

Review

Sentence processing in the cerebral cortex

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Abstract

Human language is a unique faculty of the mind. It has been the ultimate mystery throughout the history of neuroscience. Despite many aphasia and functional imaging studies, the exact correlation between cortical language areas and subcomponents of the linguistic system has not been established. One notable drawback is that most functional imaging studies have tested language tasks at the word level, such as lexical decision and word generation tasks, thereby neglecting the syntactic aspects of the language faculty. As proposed by Chomsky, the critical knowledge of language involves universal grammar (UG), which governs the syntactic structure of sentences. In this article, we will review recent advances made by functional neuroimaging studies of language, focusing especially on sentence processing in the cerebral cortex. We also present the recent results of our functional magnetic resonance imaging (fMRI) study intended to identify cortical areas specifically involved in syntactic processing. A study of sentence processing that employs a newly developed technique, optical topography (OT), is also presented. Based on these findings, we propose a modular specialization of Broca's area, Wernicke's area, and the angular gyrus/supramarginal gyrus. The current direction of research in neuroscience is beginning to establish the existence of distinct modules responsible for our knowledge of language. © 2001 Elsevier Science Ireland Ltd and the Japan Neuroscience Society. All rights reserved.

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1. Introduction

Linguistics has addressed the following key questions:

1. What constitutes the knowledge of language?
2. How is the knowledge of language acquired?

Evidently, we know about language and can intuitively judge the grammaticality of a sentence as far as our native language is concerned. But such knowledge about grammatical rules is mostly implicit, and we cannot fully explain why it is grammatical. An adequate explanation of linguistic knowledge would require a detailed analysis of various sentences in accordance with a theoretical framework for linguistic structures. On the other hand, a human child can

acquire any natural language within a few years, without the aid of analytical thinking and without explicit instruction of 'grammars' usually taught at school. Therefore, the origin of grammatical rules should be ascribed to an innate system located in the human brain. Since language is a subsystem of the mind and the mind itself has biological constraints of the brain, language inherently reflects some aspects of biological properties. Linguistics can be regarded as an effort to discover the fundamental laws and general principles that explain the properties and constraints of language systems. Noam Chomsky has proposed a general framework for these inquiries as universal grammar (UG), a concept that revolutionized linguistics and cognitive science (Chomsky, 1957; Smith, 1999; Chomsky, 2000).

It is important to ask how language is related to or separated from other aspects of the mind. Probably

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inspired by Chomsky's modular approach to the study of mind (Chomsky, 1980), Fodor (1983) postulated 'the modularity of mind', which attributed language to an input system as one of modules like sensory systems. However, Chomsky claimed that it is too narrow to regard the 'language module' solely as an input system, and that it is rather a 'central system' (Chomsky, 1986). Our position is that the language system does indeed represent a distinct module, which is segregated from other systems of the mind, i.e. the modules of perception, memory, and consciousness (Fig. 1). Nevertheless, language closely interacts with these cognitive faculties of the mind. First, language is encoded by a series of phonemes (segmental units), and its phonological form can be perceived either through the auditory perception of speech sounds or through the visual perception of letters and signs. Phonemes are further recognized as meaningful units or semantic representation of words, in reference to stored information in long-term memory. As to the modularity of language and memory, there is experimental evidence that syntactic processing is separable from the working memory system underlying other general functions (Caplan and Waters, 1999). Further, normal speech comprehension and speech production is only possible in a conscious state. As Dennett (1978) noted, 'If one supposes...that one's thinking is one's 'stream of consciousness',... then we must grant that thinking is an activity restricted to language-users.' On the other hand, syntactic operations themselves, which govern the hierarchical organization of words and phrases in sentences, are mostly unconscious. These multiple processes of linguistic information suggest that the language system itself has internal modularity (Chomsky, 1984), and that it is further divided into distinct modules or subsystems, such as phonology, semantics, and syntax, which interact systematically with each other (Fig. 2).

The hypothesis of functional modules states that individual modules constitute a system as a whole. If modules of phonology, semantics, and syntax conceivably exist in the language system, information flow among these modules, as well as the roles of their

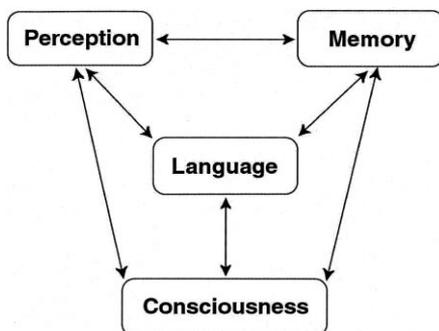


Fig. 1. A model of reciprocal interactions between cognitive components of mind and language

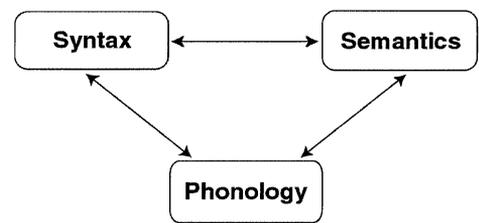


Fig. 2. Modules of language and their interactions.

