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Update article

Sentence processing is uniquely human

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Abstract

In this article, we will focus on three fundamental issues concerning language processing in the human brain, and update recent advances made by functional neuroimaging and magnetic stimulation studies of language. First, we will provide the first experimental evidence that the neural basis of sentence comprehension is indeed specialized. Specifically, our recent functional magnetic resonance imaging (fMRI) study has clarified that the human left prefrontal cortex (PFC) is more specialized in the syntactic processes of sentence comprehension than other domain-general processes such as short-term memory. Second, the distinction between explicit and implicit syntactic processes will be clarified, based on our fMRI studies that elucidate syntactic specialization in the left PFC. Third, we will advance a hypothesis stating that distinct subregions of the left PFC are recruited for the syntactic integration of lexico-semantic information. The current direction of research in the neuroscience of language is beginning to reveal the uniqueness of the human mind.
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1. The uniqueness of sentence processing

There is a tacit assumption in neuroscience from the genetic to the systemic level, which holds that the biological foundations of humans are essentially similar to those of non-human primates, and that even human language can be understood by extending experiments with monkeys and apes (Trefil, 1997; Gannon et al., 1998; Ramus et al., 2000; Cantalupo and Hopkins, 2001; Fujiyama et al., 2002). Language function closely interacts with other cognitive faculties of the mind, such as perception, memory, and consciousness, which have hampered the study of essential processes involving linguistic components alone (Sakai et al., 2001). Previous studies have examined various cognitive functions in the prefrontal cortex (PFC) of monkeys to find homologs of human cognitive functions, and have claimed that there are anatomical and functional commonalities between the PFCs of monkeys and humans (Barbas and Pandya, 1989; Rizzolatti and Arbib, 1998; Nakahara et al., 2002). Both monkey and human studies have reported that the PFC plays a critical role in executive processes, which operate on short-term memory and contribute to general cognitive functions (Fuster, 1989; Smith and Jonides, 1999; Levy and Goldman-Rakic, 2000). In accordance with these prevailing views, it has been assumed that language processing is, in principle, not entirely different from the combination of other cognitive functions commonly found in monkeys and humans.

However, it has been known that human language is radically different from what is known as animal communication. 'Ape language' should not be called a language, because there is no convincing evidence of syntactic structures or word orders in ape language. According to critical assessment of a chimpanzee's signs, the mean length of each utterance is no more than 1.6 words, and even longer utterances lack rule-governed combinations of signs (Terrace, 1979). Although dissenting views continue to be voiced (Savage-Rumbaugh

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and Lewin, 1994), the evidence of Kanzi's 'program-mar' is far from rule systems found in natural languages, and it has not been shown that Kanzi's understanding of human utterances is grammatical in nature, which would be based on associative mechanisms of learning instead (Sakai and Miyashita, 1993). It is known that apes are able to use a few hundred words, but the numbers of words are clearly limited, while children in contrast exhibit the explosive expansion of words in their first several years (Lieberman, 1991). Given these contrasting abilities between humans and non-human primates, we have to ask if there is something unique both to humans and to human language. Recently, Hauser, Chomsky, and Fitch have proposed that *recursion* is the only uniquely human component of the faculty of language (Hauser et al., 2002), which is also known as the property of *discrete infinity*, the ability to generate an infinite range of discrete expressions from a finite set of elements. Sentences are indeed such infinite expressions generated from a limited set of sounds, signs, or letters. Chomsky has proposed that this property is instantiated in human languages by syntactic mechanisms (Chomsky, 2000). Our position is that sentence comprehension characterizes human languages, and that its neural basis is uniquely human.

