

Functional Segregation of Semantic Memory and Processing in Ventral Inferior Frontal Gyrus

Mi Li^{1,2}, Shengfu Lu^{1*}, Xiaofei Xue¹ and Ning Zhong^{1,3}

1 The International WIC Institute
Beijing University of Technology
Beijing, China
lusf@bjut.edu.cn, xfx@emails.bjut.edu.cn

2 Liaoning ShiHua University
Liaoning, China
limi135@gmail.com

3 The Department of Life Science and Informatics
Maebashi Institute of Technology
Maebashi-City, Japan
zhong@maebashi-it.ac.jp

Abstract—Although many studies in neuroimaging showed that semantic tasks activated the left ventral inferior frontal gyrus (LvIFG), whether there is the functional segregation of LvIFG in the semantic memory and semantic processing remains unclear. In order to determine neural differences of semantic memory and processing in LvIFG with functional MRI, thirty-six subjects performed reading tasks on triplets of either text or figure or text-figure. The text/figure/figure+text tasks activated two common areas located in an anterior portion of LvIFG and a posterior portion of LvIFG. The BOLD signal change of the posterior portion of LvIFG has semantic working memory characteristics because semantic repetition priming and the BOLD signal change of anterior portion of LvIFG has information processing characteristics. The results suggest that the posterior portion of LvIFG unrelated to information forms is for semantic memory, whereas the anterior portion of LvIFG related to information forms is for semantic processing.

Keywords—left ventral inferior frontal gyrus(LvIFG); function MRI; semantic memory; semantic processing; BOLD signal change

I. INTRODUCTION

Since the findings of Petersen et al. with Positron emission tomographic (PET) suggested that the left inferior frontal gyrus (LIFG) was identified in processing for semantic association [1], many researchers have focused on the study of the LIFG in neuroimaging. These functional neuroimaging studies have implied that the LIFG is involved in semantic processing, such as semantic judgement [1-6], the control of semantic retrieval [4,7], and the selection of semantic information [8]. Moreover, this region is also related to the processing nonverbal tasks such as object naming [2,9] and unfamiliar faces recognition [10].

Further studies showed that the LIFG was separated into two functional areas, including the dorsal (near the inferior

frontal sulcus involving BA44/45) and ventral parts (BA45/47), and the posterior and dorsal aspect of the left IFG related to phonological processing and the anterior and ventral aspect involved selectively in semantic processing [11-13]. For example, phonetic relative to pitch judgments for auditorily presented syllables activates BA44/6 and BA44/45 [14,15]. Similarly, BA45 is more significantly activated for phonemic orthographic decisions in the visual domain [16]. By contrast, the anterior and ventral LIFG appears to be involved in semantic processing. Kapur et al. [17] demonstrated that semantic-related activity in BA45/47, while others found such activity in the mid-ventrolateral frontal cortex (BA47) [18]. Additionally, most previous studies reported that the LIFG was also activated during the sentence comprehension [19-23]. The cognitive process at the sentence level is not only the semantic processing of words alone, but also refers to syntactic processing [19, 20], semantic working memory [21], and the integration of world knowledge [22,23]. Peter et al using ERP and FMRI demonstrated that the LIFG (BA45/47) is involved in the integration of both word meaning and world knowledge during reading a sentence, and the brain retrieves and integrates them at the same time [22].

Besides the LIFG (BA45/47) is directly related to semantic processing of words, the similar area is decreased activation during repeated semantic processing of those same words (namely semantic priming) [4][24-26]. Gabrieli et al. found that, when making semantic decisions about words, the repeated semantic processing is decreased activation in LIFG relative to initial semantic processing. This decrease in activation represents a semantic repetition priming effect that occurs under implicit test instruction [25]. Further, such repetition-induced decreases in LIFG activation appear specific to semantic processing: Repeated nonsemantic processing of words does not reduce LIFG activation [4]. Another study about the semantic repetition priming examined the stimulus generality of LIFG function during repeated relative to initial semantic processing of

words and of pictures. Their results suggested that the LIFG area (approximately to BA45/47 posteriorly) is decreased activation with repetition regardless of perceptual form [26].

