The Left Anterior Inferior Frontal Gyrus Processes the Semantic Relations between Adjectives and Nouns:

An Event-Related Functional Magnetic Resonance Imaging Study

KAY MARUYAMA ATSUSHI YUHAKU SATORU NAKAI

Summary

Although recent functional imaging studies have revealed that various cortical regions are related to the processing of various linguistic constructions, it has not yet been discovered which brain areas are directly associated with the modification process, i.e., the processing of the relationship between the adjective and the subsequent noun in adjective-noun constructions. In the present study, we used event-related functional magnetic resonance imaging (fMRI) to identify the brain regions that underlie the processing of the semantic relationship between adjectives and subsequent nouns in adjective-noun constructions. We used four types of stimulus sentences: correct sentences (filler), sentences containing semantic errors in the adjective-noun relationship, sentences containing syntactic errors, and sentences containing lexical errors (baseline). In the result, the stimulus sentences, which contained semantically erroneous relations between adjectives and nouns relative to baseline lexically erroneous stimulus sentences, activated the left anterior inferior frontal gyrus (IFG): [(x, y, z) = (-44, 25, -2), Z = 4.50]. This region was also observed on coordinates [(-44, 25, -4), Z = 5.60] even in the comparison of the semantically erroneous stimulus sentences relative to the syntactically erroneous stimulus sentences. These two coordinates nearly overlapped. Coupled with recent fMRI studies focusing on semantic processing, these data indicate that the left anterior IFG is closely associated with the processing of the adjective-noun construction and/or semantic relational computation.

Introduction

Recent research on aphasia and functional imaging studies has revealed the existence of distinct modules for the faculty of language, such as syntactic, phonological, and semantic systems (Embick, *et al.* 2000; Sakai *et al.*, 2001; Ullman, 2001; Homae *et al.*, 2003; Wartenburger *et al.*, 2003; Meyer *et al.*, 2003). Concerning semantic modules, some involvement of the left temporal regions in semantic processing has been proven (Thompson-Schill *et al.*, 1999; Malogiannis *et al.*, 2003; Friederici *et al.*, 2000).

Semantic processing studies have used various tasks. For example, subjects have judged whether a presented word is concrete or abstract (Binder et al., 1997; Friederici et al., 2000); whether the lexicosemantic relationship (selectional restrictions) between a noun and a verb is normal (Suzuki and Sakai, 2003; Friederici et al., 2003); and whether two presented sentences are semantically identical (Dapretto and Bookheimer, 1999). Many of these studies have indicated the participation of regions of the left temporal lobe, such as Wernicke's area, the left superior and middle temporal gyri in semantic processing (Sakai et al., 2000; Malogiannis et al., 2003; Friederici et al., 2000). But it should be emphasized that most of these studies hardly controlled the number of syllables or the novelty of words used in the experiments, which could cause unexpected activations. Moreover, in some of these studies, words instead of sentences have been used as stimuli. It is indispensable to use sentence-level stimuli to search for the loci of syntactic and semantic modules.

In our study, we used sentences as the stimuli that contained the adjective-noun construction because computation of modification is an unexplored research topic. The present study is, therefore, an attempt to specify the locus subserving the computation of modifications, and we expect that its results will contribute to further specifications of the brain area for semantic processing and/or retrieval

Material and methods

Subjects

Six male volunteers, mean age 23.8 years ranging from 21 to 27 (SD 2.19) participated in the experiment. None had a history of neurological or psychiatric disease. Japanese was their first language, and all showed right-handedness (laterality quotients, 60-100) as determined by the Edinburgh Inventory (Oldfield, 1971). They all had normal or corrected to normal vision. Written informed consent was obtained from all the subjects prior to the experiment whose protocol was approved by the Ethical Committee of Advanced Telecommunication Research Center (ATR), whose fMRI we used for our experiment.

