ~ 510 and 570 ~ 590 ms, we observed a significant N > C effect in the left SMG, which may reflect the difficulty in processing lexical information for semantic-role assignment within noncanonical sentences. According to a cortical stimulation mapping study (Corina et al., 2005), the left SMG has been implicated in lexical retrieval during verb-naming. In our paradigm, a subject and another NP were scrambled in most noncanonical modified sentences (except monotransitive sentences with locative postposition '*-de*', see Table 3). The N > C effect in the left pSTG at 600 ~ 650 ms was consistent with previous fMRI studies, which have contrasted noncanonical object-initial and canonical subject-initial sentences (Bornkessel et al., 2005; Kinno et al., 2008). We have previously reported that a focal region in the left pMTG/STG was significantly activated by sentences containing syntactic or semantic anomalies (Suzuki and Sakai, 2003). The activation in the left pSTG may reflect reanalyses of anomalous or scrambled sentences, which are more confusing than canonical sentences. The N > C effect in the right aMTG/ITG at 650 ~ 670 ms was consistent with a transcranial magnetic stimulation (TMS) study with a synonym judgment task (Lambon Ralph et al., 2009), suggesting that this effect may reflect the difficulty in processing semantic relationships between NPs for noncanonical sentences.

CHAPTER 3.

Functional and Anatomical Correlates of Word-, Sentence-, and Discourse-Level Integration in Sign Language

3.1. Introduction

All human languages involve various elements at different levels of hierarchical linguistic processing (Chomsky, 1995; Jackendoff, 2002). Indeed, multiple phonemes or morphemes are combined into single words through word-level integration; multiple content words and function words are merged into single sentences through sentence-level integration, and multiple sentences are further incorporated into discourses through discourse-level integration. While higher-level elements integrate linguistic information from lower-level elements, associated meanings and contextual information emerge simultaneously. It has been proposed that unification processes of phonological, syntactic, and semantic elements are gradually represented from the ventral part of the left LPMC to the pars orbitalis of the left inferior frontal gyrus (F3O, BA 47) with a *caudo-rostral* gradient (Hagoort, 2005; Uddén and Bahlmann, 2012). In contrast, we have proposed that syntax and sentence comprehension are organized in the *dorso-ventral* axis of the left lateral side of BAs 6/8, 44/45, and 47 (Sakai, 2005). Consistent with this latter possibility, previous neuroimaging studies have reported selective activation in the left LPMC and/or F3op/F3t for syntactic processing (Stromswold et al., 1996; Dapretto and Bookheimer, 1999; Embick et al., 2000; Indefrey et al., 2001; Hashimoto and Sakai, 2002; Sakai et al., 2002; Friederici et al., 2003; Musso et al., 2003; Ben-Shachar et al., 2004; Sahin et al., 2006; Iijima et al., 2009), and in the left F3O for sentence comprehension (Dapretto and Bookheimer, 1999; Homae et al., 2002; Homae et al., 2003; Sakai et al., 2005). Here we define the *frontal language areas* as the regions consisting of the left LPMC, F3op/F3t, and F3O. The goal of the present study was to determine the functional organization of these frontal language areas. Although linguistic processes are localized in different regions according to these postulates, there has been no direct evidence regarding *how* these multiple regions are organized. Indeed, it is unknown whether each specific region within the frontal language areas is overactivated, unchanged, or underactivated at higher levels of linguistic integration, when compared with lower levels. Furthermore, if the frontal language areas play fundamental roles in various linguistic processes, then the functional organization of these regions should be independent of input modalities,

Figure 5. An experimental paradigm with language tasks in Japanese Sign Language (JSL). There were three language tasks: a word-level (Word), a sentence-level (Sent), and a discourse-level decision (Disc) task. The stimuli used in the Disc task were a long dialogue articulated by two signers who were taking turns (see Table 5). In both the Word and Sent tasks, the sentences from this dialogue were presented in a randomized order. In these three language tasks, some words or phrases were replaced with anomalous probes (indicated by asterisks before the translated words in the figure), to which the participants were asked to respond by pressing a button. For example, in the Word task, the word "*do?*" (denoted by †1) articulated by the first signer was replaced by a pseudo-sign (the picture with a red border). In the Sent task, the word "*do?*" was replaced by a syntactically anomalous JSL sign "*done?*" (the picture with a light green border) as a perfective aspect marker expressing the past tense. In the Disc task, the word "*do*" (denoted by †2) articulated by the second signer was replaced by a contextually anomalous sign "*sleep*" (the picture with a blue border). The linguistic units for these three tasks are shown in color bars separated by dots: Word (red), Sent (light green), and Disc (blue)

including speech sounds, letters, and signs. We predicted that different levels of integration would be associated with increased activations in the dorso-ventral axis of the frontal language areas.

In the present study, we used the Japanese Sign Language (JSL). It might be thought that a sign language is a unique or atypical language, because it is used only in a visual mode without auditory representations for most words. It is true that Deaf (we follow the recent trend in capitalizing this term to refer to a cultural group) participants almost exclusively rely on visual information for language processing throughout their lives, which is not the case for individuals with normal hearing. However, sign languages share the same basic properties of word-, sentence-, and discourse-level processes with vocal languages (Sandler and Lillo-Martin, 2006), which can be easily illustrated by the JSL sentences we used (Figure 5, Table 5). On the other hand, we included some children (seven participants younger than 19 years old), and recruited disproportionate numbers of females (20 females out of 28 participants). Moreover, the Deaf participants showed the individual variability in JSL proficiency, which has been primarily due to limited opportunities for communication and education in JSL and the written Japanese (JPN) for deaf children (Table 6). While the specific developmental changes associated with maturation of the language system, as well as the role of left lateralization in various brain regions, are still under intensive investigation, it is nevertheless well accepted that the representation of language varies with experience and the acquisition of language skills. The relationship between language processing and neural activity may be also different as a function of gender and age. We acknowledge a source of variance within the study population from the inclusion of children and disproportionate numbers of females in the sample, as well as from the

Table 5. English translation of JSL discourse sentences.

A (a Deaf woman): *Next time, would you like to do a "Momo-taro" play?*
("Momo-taro" is a Japanese folk tale translating as "Peach Boy".)
B (a Deaf man): *Let me see... Yes, I would.*
A: *Where would you like to do the play?*
B: *In the backyard of my house.*
A: *Isn't it small for a play?*
B: *No, it isn't. It's large enough for 20 people to gather.*
A: *Cool! I'm sure to come.*
B: *We can watch the play while having BBQ.*
A: *That sounds great! Should it be free?*
B: *Nonsense! I'll ask a thousand yen including BBQ and the play.*
A: *What roles are included in the play?*
B: *There are an old man, an old woman, Momo-taro, a dog, a bird, a monkey...*
A: *Yeah, the dog, bird, and monkey.*
B: *Right. They went to Oni-ga-shima* (the "Demons' Island").
A: *Which won?*
B: *Momo-taro won.*
A: *Watching the play seems boring to me. BBQ and talking would be more fun.*
B: *No, you must take part in the play, too.*
A: *No way! I'm too nervous.*
B: *Really? For the BBQ, we will have thick, juicy, and delicious steak...*
A: *Oh, you're drooling...*
B: *Now, will you take part in the play?*
A: *OK, I want to take the role of Momo-taro.*
B: *No, you should take a Demon, and I'll take Momo-taro.*
A: *It's not fair! Let's toss a coin to decide.*
B: *Which do you prefer, Momo-taro or a steak?*
A: *Wait a minute... a steak.*
B: *You can have a steak, if you play a Demon.*
A: *All right. Who cares, I'll be a Demon.*
B: *Heh-heh-heh.*

Table 6. Participants' profiles and behavioral data for the task.

		range	mean	SD
Age (years old)		12 ~ 54	30	14
LQ		50 ~ 100	93	14
Age of hearing loss (years old)		0 ~ 3	0.5	1.0
AOA (years old)	JSL	0 ~ 22	8.7	7.3
	JPN	0 ~ 18	4.2	4.6
DOE (years)	JSL	1 ~ 54	21	17
	JPN	6 ~ 50	26	13
Hit rate	Word	0.20 ~ 1.00	0.78	0.22
	Sent	0.10 ~ 1.00	0.57	0.23
	Disc	0.50 ~ 1.00	0.76	0.12
	R	0.78 ~ 1.00	0.97	0.05
Correct rejection rate	Word	0.84 ~ 1.00	0.97	0.05
	Sent	0.79 ~ 1.00	0.94	0.07
	Disc	0.79 ~ 1.00	0.91	0.05
	R	0.97 ~ 1.00	1.00	0.01
d'	Word	0.16 ~ 3.58	2.63	0.84
	Sent	0.16 ~ 3.26	1.78	0.75
	Disc	1.34 ~ 3.81	2.18	0.54
	R	3.24 ~ 4.76	4.44	0.44
RTs (ms)	Word	5857 ~ 11753	7747	1097
	Sent	4223 ~ 9472	6696	902
	Disc	4714 ~ 7890	5910	703
	R	543 ~ 4802	2549	1180

LQ, laterality quotients; AOA, age of acquisition; DOE, duration of exposure; JSL, Japanese Sign Language; JPN, Japanese; Word, word-level decision; Sent, sentence-level decision; Disc, discourse-level decision; R, repetition.

wide range in experience and duration of exposure (DOE) to JSL and JPN. All of these factors may limit the generalization of the results to an adult population with typical language development, but it is still challenging to examine whether the functional organization predicted from the previous neuroimaging studies can be demonstrated by such a unique sample of participants. We believe that our participants provide us a rare opportunity to examine the universality of language processing in the brain beyond modality differences and human diversities, and to elucidate the universal relationship between the underlying neural organization and hierarchical linguistic processes.