The most critical question to be addressed here is whether there exists a specialized (*domain-special*) neural system for human language processing that is separable from other *domain-general* systems. Activations of the left PFC have been attributed to the executive processes for working memory or to cognitive demands in general (Smith and Jonides, 1999; Duncan and Owen, 2000). However, there is no direct proof of one-to-one correspondence between brain functions and cortical regions, and it is possible that the left PFC is modulated primarily by domain-special factors and secondarily by domain-general factors. We recently tested this hypothesis by directly comparing the brain activations in syntactic decision tasks with those in verbal short-term memory tasks (Hashimoto and Sakai, 2002). In each trial of syntactic decision tasks, one complete sentence was presented to judge whether the subject of a verb corresponded to one of two persons, or to judge whether a pronoun was able to refer to one of two persons in the sentence. These tasks explicitly required to utilize the structure-dependent rules. One example of a Japanese sentence used to represent the syntactic decision tasks was '*Taro-wa Saburo-ga kare-wo homeru-to omou*' ('*Taro thinks that Saburo praises him*'). In a verbal short-term memory task for words, phrases of one sentence were rearranged into separate groups of nouns and verbs, so that they were syntactically unrelated. A pair of phrases were then presented to judge their temporal orders in the original sequence. Its task requirements including memory encoding and retrieval are commonly involved in standard verbal short-term memory tasks. One example used in this task was '*kare-ni Taro-ni Saburo-ni omou homeru-to*' ('*him Taro Saburo thinks praises*'). Using functional magnetic resonance imaging (fMRI), we found that the left dorsal prefrontal cortex (DPFC, mainly in Brodmann's area (BA) 8), as well as the left pars opercularis and pars triangularis of the inferior frontal gyrus (F3op/F3t, BAs 44/45), show selective activation for syntactic decision tasks when they were directly compared with the verbal short-term memory task (Fig. 1A; red regions). The activation of these regions is related to processes of analyzing syntactic structures, and it cannot be explained either by task difficulty or by verbal short-term memory components such as the phonological store, the subvocal rehearsal system, and the central executive. Activation due to those domain-general factors was observed in the left precentral gyrus, the left parietal operculum, and the right anterior cingulate cortex (Fig. 1A; green regions). To our knowledge, this study is the first to clarify that the human left PFC is more specialized in the syntactic processes of sentence comprehension than other domain-general processes. These results further demonstrate that sentence processing is predominantly controlled by the left hemisphere, whereas there is no such clear functional lateralization for the general cognitive factors commonly found in primates, suggesting that the cerebral dominance may represent the uniqueness of human language processing. Linguists have provided a clear conceptualization of what distinctions need to be made between syntactic processing and other cognitive processes in order to account for linguistic competence (Chomsky, 1980). We believe that the identification of the cortical regions responsible for the essential properties of syntactic processing eventually leads to an understanding of how language is specialized and instantiated in the human brain.