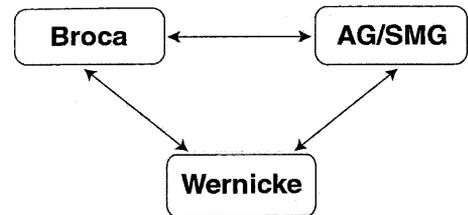


Fig. 3. Cortical language areas and their interactions.

interactions should be clarified. A further critical question is whether these modules correspond to distinct areas of the brain. The identification of specialized cortical areas responsible for these distinct aspects of linguistic competence is the first step towards understanding how language is instantiated in the brain. Lesion studies of aphasia, alexia, and agraphia have suggested three candidate areas for language function: Wernicke's area in the superior temporal cortex, AG/SMG (the angular gyrus (Brodmann's area (BA) 39) and the supramarginal gyrus (BA 40) in the parietotemporal cortex, and Broca's area (the pars opercularis (BA 44) and the pars triangularis (BA 45) in the inferior frontal cortex (Fig. 3). In this paper, we consider Wernicke's area as containing the planum temporale (BA 42/22), the superior temporal gyrus (BA 22), and the superior part of the middle temporal gyrus (BA 21). However, it should be noted that this conventional term is often too broad to specify particular areas. Despite the long history of neurolinguistic studies (Oblor and Gjerlow, 1999), the individual roles of these areas continue to be debated, and the exact correlation between cortical language areas and subcomponents of the linguistic system has not yet been established. Recently developed functional imaging techniques address these critical issues. Such imaging techniques should be combined with detailed anatomical studies in order to contribute to an understanding of both structural and functional bases of language information processing.

2. The module of syntactic processing

One key question that addresses the modular organization of language in the cerebral cortex is the undetermined role of Broca's area in syntactic processing, an