A recent fMRI study of Deaf adults reported that activations in the left frontal and some other regions during a grammatical judgment task were negatively correlated with the ages of acquisition (AOAs) of American Sign Language (ASL) (Mayberry et al., 2011). Because AOAs were also negatively correlated with the task performances in this previous study, it is critical to separate the effects of proficiency and AOAs, and to confirm common activations among all participants. For our functional analyses, we tried to exclude the effects of the following factors by regarding them as nuisance factors: the effect of age, handedness, gender, age of hearing loss, AOAs of JSL, and AOAs of JPN. On the other hand, some previous VBM studies have shown that Deaf individuals have an increased GM density in the left motor cortex (Penhune et al., 2003) and an increased GM volume in the insula (Allen et al., 2008), compared with hearing non-signers. It has also been shown that AOAs of ASL were negatively correlated with the GM density in the left precuneus (Pénicaud et al., 2013). We thus hypothesized that there would be an anatomical signature for the linguistic proficiency of individuals in the frontal language areas and these regions, even when the functional organization of the frontal language areas was common to individuals.

3.2. Materials and Methods

3.2.1. Participants

Thirty-seven Deaf signers participated in the present study. Nine participants were excluded from the data analyses because of neurological abnormalities, excessive head movements even in a single run, weak left-handedness, later onset of hearing loss (more than three years old), and/or poor task performances (null hit rates). Table 6 shows detailed profiles of the remaining 28 participants (20 females and 8 males), including two students from a bilingual-bicultural school for the Deaf (Meisei Gakuen, Shinagawa-ku, Japan) and three students from a facility for Deaf children (Kanamachi Gakuen, Katsushika-ku, Japan). All participants showed right-handedness (LQ ≥ 50), as determined by the Japanese translation of the Edinburgh inventory (Oldfield, 1971) (Appendix 1). We obtained written reports about participants' hearing status and JSL/JPN experience (Appendix 2). All participants had binaural hearing losses of > 75 dB. Most of the 28 participants had experienced the cued speech method and/or the oral method to learn JPN, but there has been no established testing in JSL or JPN for the Deaf. Neither the grouping of early/late bilinguals nor a binary distinction between native/non-native speakers (i.e., first/second languages) was taken into account in the present study. Written informed consent was obtained from all participants, as well as from their parents/guardians for the juvenile participants, according to the Declaration of Helsinki. The study was approved by both the school and facility, and by the review board of The University of Tokyo, Komaba.

3.2.2. Stimuli

A dialogue between two Deaf signers (a woman and a man) was prepared in JSL (see Table 5 for the entire dialogue). Each stimulus consisted of familiar signs, which were sufficiently easy for the juvenile participants to comprehend, and did not contain fingerspellings. Each dialogue sentence was articulated by one of two signers who were taking turns, i.e., one person questioning/proposing, then the other responding, thereby completing one or two sentences (Figure 5). The rationale for using two signers was to present samples of natural discourse with rich prosodic cues, thereby providing contextual information through an actual conversation (Sakai et al., 2005). Video-taped signers were always in a full-face shot, because gaze directions are crucial in sign languages. For example, the video images of an inquiring facial expression looking forward represented an interrogative to the other signer in the dialogue. Video images of the two signers were presented with an eyeglass-like MRI-compatible display (VisuaStim XGA; Resonance Technology, Northridge, CA) (resolution = 720 × 480, frame rate = 30 fps).

3.2.3. Tasks

There were three language tasks: word-level or lexical decision (Word), sentence-level decision (Sent), and discourse-level decision (Disc) tasks. In the Word and Sent tasks, each dialogue sentence was presented in a random order; in the Disc task, the dialogue sentences were presented in the original order, and completed in seven separate blocks. Therefore, the overall stimuli were physically equated among the language tasks. On the other hand, individual tasks imposed different “task sets” (i.e., an effective intention for a task to attend the specific operations demanded by the task) as explained below, while these tasks basically included probe detection in common in that anomalous probes *infrequently* appeared (in 10 out of 29 or 43 dialogue sentences). It should be noted that there was only one type of probes (lexical, syntactic, or contextual errors) included in each task block. The purpose of including probes was to ensure the participants’ full attention to lexical information, sentence expressions, or discourse flows, thereby allowing assessment of their linguistic proficiency for each task. A number of linguistic studies with lexical, syntactic, or contextual decision tasks inherently involved anomaly detection in the tasks, and we have already established that activations of the frontal language areas depend on the type of decisions, but not on the anomaly of stimuli themselves (Suzuki and Sakai, 2003). We performed fMRI experiments in a block design, which measured overall responses during each block, and thus was unaffected by the presence of probes (mostly less than 5 s). Trials with the sentences containing anomalous probes were included in the block design analysis. To maintain the natural flow of signs, both normal and anomalous versions of an entire sentence were filmed with the same signers and settings, as if each sentence constituted a normal continuous discourse even with a probe. Each block of the language tasks consisted of four or five dialogue sentences, and lasted for 24 ~ 48 s.

Using both JSL and written JPN, we instructed the participants to respond to a probe by pressing a button while a sentence containing the probe was presented. At the initiation of each block, the task type was visually presented for 1.3 s in Japanese: ‘*kotoba*’ (*word*) for the Word, ‘*hyougen*’ (*expression*) for the Sent, and ‘*kaiwa*’ (*conversation*) for the Disc task. In the Word task, probes were pseudo-signs freely devised by the native signers, and the participants were asked to detect the probes by focusing on word-level information among the disconnected dialogue sentences. Lexical decision critically involves word-level integration; for sign languages, elements of handshape, location, and movement are combined into real words. In the Sent task, probes were syntactically anomalous JSL expressions, and the participants were asked to detect the probes by focusing on sentence expressions (e.g., word-to-word relationships) among the disconnected dialogue sentences. These syntactic errors included violations of tense (see Figure 5), person (e.g., an agreement error between first and third persons), word order (an ungrammatical order of lexical items), etc. In the Disc task, probes were contextually anomalous signs in the flow of the dialogue, and the participants were asked to detect the probes by focusing on the flow of discourse, i.e., using discourse-level integration. Every sentence containing a probe in the Disc task was not only syntactically normal, but also *semantically plausible*, if the sentence was free from a given context. In our paradigm, the levels of linguistic integration necessary for each language task can be characterized by distinct *linguistic units*. In the Word, Sent, and Disc tasks, linguistic units were individual words, disconnected dialogue sentences, and consecutive sentences, respectively.

As a baseline for the language tasks, a repetition (R) task was tested with the same probe detection. At the initiation of each R block, the task type, '*kurikaeshi*' (*repetition*), was visually presented for 1.3 s. In the R task, normal sentences used in the three language tasks were played backward and presented in a randomized order, and a probe was a successively repeated "backward sentence". During each R block, video images of only one signer (e.g., a woman for an R block, a man for the next R block, etc.) were presented, since successive presentation of different signers could not become a probe. The participants reported that it was impossible to comprehend sentences composed of backward signs, although some of the signs were recognizable as meaningful. Here, it should be noted that the stimuli used in the language and R tasks were physically equivalent, i.e., in terms of the visual stimuli themselves, which included hand shapes, facial expressions, and body movements. Activation by the contrasts between the language and R tasks (e.g., Word – R) thus reflected the processes of individual words (in common for the language tasks) and associated linguistic integration (different among the language tasks), while general cognitive factors such as lower-level visual perception, probe detection, short-term memory, response selection, and motor responses were fully controlled.

Every participant underwent a total of eight scanning sessions, each of which had seven blocks and lasted for 220.7 ~ 221.1 s. In the first seven sessions, four blocks of the baseline R task were alternately presented with a block of the Word, Sent, or Disc task (appearing once in a pseudo-random order). In the last session, four blocks of the R and three blocks of the Disc task were alternately presented, with a part of the original dialogue being repeated once more with new probes in the Disc task. In each block of the Disc and R tasks, there was always a single probe, and in each block of the Word and Sent tasks, there were either one or two probes. There were a total of ten different probes for each of the Word, Sent, and Disc tasks, whereas there were 32 probes for the R task. In each language task, no sentence appeared more than twice. The use of more blocks for the Disc task might have increased the brain activations, but the number of blocks was largest for the R task (Figure 6). Since the number of blocks was equal for the Word and Sent tasks, the change in activation by the levels of linguistic integration, if any, cannot be explained by the differences in the number of blocks.