Recently, we further demonstrated a causal link between syntactic processing and activation in the left F3op/F3t by using transcranial magnetic stimulation (TMS) (Sakai et al., 2002). In this study, we employed a minimal-pair paradigm (Table 1; syntactic and semantic decision tasks with visual stimuli), in which only one linguistic element differs between a stimulus pair. This TMS study has provided new findings that are striking in three ways: (1) event-related TMS pulses selectively reduced reaction times (RTs) in explicit syntactic decisions but not in explicit semantic decisions, which is unexpected according to the known TMS effects on cognitive processes, (2) this effect was observed during syntactic decisions regarding both normal and anomalous sentences, and (3) this effect was observed when magnetic stimulation was administered to the left F3op/F3t at a specific timing (150 ms from a verb stimulus), but not to the left F2 (the middle frontal gyrus) (Fig. 1B). As to the first point, the temporally-restricted and
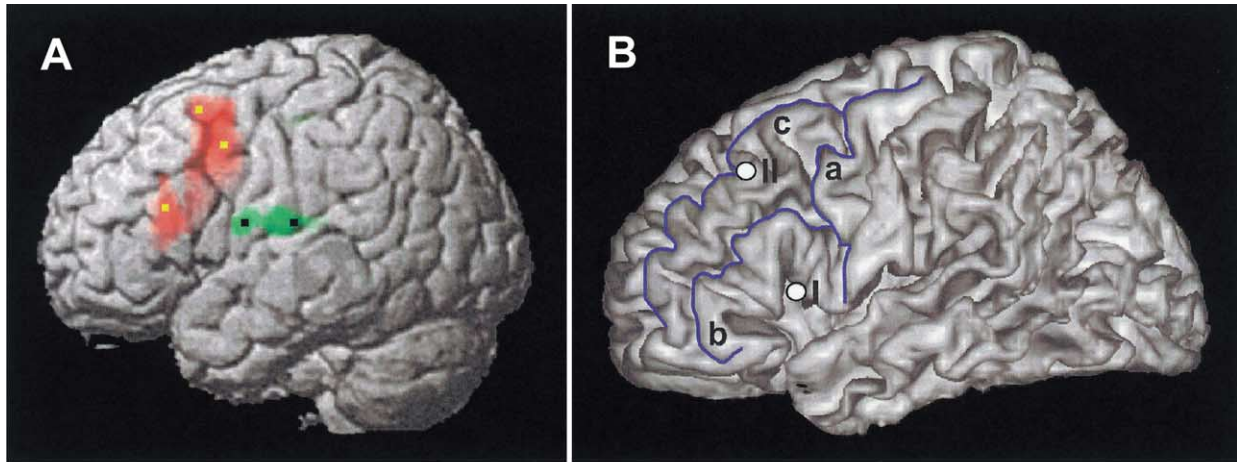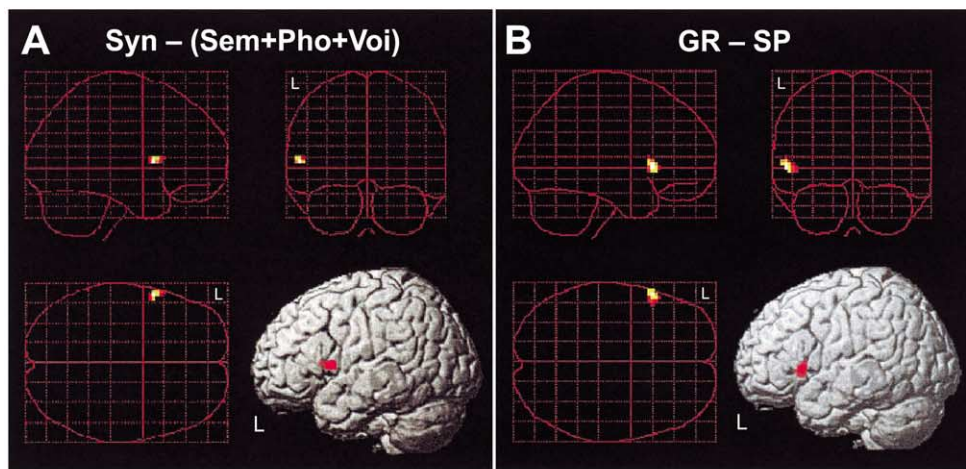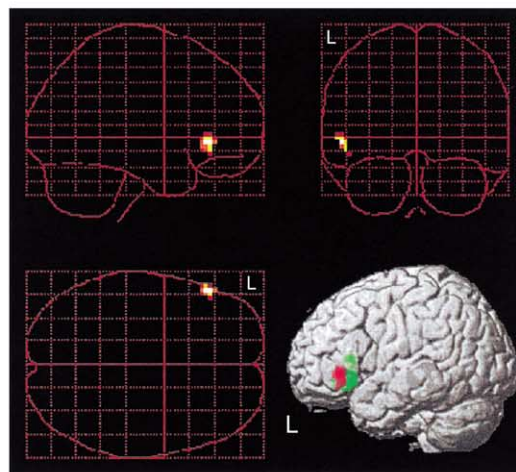
Fig. 1

