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Neuro-Anatomical Overlap Between Language and Memory Functions in the Human Brain

Satoru Yokoyama
Tohoku University
Japan

1. Introduction

In the nineteenth century, two studies in aphasiology comprise a turning point for research of brain-language relationships: Broca, 1861 and Wernicke, 1874. Based on these two studies, it was claimed that Broca's area (i.e., the pars triangularis and pars opercularis of the left inferior frontal gyrus) and Wernicke's area (i.e., the posterior part of the left superior/middle temporal gyrus, but in some situations including a part of the inferior parietal lobule) were involved in language production and comprehension, respectively (Geschwind, 1970). Recently, due to the development of functional brain imaging techniques (e.g., PET and fMRI), normal brains have been measured to examine the neuro-cognitive architecture of language processing. In particular, both Broca's and Wernicke's areas have been shown to be responsible for several language functions, such as single word processing and sentence processing (Fig. 1).

However, these two important regions are also activated for working memory-related processes, at least, including executive functions and short term memory processes of linguistic information, and the processes of storage and access to long term memory of linguistic information. This memory system could be assumed essential for language comprehension. For example, in order to comprehend a word, we have to first identify a series of sounds or letters as a certain word and to access its semantic information from long term memory. For sentence comprehension, we have to tentatively memorize several words comprising the sentence to compute the syntactic and semantic structure of the sentence. For example, it is clear that if we do not tentatively memorize words comprising the sentence, we cannot comprehend the sentence, since we have to compute the syntactic/semantic information of the sentence by using these words. Hence, in order to understand a language expression, we need the involvement of both the short and long term memory systems. In previous studies, there were essentially two types of standpoints regarding the involvement of the memory system in language comprehension. The first is that of the „specialist“, who assumes that the syntactic processing system of the language processing system exists in our brain and is independent from other cognitive functions. The second is that of the „generalist“, who assumes that the syntactic processing system has neural substrates in common with other cognitive functions, mainly the working memory system.

In this chapter, recent neuroimaging studies of the neuro-cognitive architecture of single word and sentence processing will be briefly reviewed and the relationships between language and memory in the human brain will be discussed in the context of functional neuroimaging evidence.