The stimulus presentation and button-press signal acquisition were controlled using the Lab-VIEW software package and interface (National Instruments, Austin, TX). The accuracy of each task was evaluated with *d*', which was computed from the *Z*-scores of hit rates and correct rejection rates. If these rates were 1.00, the formula of 1–1/(2 × *Num*) was used (Macmillan and Creelman, 2005), where *Num* was the total number of probes in each task (Word, 10; Sent, 10; Disc, 10; R, 32) for hit rates, and that of other stimuli in each task (Word, 19; Sent, 19; Disc, 33; R, 110) for correct

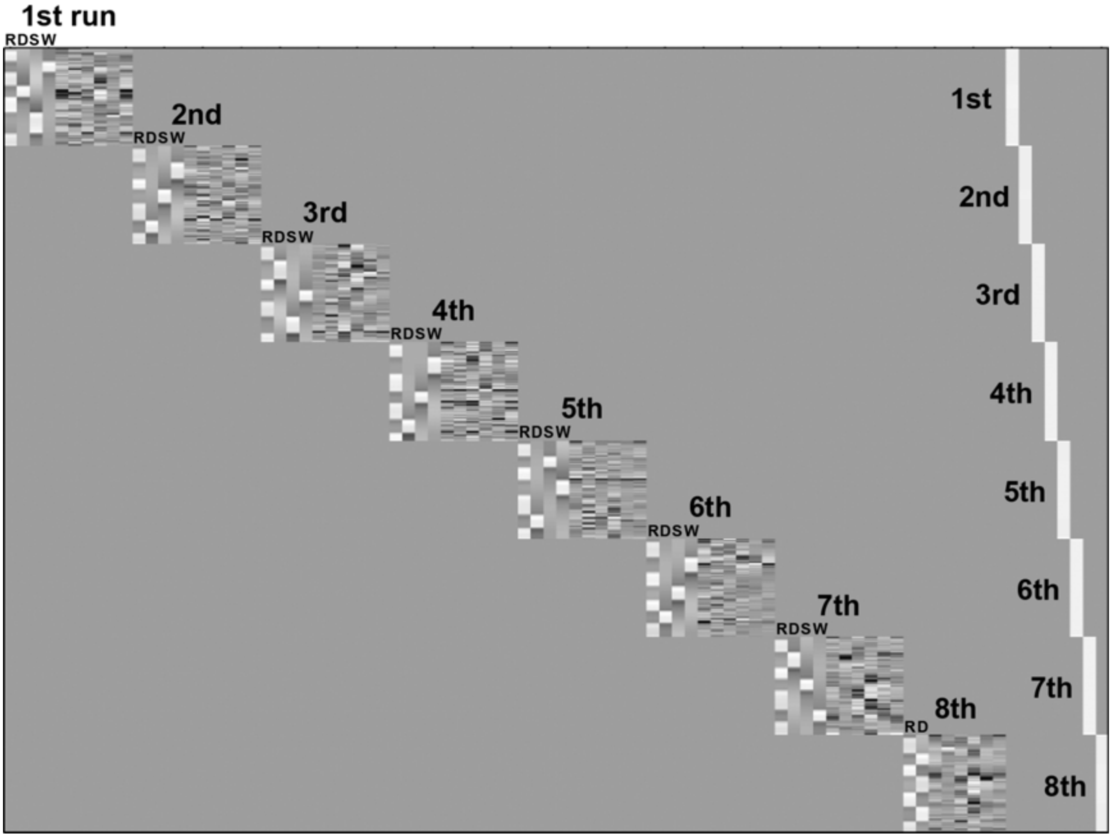

Figure 6. The general linear model design matrix for one typical participant. Run-specific predictors are shown in the right-hand columns (denoted as 1st to 8th) that model differences among individually averaged activations in eight runs. For each of the left-hand columns representing the first to seventh runs, the regressors of the R, Disc (D), Sent (S), and Word (W) tasks (convolved with a hemodynamic function), as well as the realignment parameters of three translations and three rotations obtained from preprocessing (i.e., due to head movements), were included in the design matrix in this order. For the eighth run, the regressors of the R and Disc tasks, as well as the six realignment parameters, were included in the design matrix.

rejection rates. RTs were calculated from the onset of each dialogue sentence containing a probe.

3.2.4. MRI Data Acquisition

The participants were in a supine position, and their heads were immobilized inside the radio-frequency coil with straps. The MRI scans were conducted on a 3.0 T MRI system (GE Signa HDxt 3.0T; GE Healthcare, Milwaukee, WI). We scanned 32 axial slices that were 3-mm thick with a 0.3-mm gap, covering from – 42.9 to 62.4 mm from the anterior to posterior commissure (AC-PC) line in the vertical direction, using a gradient-echo echo-planar imaging (EPI) sequence (TR = 3 s, TE = 60 ms, FA = 90°, FOV = 192 × 192 mm^2, resolution = 3 × 3 mm^2). In a single scanning run, we obtained 77 volumes following three dummy images, which allowed for the rise of the MR signals. High-resolution T1-weighted images of the whole brain (192 axial slices, 1.0 × 1.0 × 1.0 mm^3) were acquired with a three-dimensional fast spoiled gradient-echo (3D FSPGR) sequence (TR = 9 ms, TE = 3 ms, FA = 25°, FOV = 256 × 256 mm^2). These structural images were used for normalizing fMRI and VBM data.

3.2.5. fMRI Analyses

We performed group analyses with SPM8 run on MATLAB software. The acquisition timing of each slice was corrected using the middle (sixteenth in time) slice as a reference. We realigned the functional volumes to the first volume and removed runs that included data with a translation of > 4 mm in any of the three directions and with a rotation of > 2.5°. Each individual's structural image was coregistered to the mean functional image generated during realignment. The coregistered structural image was spatially normalized to the standard brain space as defined by the MNI using the unified segmentation algorithm with very light regularization, which is a generative model that combines tissue segmentation, bias correction, and spatial normalization in the inversion of a single unified model (Ashburner and Friston, 2005). After spatial normalization, the resultant deformation field was applied to the realigned functional imaging data, which was resampled every 3 mm using seventh-degree B-spline interpolation. All normalized functional images were then smoothed by using an isotropic Gaussian kernel of 9 mm FWHM. Task-specific effects were estimated with a general linear model (random effects model).

In the first-level analysis, each participant's hemodynamic responses induced by the tasks were modeled with a box-car function, and this function was convolved with a hemodynamic function. To minimize the effect of head movements, the six realignment parameters obtained from preprocessing were included as a nuisance factor in a general linear model (Figure 6). The images of the Disc, Sent, Word, and R tasks were then generated for each participant, and used for a second-level analysis. To regress out the effect of age, LQ, gender, age of hearing loss, AOAs of JSL, and AOAs of JPN, we included these nuisance factors as covariates in the design matrix of the second-level analysis. The statistical parametric maps were thresholded at a voxel level of uncorrected $p < 0.0001$, and at a cluster level of corrected $p < 0.05$ using the false discovery rate (FDR). For the anatomical identification of activated regions, we used the Anatomical Automatic Labeling method (Tzourio-Mazoyer et al., 2002) and Anatomy toolbox (Eickhoff et al., 2005).

3.2.6. VBM Analyses

VBM analyses on MR images were performed using SPM8 software. After alignment to the AC-PC line, T1-weighted images were bias-corrected and segmented to the GM, white matter, and cerebrospinal fluid by using default tissue probability maps and a New Segment tool, which uses an affine regularization to warp images to the International Consortium for Brain Mapping (ICBM) East Asian brain template. Inter-subject registration was achieved with Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL) (Ashburner, 2007). Jacobian-scaled ("modulated") and warped tissue class images were then created with DARTEL's Normalize to MNI Space tool, which spatially normalized images to the MNI space, converted voxel sizes to $1.5 \times 1.5 \times 1.5$ mm^3 (the size of the DARTEL template), and smoothed images with a standard Gaussian filter of 8-mm FWHM. To avoid possible edge effects (partial volume effects) around the border of the GM, voxels with a value greater than 0.2 were used for analyzing the modulated GM images. A multiple regression analysis was performed on the smoothed GM images to determine regions in which GM volumes showed a correlation with the *d*' value of each language task. The total GM volumes of individual brains were entered into the model as a proportional scaling factor to regress out the general size difference across the participants. The *d*' of the R task, as well as nuisance factors used in the fMRI analyses, was included as a covariate in the design matrix of VBM analyses. The statistical parametric maps of GM volumes were thresholded at a voxel level of uncorrected $p < 0.001$, and at a cluster level of FDR-corrected $p < 0.05$. To account for the nonisotropic smoothness of the

VBM data (Ashburner and Friston, 2000), nonstationary cluster correction implemented in SPM8 was applied.

3.3. Results

3.3.1. Behavioral Data

The task performances were well above the chance level, as indicated by the fact that the value of *d*' was significantly larger than zero (all, $p < 0.0001$) (Table 6). These high task performances suggest that the participants successfully detected different types of probes. According to a one-way rANOVA on the *d*' data, there was a significant main effect of the task [$F(3, 81) = 129$, $p < 0.0001$]. Paired *t*-tests showed that the R task was significantly easier than the other three tasks (Bonferroni corrected

Table 7. Correlation matrix of participants' profiles and behavioral data.

	Age	AOA (JSL)	DOE (JSL)	*d*'(Word)	*d*'(Sent)	*d*'(Disc)	*d*'(R)
Age	1.00	–0.25	0.91*	–0.18	–0.06	0.02	–0.03
AOA (JSL)		1.00	–0.62*	0.04	0.22	–0.05	0.15
DOE (JSL)			1.00	–0.16	–0.14	0.00	–0.08
d'(Word)				1.00	0.61*	0.40	0.29
d'(Sent)					1.00	0.29	0.17
d'(Disc)						1.00	–0.03
d'(R)							1.00

Correlation coefficients (*r*) are shown here. Asterisks denote significant correlations (corrected $p < 0.05$).