Fig. 2

Fig. 3

Fig. 1. (A) Selective activation for syntactic processing in the left PFC. Regions identified by directly comparing syntactic decision tasks and a short-term memory task for words (red) are projected together onto the left hemisphere of a surface-rendered standard brain (Hashimoto and Sakai, 2002). When the short-term memory task for words was compared with an easier short-term memory task, activation was observed in the left precentral gyrus and the left parietal operculum (green). (B) The sites for TMS in the left F3op/F3t (site I) and in the left F2 (site II) on the left lateral surface image of the standard brain (Sakai et al., 2002). a, the precentral sulcus; b, the inferior frontal sulcus; c, the superior frontal sulcus.

Fig. 2. (A) Selective activation for explicit syntactic processing in the left F3op/F3t. Activated regions were identified by comparing a syntactic decision task (Syn) and other tasks (Sem, Pho, and Voi; Table 1), combining normal and anomalous sentence conditions for each task (Suzuki and Sakai, 2003). They are projected in three orthogonal planes and onto the left hemisphere (L) of a surface-rendered standard brain. A voice-pitch comparison (Voi) task was also included in the comparison. (B) A syntactic specialization in the left F3op/F3t for detecting syntactic anomaly. Activation in a grammatical error-detection task (GR, explicit syntactic processing of ungrammatical sentences) was directly compared with that in a spelling error-detection task (SP, implicit syntactic processing of sentences containing spelling errors), revealing a single locus in the left F3op/F3t (Embick et al., 2000). The threshold was set at $P < 0.05$, corrected for multiple comparisons.

syntax-selective reduction of RTs suggests the physiological effects of facilitation or priming, such that the stimulation of the left F3op/F3t at a specific timing enhances its normal function. Indeed, the mean reduction of RTs for syntactic decisions (normal sentences: 14 ms, anomalous sentences: 25 ms) were comparable to that of a previous behavioral study, in which the RTs for lexical decision were reduced when primed by a syntactically appropriate word (Goodman et al., 1981). It is possible that a TMS temporarily raises the overall excitability of neurons, thus making an alerted state of 'stand-by', which leads to more effective activation when specific responses of those cells are required for syntactic decisions. With respect to the second point, the TMS effects on normal and anomalous sentences were in agreement with the left F3op/F3t activation observed in our event-related optical topography (OT) study using the same minimal-pair paradigm (Table 1) with auditory stimuli (Noguchi et al., 2002), indicating that common processes were involved both in judging a sentence to be normal and in judging it to be anomalous for each task. Therefore, explicit syntactic processing subsists not only in detecting syntactic anomalies per se, but in analyzing syntactic consistency in a sentence. This finding was achieved by utilizing event-related TMS and OT, thereby differentiating trials with normal and anomalous sentences. Even if 'normal' sentences are physically identical stimuli used in both the syntactic and semantic tasks, we have demonstrated that TMS resulted in differential effects on normal sentences that paralleled the effects on anomalous sentences, depending on the types of explicit linguistic decisions being made.

2. Explicit versus implicit syntactic processing

The results of Hashimoto and Sakai (2002) have further suggested that there is a distinction between unconscious, obligatory sentence processing and conscious, controlled sentence processing. In that study, we found that the left DPFC is activated when syntactic information is processed at the sentence level without explicit instructions, and that the left F3op/F3t is additionally activated when explicit syntactic decisions are required. Consistent with these findings, our event-related fMRI study (Suzuki and Sakai, 2003) using the minimal-pair paradigm (Table 1) with auditory stimuli clearly established that the left F3op/F3t is involved