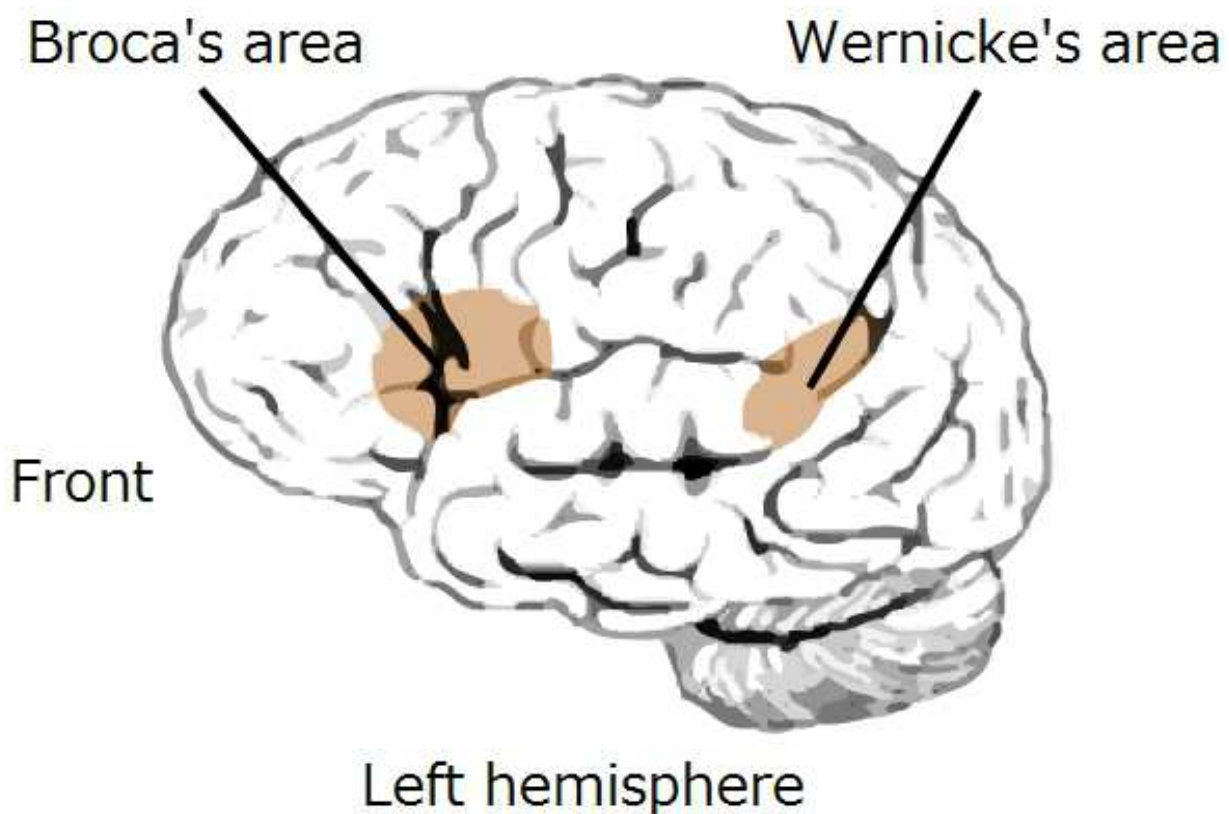


Fig. 1. Broca's area and Wernicke's area.

2. Neural basis of language comprehension

2.1 Neural basis of single word processing

There is a wealth of evidence that auditory and visual word processing have at least partly independent neural bases, particularly in the early stages of stimulus processing. While these two processes have been reported to utilize different brain regions in the early stages of processing (i.e., modality-related processes and the processing of non-linguistic to linguistic information translation), a common word recognition system exists in the late stages of processing (i.e., phonological processing and semantic processing) (e.g., Chee et al., 1999; Booth et al., 2003). Chee et al. study used semantic concreteness judgment task, non-semantic syllable counting control task for auditory stimuli, and case size judgement control task for visual stimuli, while Booth et al. study used semantic relation judgment task and rhyming control task. Both studies reported that the left inferior frontal and middle temporal gyri were commonly activated for both auditory and visual word processing. In contrast, while visual word processing activated visual-related areas including the occipital lobe, the ventral part of inferior temporal gyrus, and the fusiform gyrus, auditory word processing activated auditory-related areas including the superior temporal gyri.

2.2 Phonological working memory involvement in single-word processing

It is known that phonological working memory is essential for processing words. It is assumed that the anterior part of the left inferior frontal gyrus (i.e., the pars triangularis of

the inferior frontal gyrus/Brodmann area 45) and the left inferior parietal region (i.e., the supramarginal gyrus) comprise the verbal working memory circuit (for a recent meta-analysis see Vigneau et al., 2006). The former area is thought to be involved in articulatory rehearsal and the latter in phonological storage (e.g., Poldrack et al., 1999; Warburton et al., 1996; McGuire et al., 1996; Paulesu et al., 2000; Jessen et al., 1999; Zattore et al., 1996; Price et al., 1996). These two areas have often been reported to be active during single word processing (e.g., Hautzel et al., 2002; Jonides et al., 1998; Rypma et al., 1999; Cohen et al., 1997). The neuroimaging results are compatible with the working memory theory proposed by Baddeley, since the correlation between the sub-functions and locations of the involved brain regions reported in these neuroimaging studies is in line with the assumption of this model (e.g., Baddeley, 2003).

2.3 Lexico-semantic processing

The left inferior frontal region, the left lateral and ventral middle/inferior temporal regions, and the left inferior parietal region are activated during semantic processing tasks. It is still unclear whether the left inferior frontal region is activated by single word semantic processing per se. Demb et al. (1995) have reported that brain activity in this region is greater for more difficult semantic processing tasks than for corresponding less difficult semantic processing tasks. Similarly, the left inferior frontal region was modulated by the frequency of words (Fiebach et al., 2002). It is common knowledge that low frequency words are more difficult to process than high frequency ones. Hence, in single word semantic processing, there exists the possibility that modulation of the left inferior frontal region by word frequency is explained by access to lexico-semantic information stored in long term memory. In contrast, it has been claimed that only the orbital part of the left inferior frontal gyrus is associated with the processing of semantic information retrieval. Several meta-analysis results in particular have supported this claim (Fiez, 1997; Bookheimer, 2002; Binder et al., 2009). A meta-analysis (Vigneau et al., 2006) has also supported the report that the left parietal lobe contributes to semantic processing regardless of the difference between pictures and words (Vandenberghe et al., 1996).