$p < 0.05$). Based on a comparison of the *d*' values for the three language tasks, the Word task was the easiest, whereas the Sent task was the most difficult (corrected $p < 0.05$).

Correlation analyses on *d*' among the participants showed that the performance of the Word task was significantly correlated with that of the Sent task [$r = 0.61$, $p = 0.0004$] (Table 7). If some participants had inadvertently and partially switched between the Sent and Word tasks irrespective of task instructions, then the performances of one of the two tasks would have become worse, because the use of one task set, e.g., the detection of pseudo-signs, did not help in the proper use of the other task set, as there were no pseudo-signs at all in the Sent task. However, the performances on the Word task were found to be positively correlated with those on the Sent task, indicating that the participants, who discriminated one of the two tasks well, could also discriminate the other task, even when the same set of disconnected sentences was used.

The ages of the participants were strongly correlated with the DOE of JSL [$r = 0.91$, $p < 0.0001$]; the ages and DOE of JPN were also correlated [$r = 0.94$, $p < 0.0001$]. The AOAs and DOE of JSL were negatively correlated with each other [$r = –0.62$, $p = 0.0003$], while the AOAs and DOE of JPN were not correlated [$r = 0.08$, $p = 0.68$], probably due to the smaller variances for the AOAs of JPN. The correlation between the AOAs of JSL and JPN was not significant [$r = –0.22$, $p = 0.28$], indicating that these AOAs were independent of each other for the participants.

According to a one-way rANOVA on the RTs, there was a significant main effect of the task [$F(3, 81) = 165$, $p < 0.0001$]. Paired *t*-tests showed that the RTs for the R task were significantly shorter than those for the other three tasks (corrected $p < 0.05$). Among the RTs for the three language tasks, the RTs for the Word task were the longest, whereas those for the Disc task were the shortest (corrected $p < 0.05$). In the VBM analyses, we used the *d*' of each task to represent the linguistic proficiency of individuals, because *d*' controls for any response bias the participants may have, and thus is more reliable than RTs in this context.

3.3.2. Cortical Activations Modulated by the Levels of Linguistic Integration

To elucidate the functional organization of the frontal language areas in an unbiased manner with respect to other cortical regions, we adopted whole brain analyses for fMRI and VBM. Figures 7A-C show cortical responses in the Word, Sent, and Disc tasks compared with those in the R task (FDR-corrected $p < 0.05$). Corresponding to a difference in the linguistic units for the Word, Sent, and Disc tasks (see **3.2.3. Tasks**), activated regions in the frontal language areas gradually expanded in the dorso-ventral axis, i.e., from the left LPMC to the F3O, via the F3op/F3t. In Word – R, significant activation was observed bilaterally in the LPMC and dorsal F3op/F3t (dF3op/F3t), as well as in the pre-supplementary motor area (pre-SMA, the medial side of BAs 6/8) (Table 8). In Sent – R and Disc – R, consistent activation was observed in the bilateral LPMC/F3op/F3t, right F3O, pre-SMA, left angular gyrus (AG, BA 39), bilateral MTG/STG, and bilateral caudate. In Disc – R, activation in the F3O and AG became bilateral, indicating that the Disc task recruited exactly mirrored regions. We also observed the left cerebellum activation in Sent – R, and the medial precuneus (BA 7) activation in Disc – R. Taking these results together in an overlaid map (Figure 7D), the hierarchical integration in the frontal language areas was striking, such that the more dorsal regions activated at the lower levels of linguistic integration were almost completely included in the wider regions activated at the higher levels. In the right lateral frontal cortex, pre-SMA, and right temporal regions, in contrast, such an integration was unclear, and some regions activated at the lower levels were outside those activated at the higher levels.

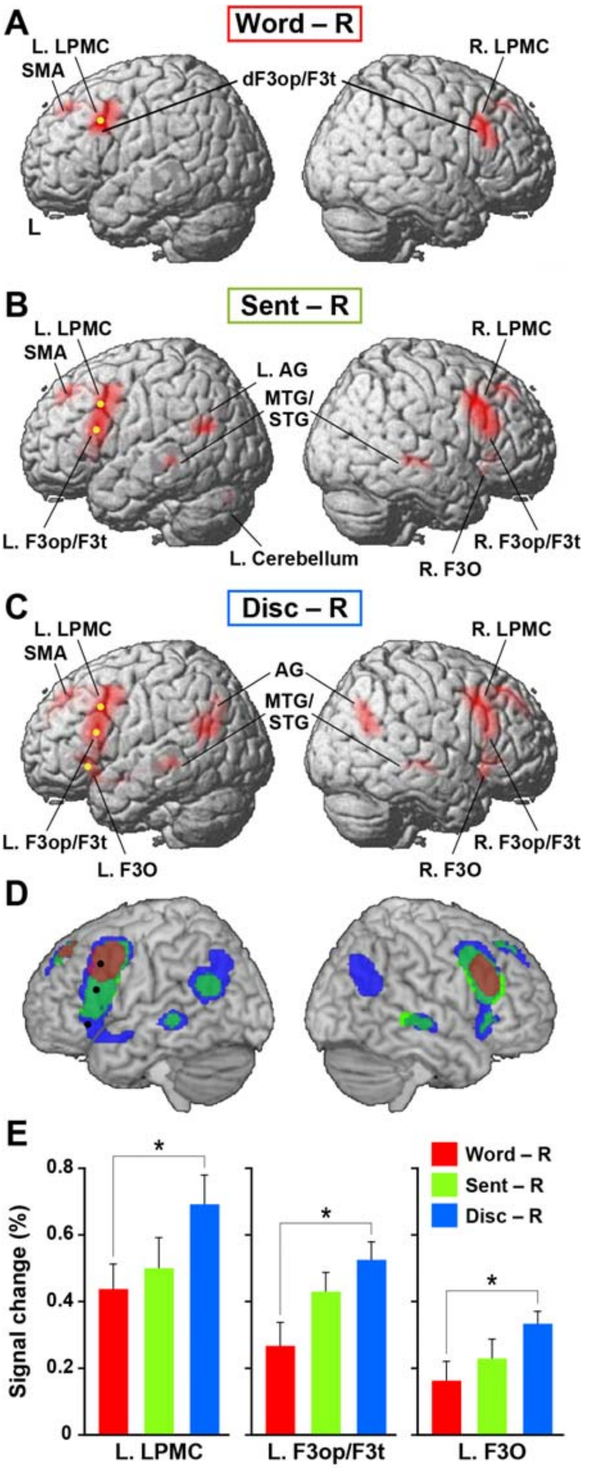

Figure 7. Cortical activations modulated by the levels of linguistic integration. (A-C) Cortical activations in each of the Word **(A)**, Sent **(B)**, and Disc **(C)** tasks, compared with the R task, are projected onto the lateral surfaces of a standard brain in the MNI space. Significantly activated regions are shown in red (FDR-corrected $p < 0.05$). Note the most prominent activation in the frontal language areas. **(D)** An overlaid map of cortical activations in Word – R (red), Sent – R (light green), and Disc – R (blue), using transparent overlays in this order (Word – R topmost). For example, when a region was activated in both Sent – R and Disc – R, its color became blue-green (see the region in the right temporal cortex). Note the gradual expansion of activation from the dorsal to ventral regions within the frontal language areas. We focused on three regions in the frontal language areas: the left LPMC, F3op/F3t, and F3O (shown as yellow dots in **(A-C)**, and as black dots in **(D)**). **(E)** Signal changes of each local maximum for Word – R (red), Sent – R (light green), and Disc – R (blue). Error bars indicate the SEM of participants, and asterisks denote the significance level of corrected $p < 0.05$.

Table 8. Cortical activations modulated by the levels of linguistic integration.

Brain region	BA	Side	*x*	*y*	*z*	*Z* value	Voxels
Word – R							
LPMC/dF3op/F3t	6/8/44/45	L	–48	17	37	5.1	224
		R	48	20	31	4.9	136
pre-SMA	6/8	M	–9	44	46	5.0	143
Sent – R							
LPMC	6/8	L	–39	11	43	5.5	538
F3op/F3t	44/45	L	–51	20	19	5.2	*
LPMC	6/8	R	39	14	37	6.2	437
F3op/F3t	44/45	R	45	29	19	5.7	*
F3O	47	R	48	26	1	4.2	47
pre-SMA	6/8	M	–9	38	46	6.2	323
AG	39	L	–42	–58	25	4.8	139
MTG/STG	21/22	L	–60	–34	–2	4.6	36
		R	48	–28	–5	5.5	103
caudate		L	–15	5	16	4.6	80
		R	12	5	13	4.5	77
cerebellum, crus I		L	–18	–76	–32	4.9	34
Disc – R							
LPMC	6/8	L	–39	8	43	6.6	966
F3op/F3t	44/45	L	–51	20	22	6.5	*
F3O	47	L	–30	26	–5	6.5	*
MTG/STG	21/22	L	–48	–31	–5	6.3	*
LPMC	6/8	R	42	17	43	6.2	577
F3op/F3t	44/45	R	54	23	16	5.6	*
F3O	47	R	36	26	–8	6.1	*
MTG/STG	21/22	R	54	–25	–5	5.6	79
pre-SMA	6/8	M	0	35	46	6.9	562
AG	39	L	–33	–70	40	5.6	333
		R	57	–64	22	5.5	195
precuneus	7	M	–3	–67	31	5.1	93
caudate		L	–15	11	10	5.2	99
		R	15	17	7	4.8	103

Stereotactic coordinates (*x*, *y*, *z*) in the MNI space (mm) are shown for each activation peak of *Z* values (corrected $p < 0.05$). BA, Brodmann's area; L, left hemisphere; R (in the Side column), right hemisphere; M, medial; LPMC, lateral premotor cortex; dF3op/F3t, pars opercularis and triangularis of the dorsal inferior frontal gyrus; F3O, pars orbitalis of the inferior frontal gyrus; pre-SMA, pre-supplementary motor area; AG, angular gyrus; MTG/STG, middle/superior temporal gyrus. The region with an asterisk is included within the same cluster shown one row above.