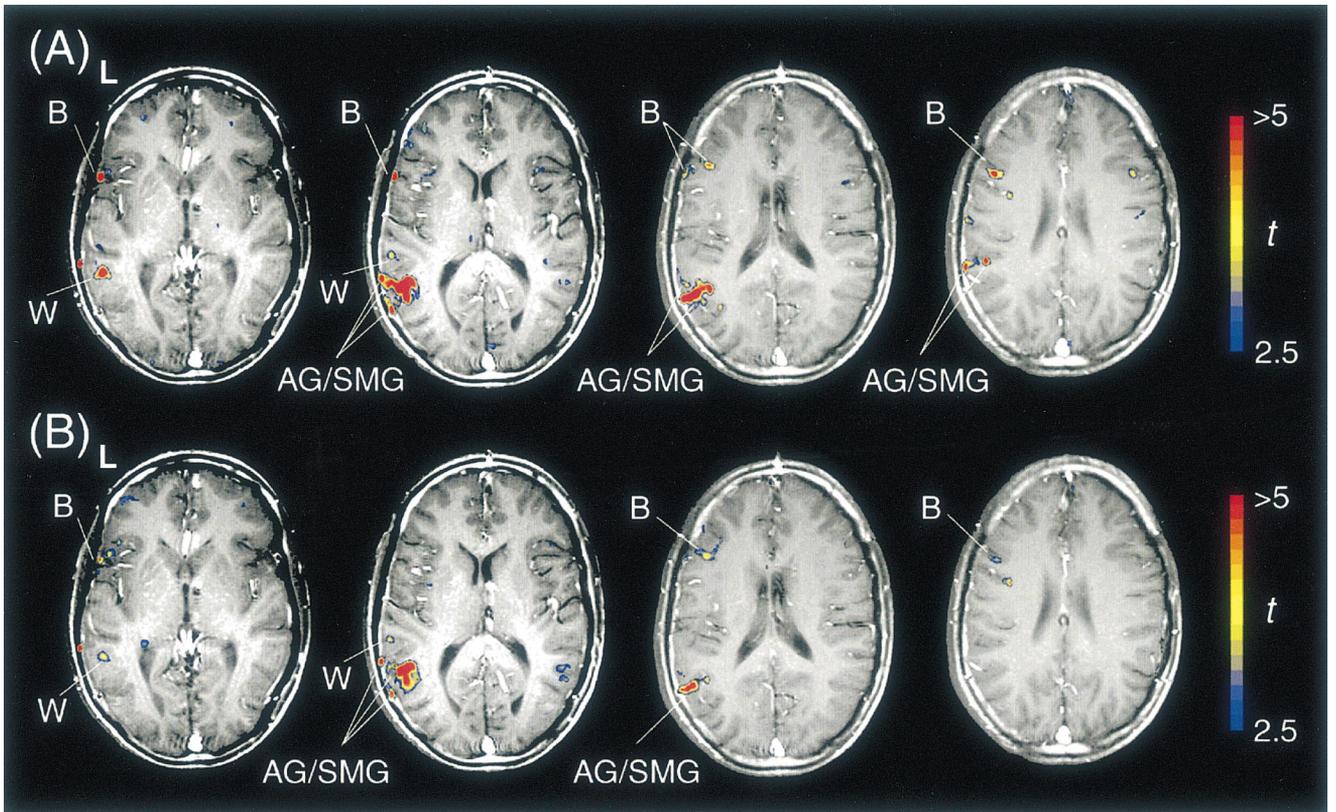


Fig. 4

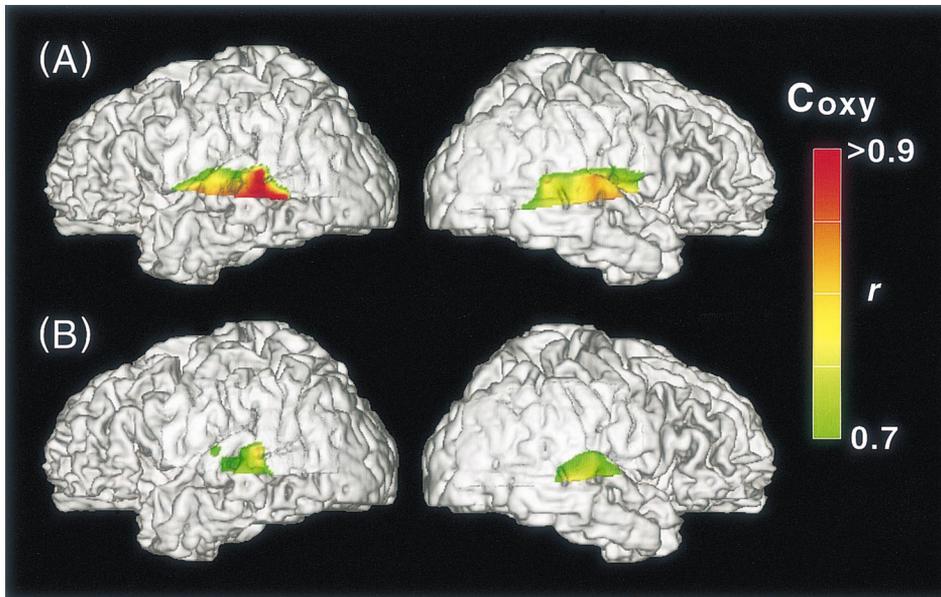


Fig. 6

Fig. 4. Cortical activation in grammar (GR) and spelling (SP) conditions. (A) GR vs CO; (B) SP vs CO. fMRI images in t -maps were superimposed on structural images showing $z = 4, 12, 20,$ and 28 horizontal slices for a single representative subject. The color bars at light indicate the t -values of the comparison. The left side (L) of the brain is shown at the left. Activation during the GR condition was generally greater in the language areas than activation during the SP condition; this difference was particularly prominent in Broca's area (B), compared with Wernicke's area (W) and AG/SMG (Embick et al., 2000).

Fig. 6. Superior temporal cortex activation during speech recognition. (A) Story task vs control; (B) Repeat task vs control. OT images in r -maps for signal changes averaged among all subjects were superimposed on lateral images of a brain. The color bars at night indicate the correlation coefficient (r) of C_{oxy} time points with a boxcar waveform (each period, 36 s; delay, 6 s). Note the prominent activation in the mid-lateral part of the bilateral temporal cortex.

issue which has been debated from a number of different perspectives. The notion that Broca's area is a locus for syntactic processing stems initially from the aphasia literature. After Broca's initial insight, Broca's area was first regarded as a speech production area, because patients diagnosed with Broca's aphasia were relatively or grossly inarticulate but were able to understand spoken language. The agrammatism of Broca's aphasics suggested that Broca's area is the locus of syntactic processing or the locus of the grammatical system (Geschwind, 1970; Goodglass, 1976). More recent studies, however, have argued that there is dissociation between Broca's aphasics' problems with syntactic processing/comprehension and lesions in Broca's area (Caplan et al., 1996; Dronkers, 1996), although dissenting views on this matter continue to be voiced (Grodzinsky, 2000).