Stimuli

In the present study, four types of stimulus sentences were presented visually for a period of 5000 ms at interstimulus intervals of 500 ms, during which a fixation cross was presented. The subjects were required to look at each stimulus and indicate whether there was an error or not by pressing a button.

All the words employed in the stimulus sentences were selected from the fundamental vocabulary for Japanese language teaching (National Language Research Institute, 1984). The fundamental vocabulary was graded from score 1 to 40 (maximum), and only words scoring over 20 were chosen. The lexical frequency of the words was also controlled according to vocabulary frequency tables (National Language Research Institute, 1970) to avoid activations related to word-frequency effect (Chee *et al.*, 2003). Although the stimulus sentences were written in *kanjis* (Chinese characters) and *kanas* (syllabled-based characters) to reflect the natural Japanese writing system, the length of all stimulus sentences was controlled, i.e., the total number of letters and morae of each sentence were the same (Nakamura *et al.*, 2000; Valaki *et al.*, 2003).

The stimulus sentences all consisted of, in this order, a subject, an adjective, a noun and a verb, and were classified into four types: both semantically and syntactically correct sentences (COR), semantically incorrect sentences, in which adjectives and nouns did not match semantically (SEM), syntactically incorrect sentences, in which adjectives followed nouns (SYN), and sentences containing lexical errors (LEX). Table 1 below shows sample stimulus sentences.

Each type had 16 stimulus sentences in total. The stimulus sentences of Types SYN and LEX were derived from the sentences of Type COR. To produce Type SYN sentences, the position of the adjective and the noun was changed from Type COR sentences, which caused syntactic errors. To produce Type LEX sentences, the order of the letters of the adjective was randomized, which produced an implausible adjective. Since all types of stimulus sentences contained the same nouns and verbs, the imageability (i.e., the load with which a stimulus can be mentally imagined) of the words employed in stimulus sentences was controlled (Casasanto, 2003).

By having the participants perform an error detection task, we expected to reveal the loci related to error detection. That is to say, we expected that Type LEX stimulus sentences would activate the region subserving

Table 1 Samples of experimental stimuli. In the sample sentences, Top stands for "topic marker" and Acc stands for "accusative case marker".

	Boku wa	shikakui	hako-o	aketa		
	I Top	square	box Acc	opened		
Type COR	"I opened a square box."					
(Filler)	The sentence is both syntactically and semantically correct. The					
	adjective-noun order is normal, and there is no semantic mis-					
	match between the adjective shikakui and the noun hako .					
	Boku wa	hageshii	hako o	aketa		
	І Тор	furious	box Acc	opened		
Type SEM	"I opened a furious box."					
(active task)	The sentence is semantically incorrect. The adjective hageshii					
	cannot modify the noun hako . Hagesii hako is an unacceptable					
	expression in Japanese.					
	Boku wa	hako o	shikakui	aketa		
	І Тор	box Acc	square	opened		
Type SYN	"I opened a box square."					
(active task)	The sentence is syntactically incorrect. The noun-adjective order					
	does not follow the Japanese grammar rules that require adjec-					
	tives to precede the head noun.					
Type LEX	Boku wa	ishikaku	hako o	aketa		
	I Top	(lexical error)	box Acc	opened		
	"I opened **** box."					
(baseline)	The adjective ishikaku is produced from shikakui by randomiz-					
	ing the order of its letters.					

the lexical knowledge; Type SYN stimulus sentences would reveal activation related to syntactic processing; and Type SEM stimulus sentences would activate the region associated with the semantic computation related to adjective-noun modification.