While the temporal lobe plays a role in storing long term memory, the role of the left posterior part of superior/middle temporal gyri is still unclear. As evidence, most neuroimaging studies using comparisons between real word and pseudoword comprehension have reported that this region is more active for real word comprehension than for pseudoword comprehension (e.g., Pugh et al., 1996; Price et al., 1997; Friederici et al., 2000; Booth et al., 2002; Fiebach et al., 2002; Perani et al., 1999; Yokoyama et al., 2006b, and others). In contrast, Fiebach et al. (2002) showed that the left inferior frontal region is modulated by word frequency while the left posterior part of the middle temporal gyrus is not. Hence, at least the role of the left posterior part of the middle (and/or superior) temporal gyrus differs from that of the left inferior frontal region in lexico-semantic processing.

It has been made clear that the left inferior temporal region contributes to semantic processing. The inferior temporal region is commonly known to be involved in the storage or the long term memory of word information. Lesion studies have reported that damage to the temporal lobe cause category-related deficits (Kapur et al., 1994; Gitelman et al., 2001; Lambon Ralph et al., 2007; Noppeney et al., 2007; Warrington, 1975; Hodges et al., 1992, 1995; Mummery et al., 2000). Patients with anterior temporal damage show more difficulty processing the concept of living things than that of artifacts, while patients with posterior

temporal and parietal damage show the opposite pattern (Warrington & Shallice, 1984; Warrington & McCarthy, 1987; Forde & Humphreys, 1999; Gainotti, 2000; Lambon Ralph et al., 2007; Warrington & McCarthy, 1987, 1994; Hillis & Caramazza, 1991). Functional brain imaging studies have replicated such results from lesion studies (Cappa et al., 1998; Moore & Price, 1999; Perani et al., 1999; Grossman et al., 2002; Kable et al., 2002; Tyler et al., 2003; Davis et al., 2004; Kable et al., 2005).

2.4 The role of sensorimotor areas on language comprehension

It has recently been reported that sensorimotor areas are active during language comprehension. Even in language or picture comprehension without sensorimotor input, sensorimotor areas are active (Pulvermuller, 1999; Malach et al., 2002; Gainotti, 2004; Kable et al., 2002; Grossmann et al., 2002; Hauk et al., 2004; Pulvermuller et al., 2005; Tettamanti et al., 2005; Kemmerer et al., 2008; Desai et al., 2009; Hwang et al., 2009). Hauk et al. (2004) reported that the silent reading of action words related to face, arm, and leg movements activates the motor areas related to the movement of the tongue, fingers, and feet. Such sensorimotor activation has also been found during sentence listening stimuli describing hand movements and visual events (Desai et al., 2010). According to sensorimotor theories, sensorimotor areas play a role in category-related long term memory through the encoding process of sensorimotor experiences (e.g., Martin, 2007). Hence, it has been assumed that concepts are wholly or partially organized by sensorimotor experience (Barsalou et al., 2003; Gallese & Lakoff, 2005; Pulvermuller, 1999).

2.5 Grammatical category

Regarding grammatical category, the neural dissociation between nouns and verbs in the brain has been investigated by neuroimaging techniques. However, there exists some discrepancy at this time. In lesion studies, it has been reported that nouns and verbs are distinctly processed in the human brain (e.g., Bates et al., 1991; Miceli et al., 1988; Shapiro & Caramazza, 2003). In contrast, in neuroimaging studies, while several studies reported that different brain activations exist between noun and verb processing (Perani et al., 1999; Tyler et al., 2004; Yokoyama et al., 2006b), others find no difference between them (Tyler et al., 2001; Li et al., 2004). Based on the reported findings, several possibilities are proposed at this time. One possibility is that a cross-linguistic difference influences such discrepancy as the reported neuroimaging studies used different languages as stimuli (Yokoyama et al., 2006b). Still, despite the discrepancy among languages, the reported brain activations were located in the left inferior frontal gyrus and posterior superior/middle temporal gyrus. Hence, at least the word information related to grammatical category information, such as nouns and verbs, and is consistent with the hypothesis that long term memory of word information is stored in the temporal lobe.