We focused on the frontal language areas with clear hierarchical integration, and chose three ROIs. The local maximum of each region of the left LPMC, F3op/F3t, and F3O was taken serially from significant activation in Word – R, Sent – R, and Disc – R, respectively (Table 8), to ensure an unbiased selection of local maxima (i.e., not necessarily selective to Disc – R alone). We examined whether activations of these ROIs were incrementally modulated with the level of linguistic integration (Figure 7E). A two-way rANOVA with the ROI [LPMC, F3op/F3t, F3O] × task [Word, Sent, Disc] showed significant main effects of ROI [$F(2, 54) = 14$, $p < 0.0001$] and task [$F(2, 54) = 8.2$, $p = 0.0008$] with no significant interaction [$F(4, 108) = 1.0$, $p = 0.39$]. Paired *t*-tests showed that the signal changes for Disc – R were significantly higher than those for Word – R in all three regions (Bonferroni corrected $p < 0.05$). Task difficulty cannot explain these modulation patterns, as the Sent task was the hardest among the three language tasks; the patterns were also independent of general short-term memory, because we subtracted responses in the R task. Therefore, not only the dorso-ventral expansion of activated regions in the frontal language areas, but also overactivation in each of these regions was primarily influenced by the level of linguistic integration.

3.3.3. Lateralization and Functional Localization of Cortical Activations

To determine which regions showed significant lateralization, we further performed a flip method with voxel-wise analyses, which has been shown to be superior to the ROI-based lateralization indices method for such determination (Baciu et al., 2005). For this purpose, activations (i.e., in Word – R, Sent – R, or Disc – R) of the brain images flipped from side to side (i.e., mirror-reversed images derived from fMRI first-level analyses) were subtracted from the cortical activations of the normal images shown in Figures 7A-C. These comparisons correspond to the interaction of task and hemisphere (left versus right); the resultant activations in the left brain represent [Disc – R] × [left – right], etc., whereas those in the right brain represent [Disc – R] × [right – left], etc. (FDR-corrected $p < 0.05$). In Sent – R, we observed clear left-lateralized activations in the left F3op/F3t and LPMC, as well as right-lateralized activations in the MTG/STG (Figure 8A, Table 9). In Disc – R, we observed clear left-lateralized activations in the left LPMC alone (Figure 8B), while there was no significant lateralization of activations in Word – R.

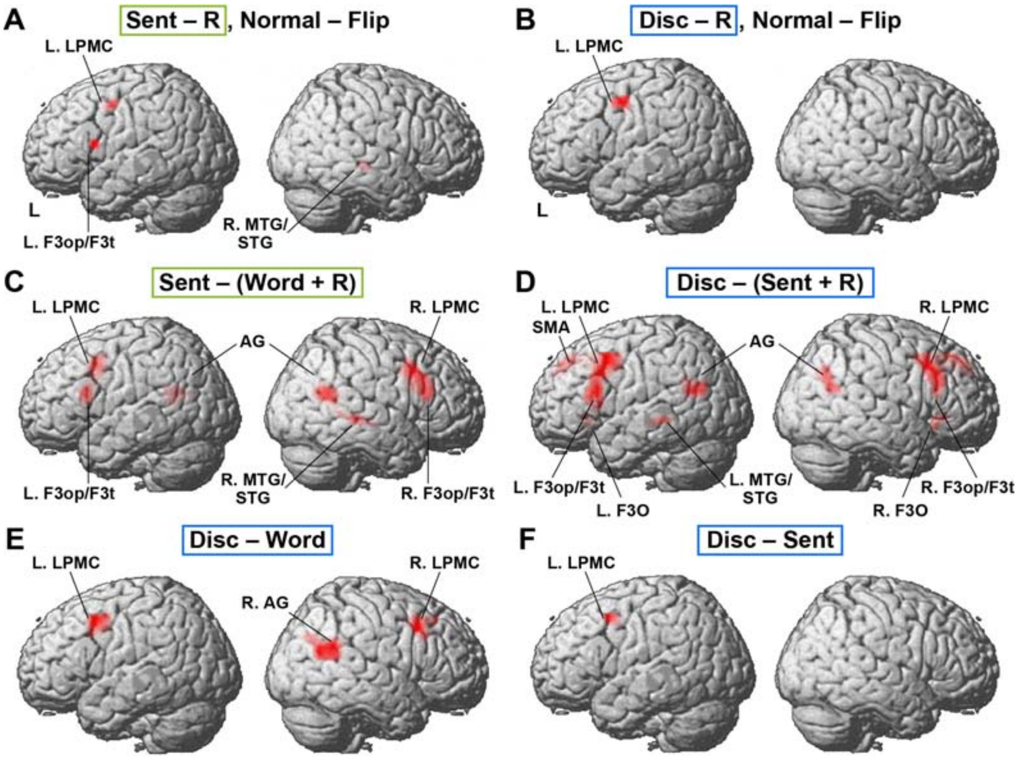

Figure 8. Lateralization and functional localization of cortical activations. (A-B) Cortical activations in the Sent – R or Disc – R of the brain images flipped from side to side (Flip) were subtracted from those of the normal images (Normal). In Sent – R, Normal – Flip **(A)**, note the significant effect of hemispheres in the left LPMC, F3op/F3t, and right MTG/STG. In Disc – R, Normal – Flip **(B)**, there was a significant effect of hemispheres in the left LPMC alone. **(C)** Regions identified by Sent – (Word + R). **(D)** Regions identified by Disc – (Sent + R). **(E)** Regions identified by Disc – Word. **(F)** Regions identified by Disc –Sent.

Table 9. Lateralization and functional localization of cortical activations.

Brain region	BA	Side	*x*	*y*	*z*	*Z* Value	Voxels
Sent – R, Normal – Flip							
LPMC	6/8	L	–42	–4	52	4.2	25
F3op/F3t	44/45	L	–51	14	13	4.5	21
MTG/STG	21/22	R	39	–28	–5	4.6	31
Disc – R, Normal – Flip							
LPMC	6/8	L	–45	2	46	4.9	56
Sent – (Word + R)							
LPMC	6/8	L	–42	11	43	5.0	208
F3op/F3t	44/45	L	–51	20	19	4.5	*
LPMC	6/8	R	39	11	37	6.1	342
F3op/F3t	44/45	R	45	26	19	5.4	*
AG	39	L	–42	–49	16	4.9	103
		R	57	–58	19	5.7	151
MTG/STG	21/22	R	48	–31	–2	5.1	106
Disc – (Sent + R)							
LPMC	6/8	L	–42	8	46	6.5	491
F3op/F3t	44/45	L	–57	20	19	5.8	*
LPMC	6/8	R	39	17	46	5.6	290
F3op/F3t	44/45	R	54	23	19	4.6	*
F3O	47	L	–30	26	–2	4.7	38
		R	36	29	–5	5.9	62
pre-SMA	6/8	M	9	29	49	6.0	352
AG	39	L	–45	–64	22	4.6	130
		R	57	–61	22	4.6	114
MTG/STG	21/22	L	–48	–28	–8	5.3	58
Disc – Word							
LPMC	6/8	L	–39	8	46	5.6	159
		R	39	17	46	4.7	151
AG	39	R	57	–64	19	4.9	197
Disc – Sent							
LPMC	6/8	L	–36	8	49	4.6	50

The region with an asterisk is included within the same cluster shown one row above.

Next, we compared activations among the language tasks. By adding the Word task to the R task in Sent – R, i.e., Sent – (Word + R), we examined overactivation during sentence-level processes when compared with lower levels. This contrast exhibited more focal activation in the left LPMC and F3op/F3t (Figure 8C, Table 9), consistent with the left-lateralized activation in these regions (Figure 8A). On the other hand, the Disc – (Sent + R) contrast resulted in an activation pattern (Figure 8D) similar to that in Disc – R (Figure 7C), but the left F3O activation was clearly separated. A direct comparison of activations between the Disc and Word tasks showed significant activation in the bilateral LPMC and right AG (Figure 8E), while a direct comparison between the Disc and Sent tasks showed focal activation in the left LPMC (Figure 8F). This left LPMC activation is consistent with the left-lateralized activation in this region (Figure 8B). These results clarified the functional localization of the left LPMC, F3op/F3t, and F3O.