Event-related brain potential (ERP) studies have identified a component, the P600, which correlates with a subject's recognition of syntactic ill-formedness (Osterhout and Holcomb, 1992; Gunter et al., 1997). However, the language specificity of this component has been challenged (Patel et al., 1998), and the specific cortical generator of the component has not been localized. A second component, the left anterior negativity (LAN), has also been associated with error detection in grammatical processing (Friederici et al., 1993; Münte et al., 1993). Its source is once again unclear, but its detection by left-anterior electrodes is suggestive of the involvement of Broca's area. In the imaging literature, activation in Broca's area has been found during the performance of some linguistic tasks, while other studies have argued for the involvement of Broca's area in decidedly nonsyntactic processing, such as in the phonological processing of words or letters (Poeppel, 1996; Fiez and Petersen, 1998). Two prior imaging studies (Stromswold et al., 1996; Just et al., 1996) have attributed activation in Broca's area during syntactic tasks to an increase in general complexity, rather than to any specific role played by this area as to syntax. In these studies, increased sentential complexity correlated with an increase in activity in Broca's area. Activity in Broca's area in these experiments might stem from the fact that Broca's area is specifically involved in syntactic processing, but it may simply reflect a general increase in demands on the entire linguistic system. In addition, verbal short-term memory may be primarily involved, rather than syntactic processing per se. The task used in one study was to judge the semantic plausibility of a visually presented sentence, and sentences with center-embedded and right-branching relative clauses were compared (Stromswold et al., 1996). Increased activity in Broca's area was observed in the same task under interference conditions that inhibited the subvocal rehearsal of sentences (Caplan et al., 2000), as well as in a task with auditorily presented cleft

object vs cleft subject sentences (Caplan et al., 1998). Another study (Just et al., 1996), noting an increase in activated voxels in both Broca's and Wernicke's areas that correlated with sentential complexity, concluded that increased sentential complexity resulted in the recruitment of more neural tissue in each of a network of cortical areas, with no single region more specifically involved in sentence processing than any other.

Three recent fMRI studies (Dapretto and Bookheimer, 1999; Kang et al., 1999; Ni et al., 2000) have claimed to have evoked differential activity in part of Broca's area (BA 44) during syntactic as opposed to semantic processing of sentences or phrases. However, each contrastive experimental condition in these studies involved both syntactic and semantic processing under the same task instructions. In neither study was there any experimental history or independent evidence to support the authors' claims about implicit and conflicting task demands across conditions. In addition, different sets of sentences were used for the two conditions, thus involving uncontrolled cognitive factors. These three studies used 'implicit' tasks for both syntactic and semantic conditions which involve: (i) listening to a pair of sentences to decide whether they have the same literal meaning (Dapretto and Bookheimer, 1999), (ii) simple reading (Kang et al., 1999), and (iii) listening to decide whether a sentence contained a 'living thing' (Ni et al., 2000). These task designs lack a control for the apparent attention to syntactic/semantic anomaly and difference involved. Therefore, it is premature to conclude that these studies dissociate 'form' from 'content'. Indeed, cortical areas implicated in processing semantic information as opposed to syntactic information are left BA 47 (Dapretto and Bookheimer, 1999), right BA 10, 45, 46 (Kang et al., 1999), and various other widespread areas in both of the hemispheres (Ni et al., 2000). These conflicting results may stem from the multiplicity of cognitive factors involved in those tasks, especially in the 'semantic' tasks. Moreover, it is not clear whether Broca's area is activated during 'explicit' detection of a syntactic anomaly, which is a key issue in establishing its involvement in syntactic processing. In one study with an explicit anomaly detection task, there was little difference between cortical areas activated during syntactic and semantic conditions (Ni et al., 2000).

Given this uncertainty about the role played by Broca's area in syntactic processing, we have tried to identify cortical areas associated specifically with syntactic processing, independent of error detection requiring verbal short-term memory and of error detection in a linguistic context (Embick et al., 2000). We used an explicit syntactic paradigm with an established experimental history and cognitive theory of the task. Furthermore, the same lexical material was employed across conditions. Our study combines a version of the

Table 1
Sample stimuli used in grammar (GR) and spelling (SP) conditions

Error	GR	SP
1	Bill wrote paper a about the discussion of the treaty.	Bill wrote a papger about the discussion of the treaty.
1	Mary wanted to read about the destruction the of city.	Mary waanted to read about the destruction of the city.
1	John drove to store the in a very fast car two weeks ago.	John drove to the store in a very fasvt car two weeks ago.
2	Mary asked question a about theorem the in class.	Mary askepd a question about the theorem in cllass.
2	The editor read article the with revisions Anne's after lunch.	The editor read the artilce with Anne's rezvisions after lunch.
2	Tom drove the to beach on Will's fast extremely motorcycle.	Tom drove to tfe beach on Will's extremely fqast motorcycle.