2.6 Morphological processing of words

Regarding the morphological processing of words, one plausible hypothesis exists, namely that of „rule and memory“ (Pinker, 1999; Ullman, 2001; 2004). However, actual neuroimaging results have not completely support this hypothesis. In this hypothesis, while rule-based morphological processing of words (e.g., “-ed” past tense form) would be processed as a procedural memory circuit in the left inferior frontal region and basal ganglia, words with irregular morphological changes would be stored in an independent

form in the temporal lobe (Ullman, 2001; 2004). Since rule-based computation is reflected by task difficulty or task performance, this hypothesis is consistent with the above results in neuroimaging studies reporting that the left inferior frontal gyrus is related to task performance or working memory load. Also, since the temporal lobe plays a role in the storage of word information, this hypothesis is fully in line with the results of neuroimaging studies on the long term memory of semantic information, as described in section 2.3.

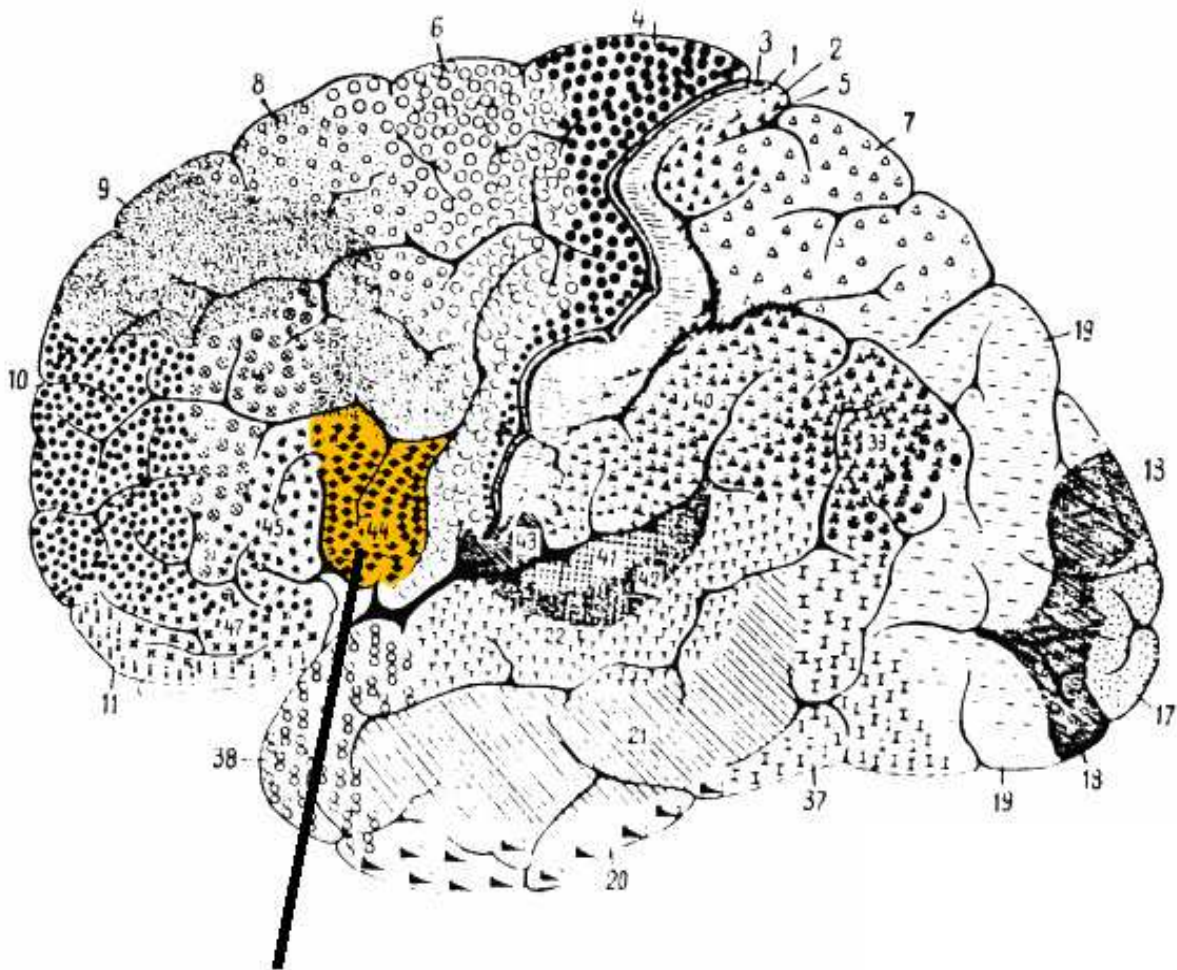
Additionally, Yokoyama et al. (2006b) showed partially supportive evidence that the left inferior frontal gyrus (and also the left premotor area) are active during the morphological processing of verbs. Yokoyama et al. (2009a) further showed that the developmental change of brain activity in L2 verb acquisition is observed, not in the temporal region which would be related to semantic memory, but in the inferior frontal gyrus which would be related to procedural memory. These results are in line with the above hypothesis. Also, fMRI results reported in Beretta et al. (2003) support the rule and memory hypothesis but show no clear dissociation in the brain activation between rule processing and memory processing of words. Hence, while supportive evidence at this time has been reported in several previous neuroimaging studies, it remains unclear whether the rule and computation hypothesis is correct or not.