Prior to the task

Prior to the experiment, whether the adjectives could really modify the following nouns was checked through three questionnaires, answered by 43 people ranging 17 to 27 years of age. Type COR stimulus sentences were selected from answers whose modifying relations were judged to be correct by a 98.76% majority, while Type SEM sentences were chosen from the answers whose modifying relations were judged strange by a majority of 95.73%.

fMRI acquisition

The image scanning was performed on a 1.5 T scanning system (MAG-NEX ECLIPSE 1.5 T Power Drive 250, Shimadzu Marconi) that used a standard radiofrequency head coil for signal transmission and reception and employed the following parameters: TR (repetition time) 6000 msec, TE (echo time) 43 msec, flip angle 90°, field of view (FOV) 19.2×19.2 cm, pixel matrix dimensions 64×64 mm, and voxel size $3 \times 3 \times 5$ mm. Thirty contiguous 5 mm thick slices without gaps were obtained in the axial plane for each subject. For each task, there were two scanning sessions that lasted 234 seconds and yielded 78 functional images (4 scans for signal stabilization) for each subject.

Image analysis

Image and statistical analyses were performed on MATLAB (Math Works, Natick, MA) using statistical parametric mapping (Software SPM2 [Wellcome Department of Cognitive Neurology, London, UK]). The acquisition timing of each slice was corrected, and the functional images of each run were realigned. Each individual brain was spatially normalized using the first scan as a reference and then was smoothed by using a Gaussian kernel of $6 \times 6 \times 10$ mm.

A fixed effects model, with a threshold of P < .05, corrected for analyses across the entire volume of the brain, was used to establish distribution of activation, since the number of subjects were too small to use a ran-

dom effects model (Friston *et al*, 1998). The effects of all event types in each run were modeled by means of canonical hemodynamic response functions. All cortical responses with P < .05 are reported. Activated brain structures were identified by using Talairach Daemon (Talairach and Tournoux, 1988).

Results

Behavioral data

Response accuracy rates and reaction times were recorded for all responses in all sentence types to verify that the subjects were performing the task correctly (Table 2). There was a significant main effect of active tasks. According to the rates, Types SYN and LEX showed similarity in task difficulty, while some rates in Type COR showed that the tasks were slightly more difficult because, to certify Type COR sentences were correct, subjects had to confirm that no modifying, syntactic, or lexical errors existed.

Tyeps	Average	Correct	Average	P value (F value) RT relative to LEX		
	Correct	SD	$\mathrm{RT}\left(\mathrm{ms} ight)$			
COR (filler)	89.58	13.81	1592	.004 (12.89)		
SEM	95.83	9.31	1542	.01 (7.85)		
SYN	98.96	2.32	1544	.03 (6.34)		
LEX (baseline)	98.96	2.32	1131			

Table 2 Average percent correct and average reaction time (msec)

fMRI results

The brain areas activated in Type SEM sentences relative to Type LEX sentences and the brain areas activated in Type SEM sentences relative to Type SYN sentences are listed in Tables 3 and 4, respectively. Figures 1 and 2 illustrate the activation sites projected onto the standard brain space for these two comparisons. Type SEM relative to Type LEX showed significant left frontotemporal activation including middle frontal gyrus, IFG, and superior temporal gyrus, whilst Type SEM relative to Type SYN showed the activation in the left anterior IFG. The coordinates of the left anterior IFG between Type SEM as compared to Type LEX [(x, y, g) = (-44, 25, -2)] and those of Type SEM as compared to Type SYN [(-44, 25, -4)] were crucially close and the activations around those coordinates were observed neither in Type SYN relative to Type LEX, nor in Type SYN relative to the rest condition, nor in Type LEX relative to the rest condition.



Fig 1 Cortical activation in Type SEM relative to Type LEX. The activated areas are projected onto a template anatomical MRI scan. The activation map is thresholded at P = .005. Talairach coordinates and Z score of local activation are given in Table 3.

Table 3 Brain regions activated by Type SEM relative to Type LEX (P < 0.05, Z > 4.00)

Region	Cluster-level		ordina	Z-score	
	Max P value	x	у	z	
L. inferior frontal gyrus BA8	0.000	- 8	30	42	5.10
L. superior frontal gyrus BA 8	0.000	0	32	48	5.00
L. medial frontal gyrus	0.000	0	46	36	4.06
L. middle frontal gyrus	0.000	-44	18	26	4.96
L. inferior frontal gyrus BA 45	0.000	-52	26	18	4.29
L. inferior frontal gyrus	0.001	-44	25	-2	4.50

BA, Brodmann's area of peak activation. Coordinates: -x left hemisphere, +x right hemisphere, -y behind the anterior commisure, +y in front of the anterior commisure, -z below the anterior-posterior commisure plane, +z above the anterior posterior commisure plane. Regions written in boldface designate the main peak activation within an area whereas regions written in roman designate associated peaks. Threshold was set at P<.05.