3.3.4. Positive Correlations between Individual Task Performances and GM Volumes

We examined correlations between the individual task performances and regional GM volumes. Multiple regression analyses revealed a significantly positive correlation between the *d*’ of each language task and GM volumes in localized regions (FDR-corrected $p < 0.05$). Between the *d*’ of the Word task and GM volumes, we found a prominent correlation in the dorsolateral surface of the left precentral gyrus and postcentral gyrus (PreCG/PostCG, BAs 4/3/1/2) [MNI coordinates of its peak: $(x, y, z) = (-49, -22, 59)$, $Z(19) = 4.6$, $p < 0.001$, 1227 voxels] (Figure 9A). This region corresponded to the “hand area” of the primary motor and somatosensory cortices.

Between the *d*' of the Sent task and GM volumes, a significant correlation was observed in the right insula [(32, –6, 17), $Z(19) = 4.9$, $p < 0.001$, 1440 voxels] (Figure 9B). The second largest cluster was located in the left insula [(–29, –9, 8), $Z(19) = 3.9$, $p < 0.001$, 449 voxels], which was just below the threshold of FDR-corrected $p < 0.05$. Finally, we also found a strong correlation between the *d*' of the Disc task and GM volumes in the

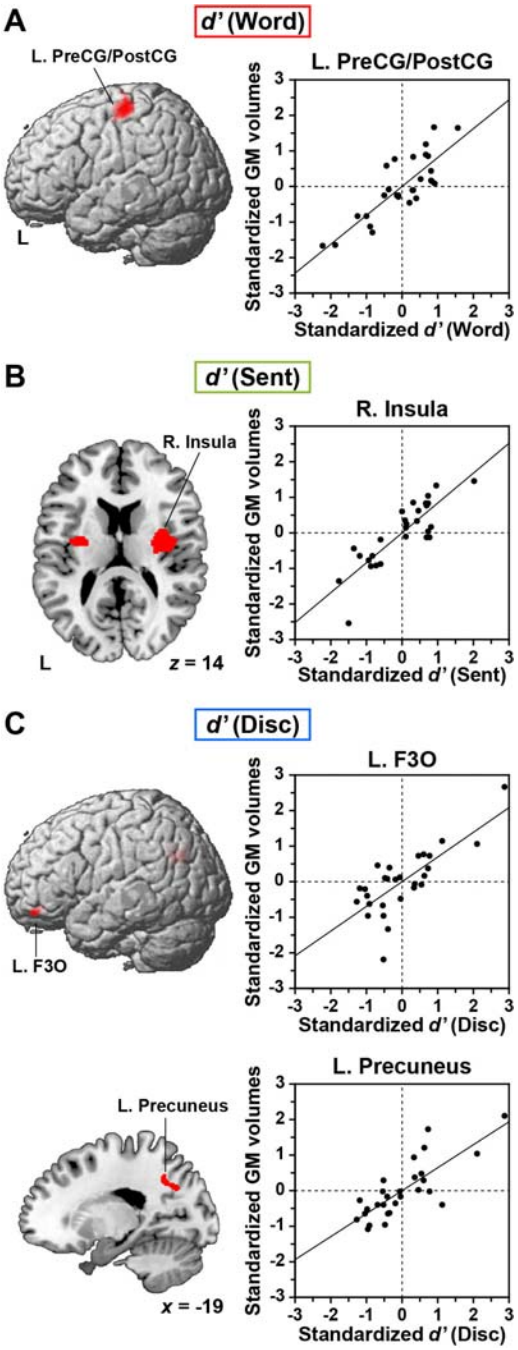

Figure 9. Anatomical signature for the linguistic proficiency of individuals in JSL. (A-C) Correlations between regional gray matter (GM) volumes and individual performances (*d*') of the Word **(A)**, Sent **(B)**, and Disc **(C)** tasks. Correlation maps (FDR-corrected $p < 0.05$) are projected onto the left lateral surfaces of a standard brain for the left PreCG/PostCG **(A)** and for the left F3O **(C)**. An axial slice ($z = 14$) is shown for the largest cluster in the right insula, as well as for the second largest cluster in the left insula **(B)**. A sagittal slice ($x = –19$) is shown for the largest cluster in the left precuneus **(C)**. Scattered plots and regression lines are shown for partial correlations between the standardized *d*' of each task and the standardized GM volumes at the peak voxel, after removing the effects of age, LQ, gender, age of hearing loss, AOAs of JSL, AOAs of JPN, and *d*' of the R task.

left F3O [(–46, 36, –24), $Z(19) = 4.0$, $p < 0.001$, 593 voxels] and in the left precuneus [(–19, –54, 41), $Z(19) = 4.2$, $p < 0.001$, 590 voxels] (Figure 9C). The left F3O cluster was anteroinferior, but very similar to the region identified in the fMRI contrast of Disc – R (Figure 7C). These results suggest an anatomical signature for the linguistic proficiency of individuals in a task-dependent manner.

3.4. Discussion

Here we analyzed cortical activity and GM volumes of Deaf participants, and clarified three major points. First, we found that activated regions in the frontal language areas gradually expanded in the dorso-ventral axis, corresponding to a difference in linguistic units for the three language tasks. Moreover, activations in each region of the frontal language areas were incrementally modulated with the level of linguistic integration. These dual mechanisms of the frontal language areas may reflect a basic organization principle of hierarchically integrating linguistic information. A previous fMRI study with passive (i.e., without on-line tasks) reading of English texts has reported that activations in the bilateral frontal and temporal regions increased in magnitude and spatial extent for each of these regions, with the greatest increase being induced by narratives, followed in order by unconnected sentences and word lists (Xu et al., 2005). However, neither hierarchical integration nor activation modulation by the linguistic levels free from stimulus differences has been previously clarified. We experimentally manipulated the task sets and linguistic units, separately from the stimuli themselves (see **3.2.3. Tasks**), and clarified that active integration processes actually modulated activations in the frontal language areas. Secondly, activations in the LPMC and F3op/F3t were left-lateralized, and direct comparisons among the language tasks exhibited more focal activation in these regions and the left F3O, suggesting their functional localization. Thirdly, we found significantly positive correlations between individual task performances and GM volumes in localized regions, even when the AOAs of JSL and JPN were factored out. More specifically, correlations with the performances of the Word and Sent tasks were found in the left PreCG/PostCG and insula, respectively, while correlations with those of the Disc task were found in the left F3O and left precuneus. These correlations suggest *anatomical* specialization of these regions related to individual abilities in sign languages, irrespective of a wide range of AOAs in both sign and vocal/written languages. These results demonstrate functional and anatomical correlates of hierarchical linguistic integration in the frontal language areas.

The present results suggest that the left LPMC, F3op/F3t, and F3O may primarily subserve word-, sentence-, and discourse-level integration, respectively. Hagoort and others have proposed a caudo-rostral gradient of the left inferior frontal cortex, in which unification processes of phonological, syntactic, and semantic elements are gradually represented in three corresponding regions from the left ventral BA 6 to BA 47 (Hagoort, 2005; Uddén and Bahlmann, 2012). In our previous fMRI and lesion studies, however, the left LPMC was more crucially recruited for processing scrambled sentences than active sentences, even when phonological factors were thoroughly controlled (Kinno et al., 2008; Kinno et al., 2009). The overactivation in the left LPMC in the Disc task compared with the Word and Sent tasks (Figures 8E, F) can be explained by the hierarchical nature of linguistic integration, such that the Disc task with discourse-level integration requires more intensive checking processes at word-and sentence-levels than do the other tasks without discourse-level integration. We propose that the input-driven information integrated at the word-level in the left LPMC is transmitted to the center of sentence-level integration in the left F3op/F3t, and that the left F3O integrates the information from these regions into coherent and meaningful discourses.

Lesion studies have shown that, as in vocal languages, damage in the left hemisphere caused aphasia in sign languages, while body movements or production of non-linguistic gestures were relatively spared (Corina et al., 1992; Hickok et al., 1996; Marshall et al., 2004). Many previous neuroimaging studies have also confirmed the left-lateralized activations in the fronto-parietal or fronto-temporal regions during phonological (MacSweeney et al., 2008), lexical (Leonard et al., 2012), and grammatical (Mayberry et al., 2011) judgment tasks in sign languages, while the spatial aspects of sign languages may activate the right hemisphere (Emmorey et al., 2002; Newman et al., 2002). In our previous fMRI study (Sakai et al., 2005), we examined cortical activity by contrasting similar Disc and Word tasks in JSL, and reported left-lateralized activation in the frontal and temporo-parietal regions in the JSL task for Deaf signers and hearing bilinguals (children of Deaf adults, CODA). By introducing the Sent task in the present study, we further demonstrated that syntax-selective activations in the left LPMC and F3op/F3t were clearly left-lateralized (Figure 8A). Our results establish that some aspects of the functional organization of frontal language areas in word-, sentence-, and discourse-level processing are common to all individuals, even if there is a considerable individual variability in linguistic proficiency.