2.7 Neural basis of sentence processing

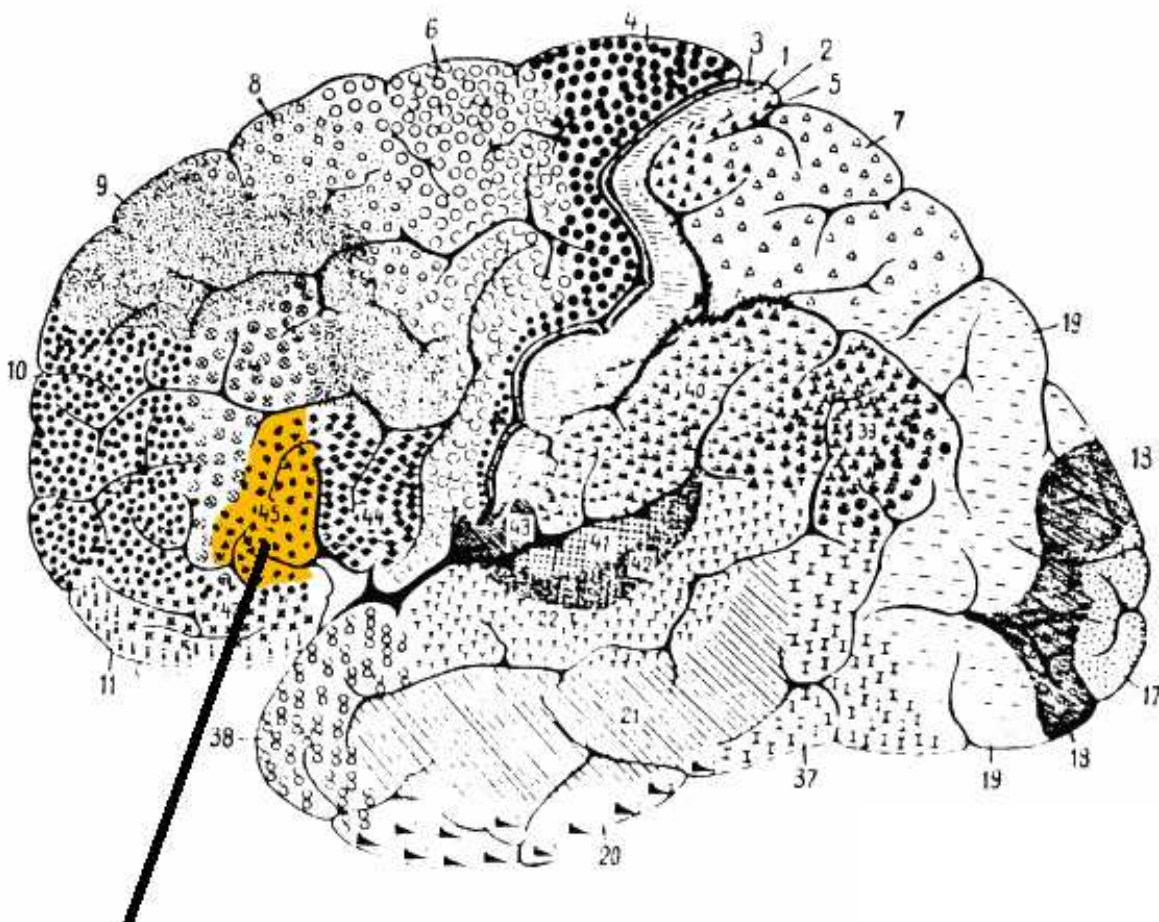
One of the main issues regarding sentence processing in cognitive neuroscience is whether lexico-semantic and syntactic processing are dissociable or not in the human brain (e.g., Fireiderici et al., 2003). In particular, it is controversial what role Broca's area and the inferior frontal gyrus play in sentence processing. Some researchers have reported that the neural basis for the syntactic computation system overlaps that of workload related to working memory (e.g., Just et al., 1996), workload related to task performance (Love et al., 2006), the phonological working memory system (Rogalsky et al., 2009), the cognitive control system for resolving competition etc. (January et al., 2008; Yokoyama et al., 2009b), or other interpretation (e.g., Bornkessel et al., 2005). These overlapped brain regions basically include the left inferior frontal gyrus (Broca's area) and the posterior part of the left superior/middle temporal gyrus (Wernicke's area). The pars opercularis (Brodmann area 44) and pars triangularis (Brodmann area 45) of the inferior frontal gyrus, which are corresponding to Broca's area (Fig. 2), were commonly activated for lexico-semantic and syntactic processing in the most recent meta-analysis study (Vigneau et al., 2006).