Fig 2 Cortical activation in Type SEM relative to Type SYN. The activated areas are projected onto a template anatomical MRI scan. The activation map is thresholded at P = .005. Talairach coordinates and Z score of local activation are given in Table 4

Table 4 Brain regions activated by Type SEM relative to Type SYN (P< 0.05, Z> 4.00)

Region	Cluster-level Max <i>P</i> value	Coordinates			Z-score
		x	у	z	
L. inferior frontal gyrus	0.000	-44	25	- 4	5.60
L. superior frontal gyrus BA 47	0.000	-48	36	-14	4.14

Discussion

The present study aimed to identify cerebral areas specifically involved in the processing of the adjective-noun modification. We expected that Type SEM sentences would activate the region subserving the computation of modification, Type LEX sentences would activate the area related to the lexical knowledge, and the activation observed in the processing of Type SYN sentences should be correlated with the syntactic knowledge. Therefore, we expected that if we compared Type SEM with Types LEX and SYN, we could reveal the region selectively associated with the computation of modification.

The result was that (1) Type SEM relative to Type LEX showed significant increase of activation in the left anterior IFG, and Type SEM relative to Type SYN also showed the activation of the left anterior IFG; (2) those two activations in the left anterior IFG had notably close Tarairach coordinates, and seemed to be closely involved in the computation of modification. The reason for this result is that (1) there was no activation in the coordinates close to these two among the other comparisons which did not involve semantic processing, such as Type SYN relative to Type LEX; (2) there was no participation of other cognitive functions such as working memory and word novelty processing because the word frequency and the number of stimulus letters and morae were controlled among all the comparisons (Buckner and Koutstaal, 1998; Siliveri *et al.*, 1998; Chien et al., 2003; Martin et al., 2003; Chee et al., 2003); (3) there were no effects of grammatical differences because grammatical functions and parts of speech employed in the stimulus sentences were controlled across all the sentence types (Perani et al., 1999; Federmeier et al., 2000; Tyler et al., 2001; Marshall, 2003; Cappa and Perani, 2003; De Bleser and Kauschke, 2003; Tyler *et al.*, 2004)

It should also be added that the activation in BA 45 observed in Type SEM as compared to Type LEX was not found in the comparison between Type SEM relative to Type SYN. BA 45 was supposed to be related to syntactic processing (Embick *et al.*, 2000), and since the sentences of

Types SEM and SYN shared the same syntactic processing subserved at the frontal areas, BA 45 seemed not to appear in the comparison between Type SEM relative to Type SYN.

The left anterior IFG

The most notable finding in the present study is that the left anterior IFG is active in Type SEM as compared to Type LEX and Type SEM as compared to Type SYN but not in the other comparisons in which the subjects did not have to operate the semantic processing to perform the given task. Moreover, these two activation sites nearly overlap on Talairach coordinates. Thus, the two activations in the left anterior IFG should be specifically correlated with the computation of modification, which is commonly implicated in Type SEM as compared to Type LEX and Type SEM relative to Type SYN.