In addition to the lateral frontal cortex, we observed consistent activation in the pre-SMA in the language tasks (Table 8). The pre-SMA has been associated with motor control for sequential articulations of syllables (Ziegler et al., 1997; Bohland and Guenther, 2006), and with visuo-spatial transformation in tasks such as mental rotation (Ecker et al., 2006), either of which may explain the consistent pre-SMA activation in the present study. In both the Sent – R and Disc – R, we also observed activation in the temporo-parietal regions, including the bilateral MTG/STG and the left AG, which are involved in phonological and lexico-semantic processes (Dronkers et al., 2004; Hickok and Poeppel, 2007). It is possible that these regions are recruited more intensively during the Sent and Disc tasks, i.e., at higher levels of integration of the phonological and lexico-semantic information. On the other hand, the right AG activation was selective to the Disc task (Figures 7D, 8E), indicating its recruitment only at the highest level of linguistic integration. In addition to these cortical activations, we observed significant activation in the cerebellum in Sent – R, and that in the caudate in both Sent – R and Disc – R. Some previous studies have suggested that on-line linguistic processing is also controlled by the internal model of the cerebellum (Ito, 2008; Lesage et al., 2012), and that the caudate plays an important role in bilingual switching (Crinion et al., 2006; Tan et al., 2011). Our task actually required on-line detection of linguistic errors with a time constraint, and most of the participants were bilinguals in JSL and JPN.

Previous VBM studies have shown that increased GM volumes in distinct regions were associated with proficiencies in different aspects of vocal languages, including vocabulary, literacy, or syntactic abilities (Mechelli et al., 2004; Lee et al., 2007; Carreiras et al., 2009; Nauchi and Sakai, 2009). The increased GM volume in the dorsolateral surface of the left PreCG/PostCG (i.e., the “hand area”) may be related to the better acquisition of subtle and complex hand movements by signers, who would therefore have better lexical knowledge in JSL as well. A previous VBM study has shown that GM volumes in the *bilateral* primary motor and somatosensory cortices were larger in professional keyboard players than non-musicians (Gaser and Schlaug, 2003). It is striking to note that the signers with right-hand dominance for general motor controls in our study showed a prominent correlation in the *left* PreCG/PostCG. Indeed, even two-hand signs have certain phonological constraints, such that the handshapes and movements must be either more complex in the dominant hand or symmetric in both hands (Sandler and Lillo-Martin, 2006). As regards the insula with a significant correlation between its GM volumes and the *d*' of the Sent task, previous voxel-based lesion symptom mapping and fMRI studies have shown that the anterior insula is critical for coordinating speech articulation (Dronkers, 1996; Bohland and Guenther, 2006; Kemeny et al., 2006; Baldo et al., 2011). The precuneus, in which we observed a significant correlation between the GM volumes and the *d*' of the Disc task, has been shown to be involved in the shifting attention between different locations in space necessary for the coordination of motor control (Wenderoth et al., 2005), and also to be necessary for the production of signs with both hands. Based on the suggested motor-related functions of the left PreCG/PostCG, insula, and precuneus, we suspect that these regions have supportive roles in accomplishing correct linguistic decisions in sign languages. In contrast, the left F3O, the GM volumes of which were significantly correlated with the *d*' of the Disc task, would also be functionally specialized in discourse-level integration, further supporting its pivotal role in sentence comprehension.

CHAPTER 4.

General Discussion

In the present MEG study, we clearly demonstrated that the left F3op/F3t plays a predictive role in syntactic processing, which depends on the canonicity determined by argument structures. Some psycholinguistic studies have reported anticipatory or predictive effects of the semantic information from precedent phrases, using a plausibility judgment task or eye-tracking method (Boland et al., 1995; Kamide et al., 2003). According to these views, semantic information of arguments can be incrementally integrated to accomplish on-line syntactic processing, such as filler-gap and semantic-role assignment. In our paradigm with P^+ vs. P^- sentences, we suggest that more abstract semantic information of animacy or possessor, directly related to syntactic processing rather than the meaning of a word itself, was utilized as cues to make predictions. As demonstrated by the responses in the left F3op/F3t here, such predictions from precedent NPs would be formulated online and facilitate syntactic processing.

Our present MEG results further indicate that predictive effects or top-down facilitation, which has been one of critical issues in the neuroscientific study of perception (Bar et al., 2006; Summerfield et al., 2006), also plays an important role in syntactic processing. We also demonstrated that syntactic predictions generated in the left F3op/F3t actually depend on the structural distance between the NPs and verb, which has been emphasized in modern linguistics (Chomsky, 2011). The neuroimaging studies, therefore, not only confirm the theory of linguistics but provide useful evidence for linguistics, auguring a future in which advances in the two fields are merged.

The hierarchical integration in the frontal language areas in the present fMRI study may be reminiscent of the recently proposed idea of a “temporal receptive window” (TRW) (Hasson et al., 2008; Lerner et al., 2011), which is the time length of effective stimuli for a cortical region, in analogy with the spatial receptive fields of neurons in the visual system (Hubel, 1988). By using an intersubject correlation analysis for fMRI data, Hasson et al. have shown a hierarchical organization of TRWs from lower- to high-order areas within the bilateral occipital and temporo-parietal cortices for silent movies and speech sounds, respectively. In the bilateral frontal cortex, however, responses were scattered and limited to longer TRWs in these previous studies. In the present study, in contrast, hierarchical integration was most prominent in the frontal language areas, and this organization was closely linked with integration of linguistic information, rather than that of sensory information. Moreover, each specific region of the frontal language areas was overactivated at higher levels of linguistic integration (Figure 7E), whereas the regions with shorter TRWs (e.g., the primary visual and early auditory cortices) responded similarly to stimuli regardless of a larger temporal context in their studies. The sources of these distinctions could be the different stimuli, tasks, or analyses employed, as well as the hierarchical nature of linguistic integration. Nevertheless, it would be interesting to imagine that specific linguistic functions take over a general organizing principle based on TRW in the frontal language areas.

In spite of the fact that we utilized JSL and examined Deaf signers, which included some children and disproportionate numbers of females, we found *consistently* left-lateralized activation in the frontal language areas among the participants we tested (Figures 7 and 8). Moreover, each of these activated regions precisely matched one of those reported by the present MEG and previous neuroimaging studies with vocal languages, which showed the involvement of the left LPMC and/or F3op/F3t in syntactic processing, as well as that of the left F3O in sentence comprehension. The new finding of the present fMRI study is that the frontal language areas in the dorso-ventral axis are hierarchically organized in correspondence with the different levels of linguistic integration. The striking consistency of the organization within our Deaf population indicates the *universality* of linguistic processing beyond modality differences and human diversities, which would also be generalizable to other individuals in any natural languages that are based on universal grammar (Chomsky, 1965). Our MRI study demonstrated the functional and anatomical correlates of hierarchical linguistic integration in the frontal language areas and other regions. The unification of functional and anatomical studies would thus be fruitful for understanding human language systems from the aspects of both universality and individuality.

Conclusions

Recent lesion and neuroimaging studies have shown that the left F3op/F3t is selectively involved in syntactic processing. In the present thesis, I explained how syntactic and other linguistic processes are temporally and spatially integrated in the left frontal cortex. For this purpose, I investigated the functional anatomy of the left frontal cortex for structure-dependent sentence processing from two different directions of research. First, using MEG, I examined temporal dynamics of the left Fop/F3t responses for syntactic processing, which was indeed influenced by semantic processes of sentences. The MEG results demonstrated that the left F3op/F3t played a predictive role in syntactic processing, which depended on the canonicity determined by argument structures. Second, using fMRI and VBM, I investigated functional organization of the left frontal cortex for different levels of linguistic integration in a sign language, and I further examined correlations between the individual task performances and regional GM volumes. The fMRI results revealed the novel dorso-ventral organization of the left frontal cortex for hierarchically integrating linguistic information. These results support the important role of the left frontal cortex in modality-independent and universal linguistic processes. On the other hand, the VBM results showed that GM volumes of the left frontal cortex and other cortical regions were related to individual differences in sign language proficiency. These results suggest a fruitful unification of functional and anatomical studies for understanding human language systems from the aspects of both universality and individuality. The present study with a paradigm based on modern linguistic theory contributes to deep understanding of the core property of the human mind.