error-detection paradigm that has been well-exemplified in ERP studies of syntactic anomaly (Neville et al., 1991), with a linguistic control condition that involves both normal sentence processing and error detection of misspelled words, comparable in difficulty to syntactic error detection. The sentential stimuli use the same lexical material in English across two conditions of grammar (GR) and spelling (SP), and differ only according to the types of errors they contain (Table 1). Sentences of the GR type contained one or two errors in word order; sentences of the SP type contained one or two errors in spelling. In each condition, stimuli were presented visually, and the task was to determine whether the sentence contained one or two errors by pressing one of two buttons. By using this one- vs two-error design, we were able to place stimuli of the same error-type in blocks, while maintaining a task that required the processing of each stimulus. In an additional Control (CO) condition, subjects viewed rows of colored Ls and Ts, with a basic association between a single color and a letter; for instance, purple Ts and yellow Ls. In this case, the task was to find matches for a target combination in the upper left-hand corner of the screen, where the letter/color violated the basic pattern; the subject, scanning the further rows of letters, determined whether there was a single match to this combination, or two matches. Each of the SP and GR conditions combined linguistic processing with an error-detection task. The difference between the two conditions lies in the different types of errors, namely, grammatical errors, which induce syntactic violations, and spelling errors, which concern orthographic representations. The CO condition controls for both a serial search and short-term memory of targets.

Eight native speakers of English (six male and two female; foreign students at The University of Tokyo, Komaba) participated in this study. All the subjects were right-handed. As to the comparison of behavioral data between GR and SP, there was no consistent significant difference in both RT and accuracy across conditions with one error and two errors. We found that each of the three cortical language areas, i.e. AG/SMG, Wernicke's area, and Broca's area, showed significant increases in signal changes during both GR and SP tasks, when each condition was compared with the CO condition (Fig. 4). In addition, the GR condition produced significantly more activation than SP across language areas. An ANOVA for the left hemisphere (region \times condition \times block) showed significant main effects of regions and conditions ($P < 0.0001$), but no main effect of blocks ($P > 0.5$). Moreover, there was a significant interaction between regions and conditions ($P < 0.05$), but there were no other significant interactions ($P > 0.1$). These results suggest that the cortical language areas were not uniformly activated under the GR and SP conditions; rather, there was a clear dissociation among language-related regions. The differential response between GR and SP was significantly greater in Broca's area than in Wernicke's area, AG/SMG, and the night homolog of Broca's area (Fig. 5). One notable feature of this study is that it did not attempt to isolate Broca's area for some task, but that it showed the differential contribution of Broca's area to a well-defined language task.

Given that the task demands were controlled across experimental conditions, these data suggest that Broca's area is selectively involved in syntactic processing. They

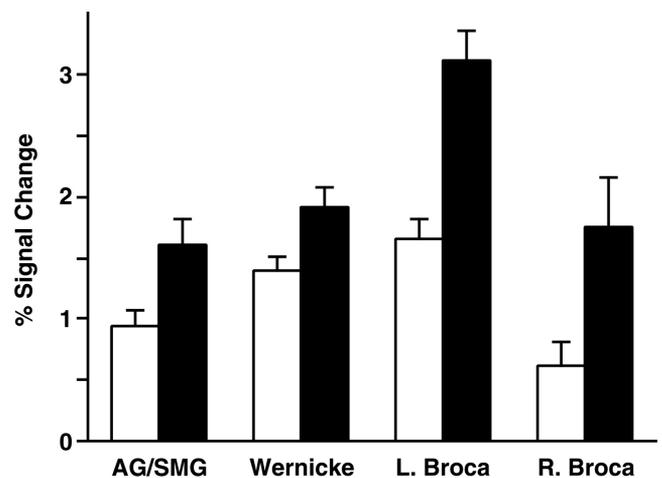


Fig. 5. A syntactic specialization for Broca's area. A histogram comparing the values for percent signal change (mean \pm SEM of subjects and blocks) for each language condition vs the control (white = SP, black = GR) is shown in each region of interest. Note the prominent condition difference in the left Broca's area (L. Broca), which is larger than in other language areas and than in the right homolog of Broca's area (R. Broca) (Embick et al., 2000).

also preclude an interpretation according to which general computational complexity would be the only difference between the GR and SP conditions, as the behavioral data did not reveal a consistent complexity contrast between these two conditions. Differences in activation observed between GR and SP can instead be attributed to the different linguistic systems involved in each condition; syntactic error detection in GR, as opposed to orthographic error detection and normal syntactic processing in SP. The source of the differences between GR and SP in Wernicke's area and AG/SMG is less clear. It could be that error detection focused in Broca's area induces an increase in activation in other language areas through feedback projections as the subject attempts reanalysis of the apparently deviant sentence. It is also possible that a certain amount of syntactic processing takes place in Wernicke's area and in AG/SMG. Finally, although we claim that Broca's area is involved in syntactic processing in a particular manner, we do not make claims about exclusivity; whether Broca's area is directly associated with other linguistic and/or non-linguistic modules remains an open question. The involvement of Broca's area in the process of speech production is another issue for future study (Levelt, 1999). Future work combining electrophysiological and hemodynamic methods will hopefully clarify the relationship between temporal response components like the LAN/P600 and the activation in Broca's area observed in this experiment.