This finding is in good accordance with the classical and increasing number of interpretation of fMRI experimental results—that the left anterior IFG is selectively engaged when subjects perform semantic processing (Gabrieli *et al.*, 1998; Poldrack *et al.*, 1999; and also Thompson-Schill *et al.*, 1997; Thompson-Schill *et al.*, 1999). The first functional neuroimaging study implicating the role of the left IFG was Petersen *et al.s'* verb generation experiment (Petersen *et al.*, 1988). They recorded brain activity when their subjects generated a plausible verb (e.g., *eat*) to a presented noun (e.g., *cake*) and when their subjects merely read the noun. Verb generation relative to noun reading produced activation in the left IFG and other areas, such as the cingulate and the right cerebellum. Subsequently, several neuroimaging studies have certified similar left IFG activation in semantic tasks. Kapur *et al.* compared the brain activation when their subjects categorized each presented nouns as living or nonliving with the activation when their subjects detected the presence

of the letter a in presented nouns (Kapur et al., 1994). Categorizing task as compared to perceptual tasks revealed significant activation in the left IFG. Moreover, Dapretto and Bookheimer investigated the neural activity when their subjects judged whether or not the meaning of two presented sentences differed in terms of syntactic or semantic aspects (Dapretto and Bookheimer, 1999). In 'semantic' condition, each pair of presented sentences was identical in syntactic aspect expect for one word that was replaced with either synonym or a different word (e.g., "The lawyer questioned the witness" v.s. "The attorney questioned the witness" (same), "The man was attacked by the doberman" v.s. "The man was attacked by the pitbull" (different)), whilst, in 'syntactic' condition, the presented sentences in each pair were different in the word order and the voice (e.g., "The policeman arrested the thief" v.s. "The thief was arrested by the policeman" (same), "The teacher was outsmarted by the student" v.s. "The teacher outsmarted the student" (different)). Their finding indicated that a part of Broca's area, centered in the pars opercularis (BA 44), is critically implicated in syntactic processing, whereas the lower portion of the left IFG is selectively involved in semantic processing. Taken these results together, Bookheimer suggested that the semantic manipulation produced additional activity in the anterior IFG (Bookheimer, 2002).

Crucially, the left anterior IFG activation in our results is significantly close to the coordinates which Dapretto and Bookheimer referred to as the region critical for semantic processing [(-48, 20, -4)] (Dapretto and Bookheimer, 1999). It can, therefore, be concluded that, though it seems that the anterior IFG is not specific to adjective processing, the area subserves the computation of modification, or relating adjectives to nouns besides the production of semantically similar words (Petersen *et al.*, 1988), the distinction of words according to a category (Kapur *et al.*, 1994) and visual semantic processing (Phillips *et al.*, 2002; Noppeney *et* al., 2003).

Importantly, the results in our experiment do not contradict the theory that the left temporal language areas, such as the Wernicke's area process semantic aspects (Mummery et al., 1999; Hodges and Patterson, 1995). Rather, our results should be interpreted to indicate that the left temporal language areas and the left anterior IFG involve different semantic processing. There is, in fact, research that dissociates those two regions (Thompson-Schill et al., 1999). As an example of those researches, Thompson-Schill et al. suggest that the left inferior prefrontal cortex is likely to be involved in the selection of semantic material, and the Wernicke's area subserves semantic processing (Thompson-Schill et al., 1997; 1999). The region identified by Thompson-Schill et al. as crucial to semantic selection is, however, more superior and posterior than the semantic-related region that we observed in this experiment. Moreover, it is unclear how Selection Hypothesis explains the fact that passive listening to sentences activated the IFG (Müller et al., 1997). We cannot make a claim about the functional dissociation between the Wernicke's area and the left anterior IFG from this experiment though the Wernicke's area might subserve more basic semantic processing than the left anterior IFG does, since there is little evidence for semantic deficits in patients with damage restricted to frontal regions (Mummery et al., 1999). The Wernicke's area might integrate semantic features from sensorimotor areas and represent a lexicon, whilst the left anterior IFG might compute and process the interaction of lexicons represented in the Wernicke's area. However, there is still not enough evidence for either of these two hypotheses. Thus, further research is required to identify and dissociate the function between the left temporal language areas and the left anterior IFG.