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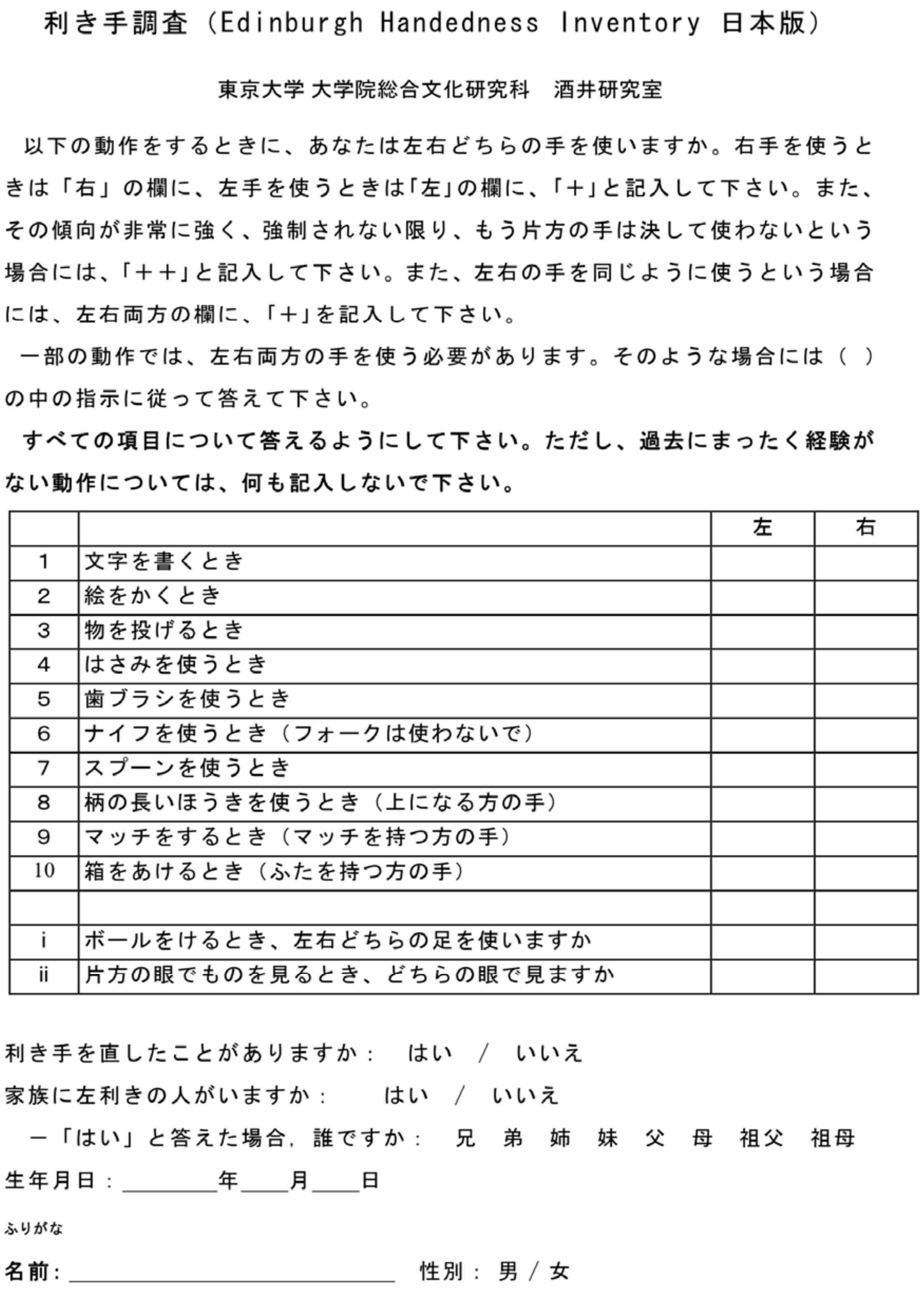
Appendices



利き手調査（Edinburgh Handedness Inventory 日本版）

東京大学 大学院総合文化研究科　酒井研究室

以下の動作をするときに、あなたは左右どちらの手を使いますか。右手を使うときは「右」の欄に、左手を使うときは「左」の欄に、「＋」と記入して下さい。また、その傾向が非常に強く、強制されない限り、もう片方の手は決して使わないという場合には、「＋＋」と記入して下さい。また、左右の手を同じように使うという場合には、左右両方の欄に、「＋」を記入して下さい。

一部の動作では、左右両方の手を使う必要があります。そのような場合には（ ）の中の指示に従って答えて下さい。

すべての項目について答えるようにして下さい。ただし、過去にまったく経験がない動作については、何も記入しないで下さい。

		左	右
1	文字を書くとき		
2	絵をかくとき		
3	物を投げるとき		
4	はさみを使うとき		
5	歯ブラシを使うとき		
6	ナイフを使うとき（フォークは使わないで）		
7	スプーンを使うとき		
8	柄の長いほうきを使うとき（上になる方の手）		
9	マッチをするとき（マッチを持つ方の手）		
10	箱をあけるとき（ふたを持つ方の手）		
i	ボールをけるとき、左右どちらの足を使いますか		
ii	片方の眼でものを見るとき、どちらの眼で見ますか		

利き手を直したことがありますか：　はい　／　いいえ

家族に左利きの人がいますか：　はい　／　いいえ

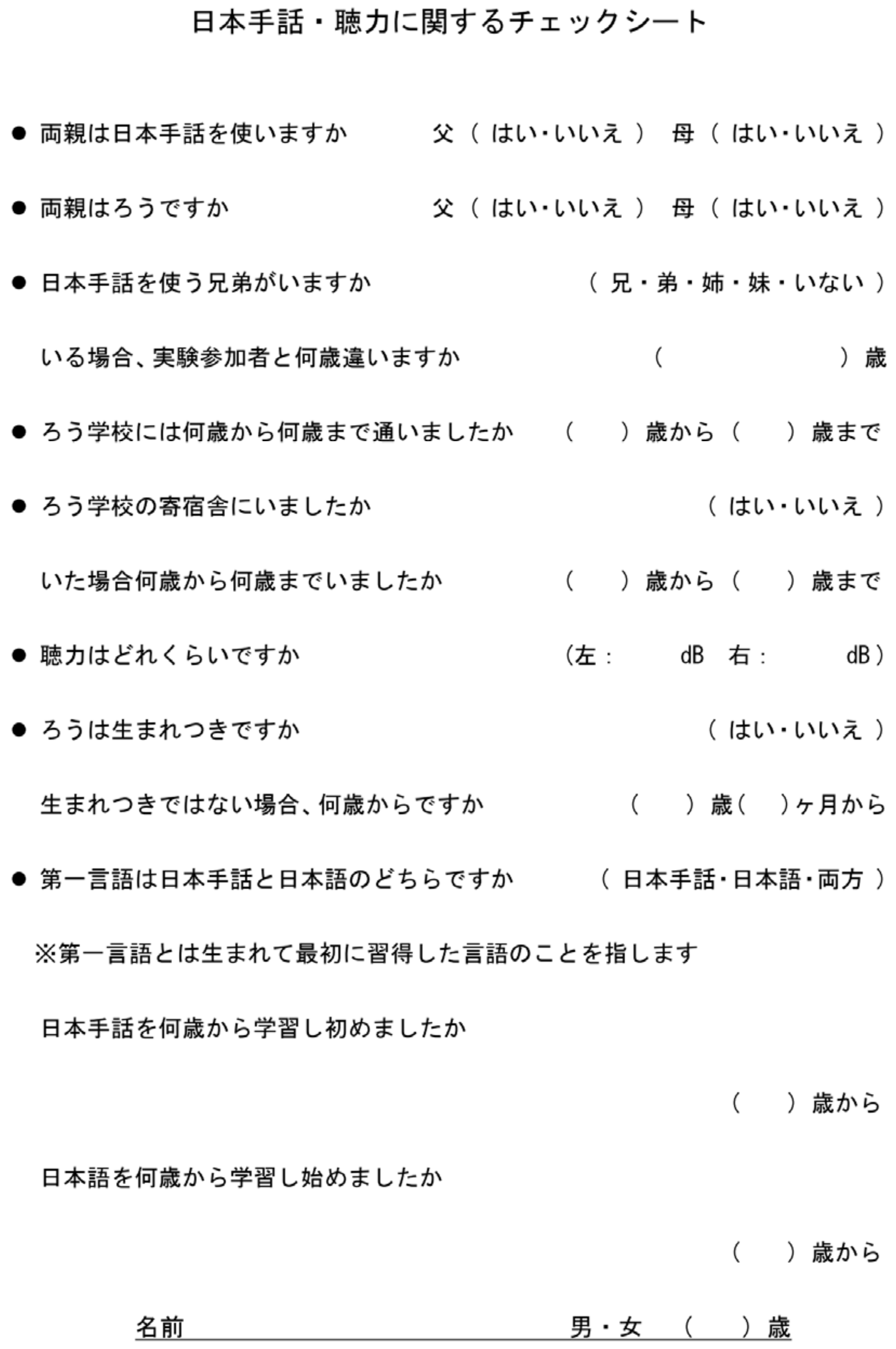
ー「はい」と答えた場合，誰ですか：　兄　弟　姉　妹　父　母　祖父　祖母

生年月日：________年____月____日

ふりがな

名前：____________________________　性別：　男 ／ 女

Appendix 1. Check sheet of LQ for the participants.



日本手話・聴力に関するチェックシート

● 両親は日本手話を使いますか　父 (はい・いいえ)　母 (はい・いいえ)

● 両親はろうですか　父 (はい・いいえ)　母 (はい・いいえ)

● 日本手話を使う兄弟がいますか　(兄・弟・姉・妹・いない)

いる場合、実験参加者と何歳違いますか　(　　　　　) 歳

● ろう学校には何歳から何歳まで通いましたか　(　　) 歳から (　　) 歳まで

● ろう学校の寄宿舎にいましたか　(はい・いいえ)

いた場合何歳から何歳までいましたか　(　　) 歳から (　　) 歳まで

● 聴力はどれくらいですか　(左：　　dB　右：　　dB)

● ろうは生まれつきですか　(はい・いいえ)

生まれつきではない場合、何歳からですか　(　　) 歳 (　　) ヶ月から

● 第一言語は日本手話と日本語のどちらですか　(日本手話・日本語・両方)

※第一言語とは生まれて最初に習得した言語のことを指します

日本手話を何歳から学習し初めましたか

(　　) 歳から

日本語を何歳から学習し始めましたか

(　　) 歳から

名前＿＿＿＿＿＿＿＿＿＿＿＿＿＿＿＿　男・女　(　　) 歳

Appendix 2. Check sheet of JSL/JPN experience and hearing status for the Deaf participants.