more in explicit syntactic processing (as in the syntactic decision task) than in *implicit* syntactic processing (as in the semantic and phonological decision tasks) (Fig. 2A). Moreover, its activation is specific to syntactic judgements regarding both normal and anomalous sentences, which is consistent with the above-mentioned TMS study (Sakai et al., 2002) and OT study (Noguchi et al., 2002). The left F3op/F3t activation in Suzuki and Sakai (2003) matched with that of our previous fMRI study using a block design (Embick et al., 2000). In the latter fMRI study, we used an error-detection paradigm that contrasted explicit syntactic processing of ungrammatical sentences and implicit syntactic processing of sentences containing spelling errors, using the same lexical material across these conditions. We found that the ungrammatical sentences produced more activation in the cortical language areas than did the sentences with spelling errors, and that the difference in activation was significantly greater in the left F3op/F3t than in other language areas (Fig. 2B). Recent imaging studies from other labs have accumulated evidence of the involvement of the left DPFC and F3op/F3t in syntactic processing (Stromswold et al., 1996; Just et al., 1996; Caplan et al., 1998; Dapretto and Bookheimer, 1999; Kang et al., 1999; Friederici et al., 2000b; Moro et al., 2001; Indefrey et al., 2001). In these studies, the syntactic knowledge of English, German, or Italian languages was tested in native speakers. Although various aspects of sentence processing are substantially different, the consistent activation of the left DPFC and F3op/F3t in these studies and in our study using Japanese, a non-Indo-European language, suggests that syntactic specialization of the left PFC reflects the existence of universal grammar (UG) in the brain.

As proposed by Fodor, modular processes are by their very nature automatic and implicit (Fodor, 1983). The suggested specialization of the left DPFC for implicit information processing in the syntactic domain indicates that it is a putative syntactic module. The activation of the left DPFC due to non-syntactic tasks and non-automatic syntactic tasks reported in some previous studies does not necessarily contradict this hypothesis, because it is always difficult to control automatic syntactic factors involved in inner speech while thinking. In normal language comprehension, one does not explicitly but automatically process syntactic information. On the other hand, explicit syntactic processing is employed when sentence comprehension

Fig. 3. Sentence-processing selective activation in the left F3t/F3O. An activated region identified by comparing a sentence comprehension task and a lexical decision task under the auditory condition is projected in three orthogonal planes and onto the left hemisphere (L) of a surface-rendered standard brain (a red region) (Homae et al., 2002). An activated region identified by comparing a sentence comprehension task and a lexical decision task under the visual condition is also rendered on the standard brain (a green region). Almost all voxels of the activated region under the auditory condition, which were localized within the left F3t/F3O, coincided with those under the visual condition.

Table 1
Examples of stimuli used in the syntactic, semantic, and phonological decision tasks

Task	Normal stimuli	Anomalous stimuli
Syntactic decision (*Syn*)	'yuki-wo sawaru' snow-Acc touch (vt) (*Someone*) *touches snow*	'yuki-wo tsumoru' snow-Acc lie (vi) (*Something*) *lies snow*
	'iro-wo mazeru' color-Acc blend (vt) (*Someone*) *blends colors*	'iro-wo medatsu' color-Acc stand out (vi) (*Something*) *stands out the color*
Semantic decision (*Sem*)	'yuki-ga tsumoru' snow-Nom lie (vi) *Snow lies* (*on the ground*)	'yuki-ga nigeru' snow-Nom escape (vi) *Snow escapes*
	'iro-ga medatsu' color-Nom stand out (vi) *The color stands out*	'iro-wo sawaru' color-Acc touch (vt) (*Someone*) *touches color*
Phonological decision (*Pho*)	'yuki-wo sawaru' (L–H–L) (L–H–H) (*Someone*) *touches snow*	'yuki-wo sawaru' (L–H–L) (H–L–L) (*Someone*) *touches snow*
	'iro-ga medatsu' (L–H–L) (L–H–L) *The color stands out*	'iro-ga medatsu' (L–H–L) (H–L–L) *The color stands out*