Conclusion

The present study demonstrated that the left anterior IFG was activated in normal subjects for the computation of modification. The anterior IFG could not be observed in other comparisons in which the subjects did not necessitate semantic processing to perform the task. Overall, the results match the hypothesized neural basis for semantic processing (Dapretto and Bookheimer, 1999; Bookheimer, 2002). Therefore, it can be concluded that the left anterior IFG subserves the computation of the semantic relation between the adjective and the following noun.

Acknowledgments

We wish to thank Dr. Shinobu Masaki, Chief of the Brain Activity Imaging Center of ATR and the staffs there for their assistance and comments.

Reference

- Binder JR, Frost JA, Hammeke TA, Cox RW, Rao SM, Prieto T. Human brain language area identified by functional magnetic resonance imaging. *The journal of neuroscience* 1997; 17(1); 353-362
- Bookheimer SY. Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. Annu. Rev. Neurosci 2002; 25; 151-188
- Buckner RL, Koutstaal W. Funcational neuroimaging studies of encoding, priming, and explicit memory retrieval. *PNAS* 1998; 95; 891-898
- Cappa SF, Perani D. The neural correlates of noun and verb processing. Journal of neurolinguistics 2003; 16; 183-189
- Casasanto D. Hemispheric specialization in prefrontal cortex: effects of verbalizability, imagenability and meaning. *Journal of neurolin*-

guistics 2003; 16; 361-382

- Chee MWL, Venkatraman V, Westphal C, Siong SC. Comparison of Block and Event-related fMRI designs in evaluating the word-frequency effect. *Human brain mapping* 2003; 18; 186-193
- Chien JM, Ravizza SM, Fiez JA. Using neuroimaging to evaluate models of working memory and their implications for language processing. *Journal of neurolinguistics* 2003; 16; 315-339
- Dapretto M, Bookheimer SY. Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron* 1999; 24; 427-432
- De Bleser R, Kauschke C. Acquisition and loss of nouns and verbs: parallel or divergent patterns? *Journal of neurolinguistics* 2003; 16; 213-229
- Embick D, Maranz A, Miyashita Y, O'Neil W, Sakai KL. A syntactic specialization for Broca's area. *PNAS* 2000; 97; 6150-6154
- Federmeier KD, Segal JB, Lombrozo T, Kutas M. Brain responses to nouns, verbs and class-ambiguous words in context. *Brain* 2000; 123; 2552 2566
- Friederici AD, Opitz B, von Cramon DY. Segregation semantic and syntactic aspects of processing in the human brain: an fMRI investigation of different word types. *Cerebral cortex* 2000; 10; 698 705
- Friederici AD, Ruschemeyer SA, Hahne A, Fiebach CJ. The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral cortex* 2003; 13; 170-177
- Friston KJ, Fletcher P, Josephs O, Holmes A, Rugg MD, Turner R. Event-related fMRI: characterizing differential responses. *Neuroimage* 1998; 12; 147-158
- Gabrieli J, Poldrack R, Desmond J. The role of left prefrontal cortex in language and memory. *PNAS* 1998; 95; 906-913

- Homae F, Yahata N, Sakai KL. Selective enhancement of functional connectivity in the left prefrontal cortex during sentence processing. *Neuroimage* 2003; 20; 578-586
- Kapur S, Craik FI, Tulving E, Wilson AA, Houle S, Brown GM. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. PNAS 1994; 91; 2008-2011
- Malogiannis IA, Valaki C, Smyrnis N, Papathanasiou M, Evdokimidis I, Baras P, Mantas A, Kelekis D, Christodoulou GN. Functional magnetic resonance imaging (fMRI) during a language comprehension task. Journal of neurolinguistics 2003; 16; 407-416
- Marshall J. Noun verb dissociations—evidence from acquisition and developmental and acquired impairments. *Journal of neurolinguistics* 2003; 16; 67-84
- Martin RC, Wu D, Freedman M, Jackson EF, Lesch M. An event-related fMRI investigation of phonological versus semantic short-term memory. *Journal of neurolingustics* 2003; 16; 341-360
- Meyer M, Alter K, Friederici A. Functional MR imaging exposes differential brain responses to syntax and prosody during auditory sentence comprehension. *Journal of neurolinguistics* 2003; 16; 277 300
- Müller R, Rothermel RD, Bchen ME, Muzick O, Mangner TJ, Chugani HT. Receptive and expressive language activations for sentences: a PET study. *Neuroreport* 1997; 8; 3767-3770
- Nakamura K, Honda M, Okada T, Hanakawa T, Toma K, Fukuyama H, Konishi J, Shibasaki H. Participation of the left posterior inferior temporal cortex in writing and mental recall of kanji orthography: a functional MRI study. *Brain* 2000; 123; 954 -967
- National Language Research Institute. Studies on the vocabulary of modern newspapers Vol 1. General descriptions and vocabulary frequency tables. [Japanese]. Tokyo: Shuei-Shuppan; 1970.