In contrast, other studies have reported that the neural basis for syntactic processing of sentence comprehension is independent from other cognitive systems. Yet to claim such dissociation, we have to pay careful attention to other confounding factors and interpretations. For example, since the left dorsal prefrontal cortex, or middle frontal gyrus, was active for sentence comprehension independent of phonological short term memory load, this region is specific to sentence comprehension (Hashimoto & Sakai, 2002). However in Baddeley's working memory theory, the working memory system has a modality-free executive processing system and modality-dependent short term memory systems. To claim that the observed brain activation is independent from the working memory system, it is necessary to compare brain activities, not only between sentence comprehension and short term memory process, but also between sentence comprehension and the executive process. Indeed, in neuroimaging studies of executive process, the left dorsal prefrontal cortex was active (e.g., Eldreth et al., 2007). This region was close to the brain region observed in

Hashimoto and Sakai (2002). Contrastively, the left posterior part of the temporal region was specifically active for sentence reading independent of phonological short term memory (Cutting et al., 2006). However, it is unfortunate that only the sentence comprehension condition included verbs in this study and the phonological short term memory condition did not. The comprehension of verbs has been reported to activate the left posterior superior/middle temporal gyrus (Perani et al., 1999; Yokoyama et al., 2006b). Therefore, the comprehension of verbs would cause brain activation in the left posterior temporal region in the sentence comprehension condition in Cutting et al. (2006). Makuuchi et al. (2009) has reported that the pars opercularis of the inferior frontal gyrus is specifically active for syntactic computation regardless of syntactic difficulty. This study did not directly consider the executive process in working memory, similar to Hashimoto and Sakai (2002). Hence future studies are necessary to at least consider each aspect of the working memory system in order to propose that the neural substrate for sentence comprehension or its syntactic computation is independent from other cognitive processes, including the working memory system.



The pars opercularis of the inferior frontal gyrus
= Brodmann area 44



The pars triangularis of the inferior frontal gyrus

= Brodmann area 45

Fig. 2. The pars opercularis (Brodmann area 44) and pars triangularis (Brodmann area 45) of the inferior frontal gyrus.

Furthermore, in such previous neuroimaging studies, experimental stimuli using sentences with highly complex syntactic structures tended to be used to manipulate working memory load in the experimental design. In our daily lives we would not often use such complex sentences with long embedded clauses or relative clauses. Since such complex sentences are thought to be incomprehensible without intentional monitoring, additional intentional cognitive control or monitoring processes would affect brain activation compared to cases using simple sentences. It is necessary to test whether a hypothesis built using such complex sentences can be applicable to cases using simplex sentences or not.

3. Regional overlap between language comprehension and memory system

According to the above review, most sub-processes for language comprehension can be observed in the frontal, temporal, and parietal lobes (Fig. 3).