A minimal-pair paradigm that distinguishes the difference among explicit syntactic, semantic, and phonological processing in sentence comprehension (Suzuki and Sakai, 2003). In the syntactic decision (Syn) task, the subjects were asked to judge whether a presented sentence was syntactically normal (N) or anomalous (A). In the semantic decision (Sem) task, the subjects judged whether a presented sentence was semantically N or A. In the phonological decision (Pho) task, the subjects judged whether a presented stimulus was phonologically N or A. In the Syn task, nouns with accusative (Acc) case particles can produce either N or A stimuli, depending on whether a transitive verb (vt) or intransitive verb (vi) is used. In the Sem task, nouns with Acc or nominative (Nom) case particles can produce either N or A stimuli, depending on the denotative meaning of the verb used. In the Pho task, verbs with different accent patterns (L: low, H: high) can produce either N or A stimuli.

becomes more difficult, as in the case of garden-path or ambiguous sentences (e.g., '*The horse raced past the barn fell*'). In the presence of explicit task requirements like the syntactic task employed in our experiments, explicit syntactic processing is employed to judge the syntactic correctness of an utterance. Thus it follows that the regions activated by explicit syntactic processing involve all regions related to implicit syntactic processing as well as any additional regions. Indeed, our fMRI studies demonstrated that both the left DPFC and the left F3op/F3t are activated when the explicit use of syntactic rules is required by the syntactic tasks (Hashimoto and

Sakai, 2002; Suzuki and Sakai, 2003). Recent imaging studies using Jabberwocky sentences, in which all content words were replaced with pseudowords while inflections and function words were maintained to preserve syntactic structures, have indicated that the left DPFC and/or the left F3op/F3t are involved in syntactic processing (Friederici et al., 2000a; Moro et al., 2001; Indefrey et al., 2001). These results support the involvement of at least two distinct prefrontal regions in syntactic processing.

The distinction between explicit and implicit syntactic processing raises a further question as to whether the left F3op/F3t is always dormant in implicit syntactic processing. Activation of the left F3op has been reported to occur in implicit syntactic processing (simple reading) of syntactically anomalous phrases (Kang et al., 1999). In another study, which required listening to a pair of sentences to determine whether they had the same literal meaning, the left F3op/F3t was activated for implicit syntactic processing of syntactically normal sentences (Dapretto and Bookheimer, 1999). The activation of the left F3op/F3t for syntactic processing may stem from the fact that the subjects explicitly paid attention to syntactic processing in spite of the absence of task requirements. The results of Suzuki and Sakai (2003) indicate that explicit tasks are more effective for clarifying the left F3op/F3t involvement in syntactic processing than are implicit tasks.

3. The syntactic integration of semantic information

Sentences convey not only lexico-semantic information for each word, but sentence meaning based on syntactic structures (Caplan, 1992; Sakai et al., 2001; Townsend and Bever, 2001; Friederici, 2002). The importance of syntactic structures has been elucidated, since Chomsky's discussion of the sentence '*Colorless green ideas sleep furiously*', in that sentence structure can be understood independently of meaning (Chomsky, 1957). Although this sentence conveys no meaningful information, it is clearly different from a list of words without syntactic structures: '*Furiously sleep ideas green colorless*'. Moreover, semantic processing at the sentence level differs from a simple summation of lexico-semantic processing for each word. For example, the meaning of '*John thinks that David praises his son*' clearly differs from that of '*John thinks that his son praises David*', though the lexical items involved in each of these sentences are identical. Thus, the processing of syntactic structures plays a critical role in the selective integration of lexico-semantic information into sentence meaning. In summary, syntactic analyses are performed in the service of semantics, and sentence meaning is derived from syntactic analyses of the sentence structures.