Taken together, the left ventral inferior frontal gyrus (LvIFG) is a crucial area for semantic processing regardless of the verbal and nonverbal stimuli, and this region is also activated in the retrieval from semantic memory that terms semantic memory for short. Semantic processing and semantic memory are two different cognitive processes. It seems that these different processes are subserved by the individual subregions of LvIFG, however, whether the functional segregation of LvIFG in the semantic memory and semantic processing remains unclear. In order to determine neural differences of semantic memory and processing in LvIFG, the experimental materials were designed as the reading tasks on triplets of either text or figure or text-figure, which can describe the same information or content. Figure 1 gives an example of textual and figure tasks used in the experiment. These complex reading tasks involve many cognitive processes such as semantic processing of words, phrases or graph and using world knowledge to construct the whole meaning, and also requires to repeated retrieval of semantic knowledge to comprehend the whole meaning. Based on the above previous studies, we hypothesized that (1) the LvIFG related to semantic memory and processing would be commonly activated by the three present form (text, figure and figure+text) tasks; (2) there would be distinct subregions activated in semantic processing and semantic memory: the subregion of the LvIFG related to semantic processing would be increased activated, which showed the semantic processing characteristics; whereas the subregion of the LvIFG related to semantic memory would be decreased activated, which showed the semantic executive function characteristics.

II. METHODS

A. Subjects

Thirty-six volunteers (eighteen female and eighteen male; mean age \pm standard deviation (*S.D.*) = 22.5 \pm 1.7) participated in this study. All of the subjects were right-handed and native-Chinese speaking. The subjects had no history of neurological or psychiatric illness, and no developmental disorders, including reading disabilities. All of the participants gave their written informed consent, and the protocol was approved by the Ethical Committee of Xuanwu Hospital of Capital Medical University and the institutional Review Board of the Beijing University of Technology.

B. Materials and Procedure

In the experiment, 20 text, figure and figure+text stimuli, as well as 8 text-baseline, figure-baseline and (figure+text)-baseline stimuli were used. Each text stimulus was presented for a period of 16 seconds, the figure was presented for 14s, and the figure+text was presented for 18s; all the baseline tasks were presented for 8s. The

presentation time was set according to the behavioral experiment, in which participants can fully understand the information of text or figure presented to them. The text, figure and figure+text tasks describing the same event were counterbalanced across subjects; no individual read the same event twice [27].

The experiment consists of 4 sessions. The order of the text, figure and figure+text stimuli was pseudo-randomized in each session. All stimuli were presented on a blank background screen. The participants were instructed to read text, figure or figure+text information attentively. After a stimulus task disappeared, a question including two options was presented, then the subjects could press the selected buttons (left button refers to the first option; right button refers to the second option). The subjects were limited to answer the question during a period of 8s, and then the following rest task was presented for 6s. Four sessions were collected per each participant. The images for the initial 10s were discarded because of unsteady magnetization; the remaining images in the session were used in the analysis.

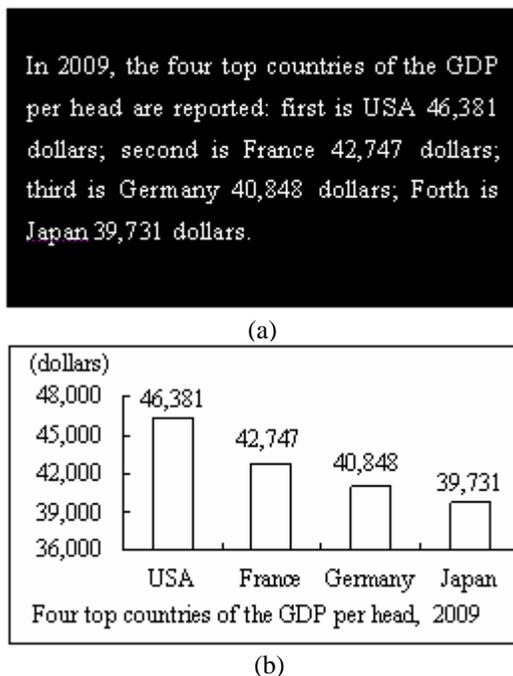


Figure 1 Examples of two types of tasks used in the experiment. (a) A figure task is an example of bar statistical graphs. (b) A text task is a paragraph ranging between 20 and 30 (mean 25) Chinese characters in length (here translated into English).