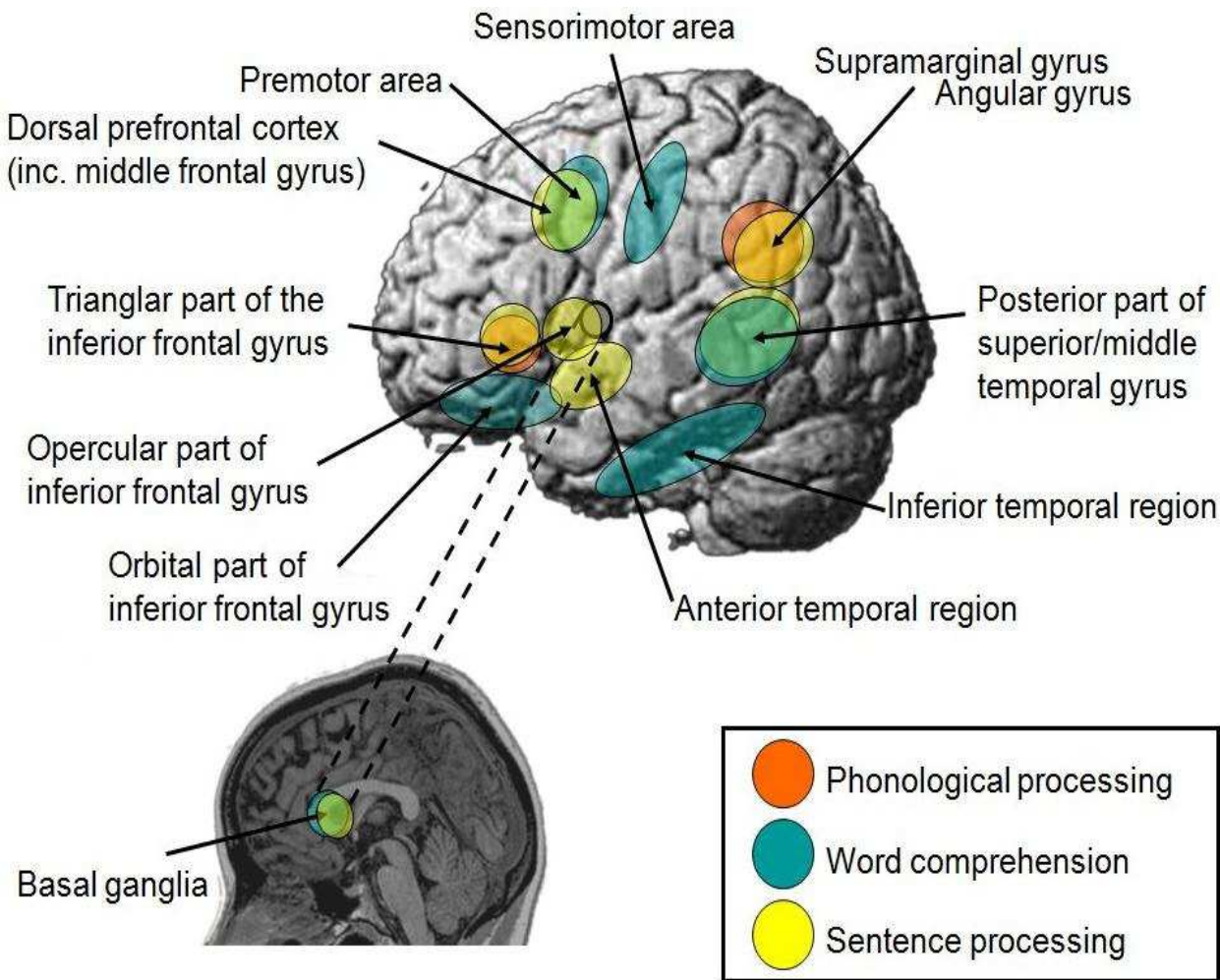


Fig. 3. Brain mapping of language function.