- National Language Research institute. A study of the fundamental vocabulary: general description and vocabulary tables. [Japanese]. Tokyo: Shuei-Shuppan; 1984.
- Noppeney U, Friston KJ, Price CJ. Effects of visual deprivation on the organization of the semantic system. *Brain* 2003; 126; 1620-1627
- Oldfield RC. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 1971; 9; 97-113.
- Perani D, Cappa SF, Schnur T, Tettamanti M, Collina S, Rosa MM, Fazio F. The neural correlates of verb and noun processing: A PET study. *Brain* 1999; 122; 2337 2344
- Petersen SE, Fox PT, Posner ML, Mintun M, Raichle ME. Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 1988; 331; 585 589
- Phillips JA, Noppeney U, Humphreys GW, Price CJ. Can segregation within the semantic system account for category-specific deficits? *Brain* 2002; 125; 2067-2080
- Poldrack R, Wagner A, Prull M, Desmond J, Glover G, Gabrieli JD. Functional specialization for semantic and phonological processing in the inferior prefrontal cortex. *Neuroimage* 1999; 10; 15 35
- Sakai KL, Hashimoto R, Homae F. Sentence Processing in the cerebral cortex. Neuroscience report 2001; 39; 1-10
- Siliveri MC, Di Betta AM, Filippini V, Leggio MG, Molinari M. Verbal short-term store-rehearsal system and the cerebellum: evidence from a patient with a right cerebelluar lesion. *Brain* 1998; 121; 2175-2187
- Suzuki K, Sakai KL. An event-related study of explicit syntactic processing of normal/anomalous sentences in contrast to implicit syntactic processing. *Cerebral Cortex* 2003; 13; 517-526

Talairach J, Tournoux P. Co-planar stereotaxic atlas of the human brain.

Stuttgart: Thieme; 1988.

- Thompson-Schill SL, D'Esposito M, Aguirre G, Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *PNAS* 1997; 94; 14792-4797
- Thompson-Schill SL, D'Esposito M, Kan IP. Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron* 1999; 23; 513-522
- Tyler LK, Russell R, Fadili J, Moss HE. The neural representation of nouns and verbs: PET studies. *Brain* 124; 1619-1634
- Tyler LK, Bright P, Fletcher P, Stamatakis EA. Neural processing of nouns and verbs: the role of inflectional morphology. *Neuropsychologia* 2004; 42; 512-523
- Ullman MT. A Neurocognitive perspective on language: the declarative/prodedural model. *Nature review/Neuroscience* 2001; 2; 717 727
- Valaki C, Maestu F, Simos PG, Ishibashi H, Fernandes A, Amo C, Ortiz T. Do different writing systems involve distinct profiles of brain activation? A magnetoencephalography study. *Journal of neurolin*guistics 2003; 16; 429-438
- Wartenburger I, Heekeren HR, Burchert F, De Bleser F, Villringer A. Grammatical judgments on sentences with and without movement of phrasal constituents an event-related fMRI study. *Journal of neurolinguistics* 2003; 16; 301-314