3. The modules of phonological and semantic processing

The phonological and semantic aspects of language processing have been studied primarily at the lexical level. A positron emission tomography (PET) study by Démonet et al. (1992) and their subsequent study (Démonet et al., 1994) clearly showed that auditory phonological processing was associated with activation in Wernicke's area, whereas semantic processing was associated with activation in the bilateral AG/SMG as well as in the left prefrontal area (BA 8, 9) and the posterior cingulate cortex (BA 30, 31). The latter result regarding semantic processing was obtained by a contrast between a lexico-semantic task for judging attributes in adjective-noun pairs and a phonological task for monitoring phonemes; no significant difference in activation was found in Broca's area and in Wernicke's area. This result is particularly notable, in that it suggests the existence of distinct functional modules for phonological and semantic processing. Furthermore, the functional role of AG/SMG and its adjacent areas in semantic processing conforms with that suggested by a previous lesion study, which showed that pure deficits in semantic comprehension at the single-word level were correlated with damage to the left posterior tem-

poral and inferior parietal regions (BA 39, 37, 22, and 21) (Hart and Gordon, 1990).

On the other hand, there has been significant controversy about the role of AG/SMG and frontal regions in the lexico-semantic tasks studied with functional imaging techniques. As to the cortical areas that are activated under both auditory and visual conditions, a PET study with word generation and association tasks suggested the involvement of the left inferior prefrontal cortex (BA 47) (Petersen et al., 1988, 1989), whereas an fMRI study with a concrete/abstract judgment task suggested the left inferior frontal gyrus (BA 44, 45) and the bilateral anterior prefrontal cortex (BA 10, 46) (Chee et al., 1999). However, the superior temporal cortex was not consistently activated in these studies. The left inferior frontal cortex (BA 45, 46, and 47) was also associated with semantic category generation and semantic memory tasks in fMRI studies (Shaywitz et al., 1995; Gabrieli et al., 1996; Crosson et al., 1999). Another recent fMRI study has reported that phonological processing in a syllable-counting task activated the dorsal portion of the left inferior frontal gyrus (BA 44, 45), and that semantic processing in a concrete/abstract judgment task activated the ventral portion of the left inferior frontal gyrus (BA 45, 47) (Poldrack et al., 1999), which is in agreement with previous proposals (Fiez, 1997; Gabrieli et al., 1998).

When these previous studies are considered together, it becomes apparent that the question remains unanswered as to the dependency of cortical responses on processing levels of language stimuli (either lexical level or sentence/discourse level), as well as their dependency on input modalities (either auditory or visual presentation). Therefore, the delineation of phonological and semantic processing as well as the exact roles of cortical language areas in these processes necessitate carefully planned experiments in the near future. The application of transcranial magnetic stimulation (TMS) may provide an additional method of overcoming the limits of imaging studies, thereby uncovering the causal link between cortical activity and the subcomponents of the linguistic system.

4. Sentence processing in the temporal cortex

There have been an increasing number of neuroimaging studies of sentence processing since a pioneering PET study by Mazoyer et al. (1993), which showed that the left middle temporal gyrus was selectively activated when subjects listened to stories in a native language, as compared with the condition of listening to semantically anomalous sentences, sentences with pseudo-words, a list of words, or story in an unknown language. These results indicate the selective involvement of the left temporal association areas (Wernicke's

area) in meaningful sentence processing. Another PET study reported significantly increased activity in the left superior temporal gyrus (BA 22, 39) and the bilateral temporal poles (BA 38), when story comprehension tasks were compared with a condition in which semantically unlinked sentences were presented (Fletcher et al., 1995). Further, the left superior temporal gyrus showed significant activation when a sentence reading task was contrasted with the presentation of consonant strings in an fMRI study (Bavelier et al., 1997). Activation in the posterior part of the left superior and middle temporal gyri (BA 22, 37) as well as in the bilateral AG/SMG correlated with linguistic complexity of visually-presented sentences (negative sentences vs. affirmatives) (Carpenter et al., 1999). The left AG was activated more consistently among tested subjects, when a task to check the order of actions (presented in phrases) was compared with a task to detect an error in the word order (Crozier et al., 1999), although this comparison involved a variety of other factors such as motor imagery. Two additional imaging studies (Maguire et al., 1999; St George et al., 1999) reported activation in the left middle temporal sulcus and the temporal pole (BA 21, 38), when story comprehension was enhanced in a paradigm developed by Bransford and Johnson (1972). Although the exact loci of activated areas were markedly different among these studies with sentence/discourse comprehension tasks, it is likely that a part of Wernicke's area, AG/SMG, and the adjacent cortices subserves as a module for sentence comprehension or semantics. This module would be complementary to Broca's area as a syntactic module. The individual roles of Wernicke's area and AG/SMG should be clarified by future studies.