We have recently proposed that a ventral region in the left PFC extending from the pars triangularis (F3t, BA 45) to the pars orbitalis (F3O, BA 47) is a putative region for the selection and integration of semantic information, which are separable from simple lexico-semantic processing (Homae et al., 2002) (Fig. 3). In this fMRI study, we directly compared cortical activations in sentence comprehension tasks with those in lexical decision tasks. One sentence example translated into English is: '*May I take a picture here?*'—'*Yes, if you can break the flash*', wherein the original phrase '*do not use*' is replaced with '*can break*', to which the subjects respond by button-pressing. In the lexical decision task, the same phrases used in the sentence comprehension tasks were presented in a completely randomized order, thereby detecting pronounceable non-words. We found sentence-processing selective activation in the left F3t/F3O, and confirmed that the left F3t/F3O is activated under both auditory and visual conditions. These results demonstrate that the sentence-related processes in this region are essentially amodal and thus beyond modality-dependent lexical processing. The remaining critical question to be answered is how lexico-semantic information is integrated by syntactic-structure analyses.

Previous neuroimaging studies have reported controversial results as to whether or not distinct cortical regions subserve the critical processes of syntax and lexico-semantics. While Röder et al. (2002) have reported that the activation of a left region of F3op/F3t reflects both syntactic and semantic effects in sentences, Dapretto and Bookheimer (1999) have claimed that F3op and F3O are differentially involved in syntactic processing and lexico-semantic processing, respectively. Regarding this controversy, we believe that the following five points should be addressed. First, each of the studies by Dapretto and Bookheimer (1999) and Röder et al. (2002) employed a single task requiring either semantic or syntactic processing under all of the contrasting conditions tested. Dapretto and Bookheimer (1999) asked the subjects to judge whether or not the meaning of two sentences differ, while Röder et al. (2002) asked the subjects to count the number of grammatical errors. It is possible that the resultant activation patterns were biased by one type of processing explicitly required in the tasks. Second, semantic processing at the sentence level is not identical to lexico-semantic processing for each word. Dapretto and Book-heimer (1999) have regarded lexico-semantic information as sentence meaning, but the two are qualitatively different, as discussed above. Röder et al. (2002) have examined sentence meaning for all-or-none conditions, in which the contribution of lexico-semantic processing cannot be separated from sentence meaning. Third, a direct comparison of syntactic versus semantic conditions, which was employed by Dapretto and Book-

heimer (1999), eliminates all regions related to the syntactic processing that is involved in both conditions. Fourth, a direct comparison between normal and Jabberwocky (nonsense) sentence types, which was employed by Röder et al. (2002), does not cancel out all syntactic processes as they proposed, but leaves behind syntactic reanalyses required for the interpretation of sentence meaning. Indeed, they reported significant interaction between sentence types and syntactic difficulty in the left F3op/F3t. Finally, it is still possible that activations related to syntactic and semantic processing of sentences reflect domain-general cognitive factors such as task difficulty and short-term memory. It has been suggested that the left F3O is related to the maintenance of letter information (Henson et al., 2000).

In contrast to the static models of separate processes (Dapretto and Bookheimer, 1999) and overlapping processes (Röder et al., 2002) for syntactic and lexico-semantic information, we propose an alternative dynamic model, such that separate processes for building syntactic structures and evaluating lexico-semantic information interact with each other in the course of sentence processing. Because semantic interpretation of sentences is clearly dependent on syntactic information, this integration process is crucial in sentence comprehension (Smith and Wilson, 1979). One theoretical model has proposed an initial stage for building syntactic structures on the basis of word-category information, and a later stage for the integration of syntactic and lexico-semantic information (Frazier, 1987). In contrast, another model has assumed an interaction between syntactic and lexico-semantic processes from an early stage (Marslen-Wilson and Tyler, 1980). Taking either model, it is true that syntactic and lexico-semantic information is integrated in the course of sentence processing, which may subsist in the functional network of the left PFC. It would therefore be necessary to elucidate the neural mechanisms responsible for the syntactic integration of lexico-semantic information. Future studies would clarify the individual roles of the subregions in the left PFC that work in concert for human-unique sentence processing.

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