While different processing systems are utilized in the early stages of the language process (i.e., modality-related processes (i.e., visual and auditory input) and the processing of non-linguistic to linguistic information translation), a common word recognition system exists in the late stages of the process (i.e., phonological processing, semantic processing, and sentence processing). Findings suggest that the inferior frontal and inferior parietal regions are associated with working memory load and/or phonological processing to perform experimental tasks for single word processing. The left inferior frontal region is malso suggested to be associated with intended acts, planning, and/or cognitive control to resolve competition, which have common processes with other cognitive functions (Owen et al., 2005; January et al., 2008; Yokoyama et al., 2009b). Thought to be involved in the semantic processing of words are the orbito-frontal and parietal “retrieval” system, and the temporal “storage” system (i.e., long term memory). Also, sensorimotor areas have been shown to be activated during word and sentence comprehension tasks. Their activation may be due to sensorimotor experiences which induce the storage of long term memories in the sensorimotor areas. While sentence comprehension activates the left inferior frontal and dorsal prefrontal cortex, these activations are thought to be based on phonological working memory and executive functions. Taken together, language comprehension would be supported by the neural substrates of the working memory and

long term memory systems, as well as other cognitive function systems (e.g., intended act, planning, and cognitive control).

While the above mentioned results reported in previous studies at least indicate that a common neural substrate supports language comprehension and memory-related processes which are functionally similar, observation of the overlapped activation between other cognitive processes might not necessarily indicate a functional overlapping of these processes. Even if both language comprehension and memory processes utilize the same brain region, the roles of the brain region are thought to be different between them. Hence, the simple subtraction analysis used in previous neuroimaging studies may not be enough to resolve this issue and functional and/or effective connectivity analysis methods might be useful or necessary in future studies. Such methods would be able to test whether a commonly activated area is connected with different regions between different conditions. If this is the case, it would mean that both language comprehension and other cognitive processes utilize common neural substrates, though the roles of the commonly activated brain regions would be different between them.

4. Conclusion

Through a review of the literature we find that, since the neural basis of language comprehension overlaps that of other cognitive systems, mainly the memory system regionwise, most previous neuroimaging studies support the „generalist“ view. However, it is to be noted that the overlaps of the neural substrate may not indicate a functional overlap since there exists a possibility that, while a brain region is commonly activated for both processes, the brain region plays different roles between them. In future studies, to clarify which brain region or cognitive process is common for language comprehension and other cognitive systems, and which is different between them, it will be necessary to develop a new experimental paradigm and also a new data analysis method, such as the functional/effective connectivity and multi-voxel pattern analysis. These methods should then be applied to language comprehension studies. Additionally, it will be necessary to consider the relationship between language and memory functions in language acquisition (i.e., Yokoyama et al., 2006a; 2009a), since, at this time, findings in neuroimaging studies regarding this issue are very few. Examination of whether or not and how semantic memory is related to the acquisition of lexico-semantic information, as well as whether or not and how procedural memory is responsible for proficient grammatical processes such as morphological processing and sentence structure computation, might also be necessary.

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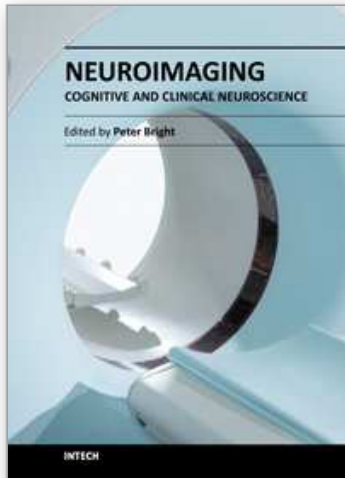
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The rate of technological progress is encouraging increasingly sophisticated lines of enquiry in cognitive neuroscience and shows no sign of slowing down in the foreseeable future. Nevertheless, it is unlikely that even the strongest advocates of the cognitive neuroscience approach would maintain that advances in cognitive theory have kept in step with methods-based developments. There are several candidate reasons for the failure of neuroimaging studies to convincingly resolve many of the most important theoretical debates in the literature. For example, a significant proportion of published functional magnetic resonance imaging (fMRI) studies are not well grounded in cognitive theory, and this represents a step away from the traditional approach in experimental psychology of methodically and systematically building on (or chipping away at) existing theoretical models using tried and tested methods. Unless the experimental study design is set up within a clearly defined theoretical framework, any inferences that are drawn are unlikely to be accepted as anything other than speculative. A second, more fundamental issue is whether neuroimaging data alone can address how cognitive functions operate (far more interesting to the cognitive scientist than establishing the neuroanatomical coordinates of a given function - the where question).

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University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
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InTech China

Unit 405, Office Block, Hotel Equatorial Shanghai
No.65, Yan An Road (West), Shanghai, 200040, China
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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