To address the issue of sentence processing in the cerebral cortex further, we adopted several new approaches in our recent study using Optical Topography (OT) (Sato et al., 1999). First, we compared two conditions, namely, listening to successive sentences of a story and listening to repeated sentences. The latter condition subserved as a control for basic sentence processing. Second, we used a dichotic listening task that required intensive tracking of speech sounds. In a previous fMRI study, we compared a similar paradigm with a diotic (binaural) listening control, and found that subregions of the auditory and language areas show enhanced activity during the dichotic listening condition (Hashimoto et al., 2000). That fMRI study is particularly notable in that it agrees with a previous anatomical study by Rivier and Clarke (1997) with respect to the anatomical location of these areas and the order of the proposed hierarchical levels. Such research will enhance the understanding of both structural and functional bases of language information processing. Third, we used a recently developed noninvasive imaging technique, OT, which measures tempo-

ral changes in hemoglobin oxygenation simultaneously at multiple regions (Maki et al., 1995; Yamashita et al., 1996; Koizumi et al., 1999). OT is a new extension of near-infrared spectroscopy (NIRS) for acquiring a topographical image; NIRS measures spectroscopic reflection and scattering at a single region with a light emitter and a detector (Chance et al., 1993; Hoshi and Tamura, 1993; Kato et al., 1993; Villringer et al., 1993). There are several advantages of using OT over other functional mapping techniques. First, it is possible to independently measure the temporal changes in oxy-hemoglobin concentration (C_{oxy}) and deoxyhemoglobin concentration (C_{deoxy}). Second, there is no scanning noise to interfere with the experimental auditory stimuli. Third, its signal-to-noise ratio is relatively high, allowing for the observation of cortical activity with a small number of trials. One major disadvantage of OT is that its measurement is restricted to the cortical surface. Nevertheless, OT has the potential to introduce a new dimension to the mapping of human cognitive functions.

In our OT study, we measured the local changes in near-infrared light absorption simultaneously from 44 points in both hemispheres. The measured region in each hemisphere centered on the Sylvian fissure and covered an area of $6 \times 12 \text{ cm}^2$. Target stimuli and non-target stimuli were simultaneously presented to opposite ears every 2 s, and a target was alternatively presented to either the left ear or the right ear at random intervals. Subjects were asked to track targets and to press a button when targets shifted from one ear to the other. We tested: (i) a control task, in which a tone and white noise were presented as targets and nontargets, respectively, (ii) a repeat task, in which the target was one repeated sentence within a task block, and (iii) a story task, in which the targets were successive, different sentences of a continuous story. In the repeat and story tasks, target sentences were read in Japanese, and non-targets were prepared by scrambling the sequence of syllables of the correspondent target. A sentence different from the target for the repeat task and contextually anomalous phrases for the story task were used as probe stimuli. Therefore, these tasks could not be completed appropriately by identifying speech sounds without paying attention to their meanings, and they were equally balanced in terms of behavioral control for task difficulty. Seven male native speakers of Japanese participated in this study. All the subjects were righthanded. The results of this study are relevant to the cortical activity of native speakers confronted with their own language.

We observed left-dominant activation in the superior temporal cortex (the superior and middle temporal gyri), preferentially during the story task over the repeat task when compared with the control task (Fig. 6). Wider regions were clearly more activated during the

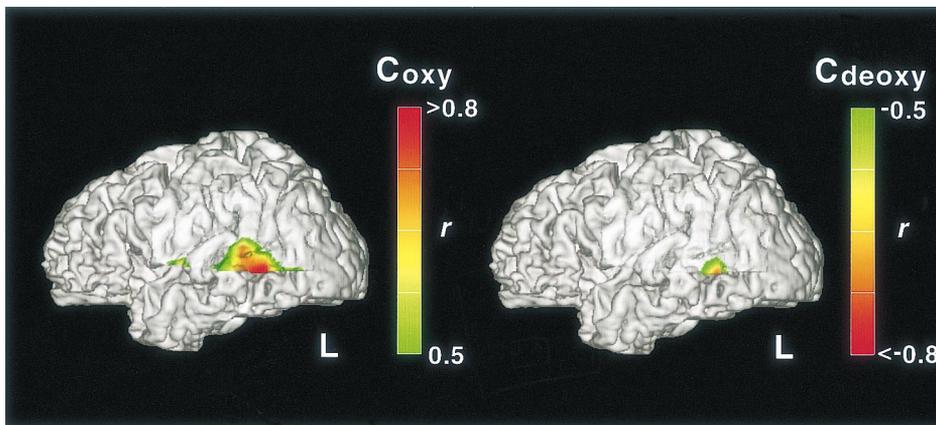


Fig. 7

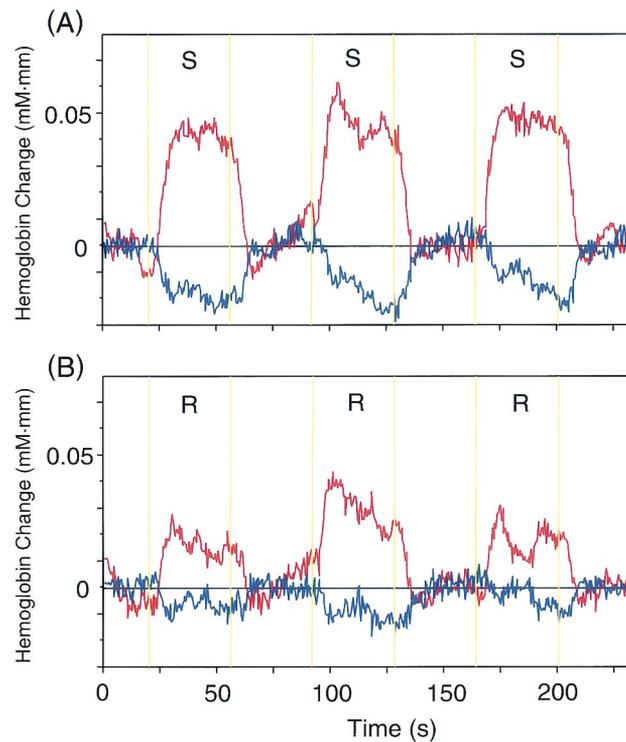


Fig. 8

Fig. 7. Focal activation in the left superior temporal cortex during sentence processing. OT images in r -maps for a direct comparison between story and repeat tasks. Left, r -maps of C_{oxy} temporal changes; Right, r -maps of C_{deoxy} temporal changes. Activation is localized in the middle temporal gyrus in both comparisons.

Fig. 8. Hemodynamics in speech-recognition tasks relative to the control task. (A) Story and control tasks; (B) Repeat and control tasks. There were three periods of either the story task (S) or the repeat task (R) in each run. Red lines show the mostly positive temporal changes of C_{oxy} , whereas the blue lines reveal the mostly negative temporal changes of C_{deoxy} . These temporal changes were calculated from averaged data among subjects.

story task than during the repeat task in both hemispheres. This finding is consistent with the results of a previous PET study that showed activation of the left superior temporal cortex when subjects listened to continuous speech in their native language (Mazoyer et al., 1993). The direct comparison between the hemodynamics in the story task and that in the repeat task showed focal activation in the left superior temporal cortex

(Fig. 7). Both an increase in C_{oxy} and a decrease in C_{deoxy} were significantly larger in the middle temporal gyrus than in the superior temporal gyrus. The temporal changes in the left superior temporal cortex are shown in Fig. 8. With a delay of 6 s, an increase in C_{oxy} was synchronized with each onset of the story task, and after reaching a plateau, C_{oxy} returned to the baseline level at the end of the task. Although a decrease in

C_{deoxy} was also synchronized with each period of the story task, C_{deoxy} did not exactly mirror the temporal dynamics of C_{oxy} . This result indicates that the temporal changes in C_{oxy} and C_{deoxy} may reflect different physiological processes whose temporal dynamics are correlated over the long term (~ 30 s) but are different in the short term (< 10 s). Similar, but smaller, changes in both C_{oxy} and C_{deoxy} were observed in the repeat run. These results suggest that the hemodynamics in the mid-lateral part of the left temporal cortex reflect cognitive factors involved in the processing of sentences. A critical difference between the story and repeat tasks would be the load of speech stimuli to be processed. Recognition of successive different sentences of a story demands more auditory, memory, and language information processing than the recognition of repeated sentences. The temporal cortex activation reported here is also consistent with the role of the primate temporal association area in memory storage and memory retrieval (Sakai and Miyashita, 1993; Sakai et al., 1994).

5. Conclusion

Based on converging evidence from aphasic and imaging studies, we propose a modular specialization of Wernicke's area, AG/SMG, and Broca's area, which is directly related to phonological, semantic, and syntactic processing. Further, the left inferior frontal regions are involved in some aspects of phonological and semantic processing, whereas the left middle temporal regions are critical for sentence processing. This rather broad delineation at the current stage of imaging studies reflects the difficulty of dissociating linguistic components from confounding cognitive factors. The language system does not stand alone but interacts with other systems of perception, memory, and consciousness, as well as with the speech output system. Future work combining electrophysiological (ERP, MEG), hemodynamic (PET, fMRI, OT), and magnetic stimulation (TMS) methods will allow us further parcellation of language processing in the cerebral cortex and will enable us to address questions about module-specific brain areas and how they actually perform linguistic computations.

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