C. Image acquisition

In each subject, functional (T_2^* weighted) images, followed by an anatomical (T_1 weighted) image, were acquired with a Siemens 3-T Trio scanner (Trio system; Siemens Magnetom scanner, Erlangen, Germany). Functional images consisted of echo-planar image volumes which were sensitive to BOLD contrast in axial orientation

(TR = 2000 ms, TE = 31ms, flip angle = 90°). Prior to each run, the first two (10 s) discarded volumes were acquired to allow stabilization of magnetization. The volume covered the whole brain with a 64 × 64 matrix and 30 slices (voxel size = 4 mm × 4 mm × 4 mm, slice thickness = 4 mm, gap = 0.8 mm).

D. Data analysis

Functional data was analyzed with statistical parametric mapping (SPM 2, Wellcome Trust Centre for Neuroimaging, London, UK) implemented in Matlab 7.0 (Mathworks, Sherborne, MA, USA). The functional images of each participant were corrected for slice timing, and all volumes were spatially realigned to the first volume (the head movement was < 2 millimeters (mm) in all cases). A mean image created from the realigned volumes was coregistered with the structural T1 volume and the structural volumes spatially normalized to the Montreal Neurological Institute (MNI) EPI template using nonlinear basis functions. Images were resampled into 2-mm cubic voxels and then spatially smoothed with a Gaussian kernel of 8 mm full-width at half-maximum (FWHM). The stimulus onsets of the trials for each condition were convolved with the canonical form of the hemodynamic response function (HRF) as defined in SPM 2. Statistical inferences were drawn on the basis of the general linear model as it is implemented in SPM 2. Linear contrasts were calculated for the comparisons between conditions. The contrast images were then entered into a second level analysis (random effects model) to extend statistical inference about activity differences to the population from which the participants were drawn. Activations are reported for clusters of 10 contiguous voxels (80 mm³) that surpassed a corrected threshold of $p < .05$ on cluster level. The coordinates given by SPM 2 were corrected to correspond to the atlas of Talairach and Tournoux (1988).

III. RESULTS

As shown in Figure 2 (a)-(d) and Table 1, we did the conjunction analysis of text, figure and figure+text, and the conjunction between them. All the results consistently showed that two distinct segregated areas were more significantly activated in the left ventral inferior frontal cortex involving an anterior portion (Talairach: -30, 30, -13, BA47/11) and a posterior portion (Talairach: -28, 13, -16, BA47) by text, figure and figure+text. The BOLD signal change percentages at the anterior portion of LvIFG showed the increased activation that has semantic processing characteristics, which suggests that the anterior portion of LvIFG is more related to semantic processing. In contrast, the BOLD signal change percentages at the posterior portion of LvIFG showed the decreased activation that has the semantic executive function characteristics because semantic repetition priming, which suggests that the posterior portion of LvIFG is more involved in semantic memory.

In addition, we also did the conjunction of tasks and rest

(text and rest, figure and rest, figure+text and rest, and text, figure, figure+text and rest), as shown in Figure 2 (e)-(h) and table1. The results showed that only the posterior portion of LvIFG (Talairach: -30, 10, -14, BA47) was more significantly activated during resting state, whereas the anterior portion of LvIFG was not activated. The BOLD signal change percentages at the posterior portion of LvIFG also showed the decreased activation.

Therefore, these results suggest that the semantic processing and semantic memory are dissociated in LvIFG, which means that the anterior portion of LvIFG is more involved in semantic processing, whereas the posterior of LvIFG is more involved in semantic memory.

TABLE I. BRAIN ACTIVATIONS WITHIN THE LEFT VENTRAL FRONTAL CORTEX WITH CONJUNCTION ANALYSIS

Region (BA)	Coordinate ^a				Cluster size (mm ³)
	x	y	z	t	
T conj. F conj. FT					
Posterior LvIFG (47)	-28	13	-16	8.87	984
Anterior LvIFG (47/11)	-30	30	-13	8.28	400
T conj. F conj. FT conj. Rest					
Posterior LvIFG (47)	-30	10	-14	8.35	97
Task conj. Task					
T conj. F					
Posterior LvIFG (47)	-28	12	-16	9.11	1752
Anterior LvIFG (47/11)	-30	30	-13	8.08	784
T conj. FT					
Posterior LvIFG (47)	-28	12	-16	8.84	1656
Anterior LvIFG (47/11)	-30	30	-13	8.19	1046
F conj. FT					
Posterior LvIFG (47)	-30	10	-14	9.28	1752
Anterior LvIFG (47/11)	-30	30	-13	8.58	800
Task conj. Rest					
T conj. Rest					
Posterior LvIFG (47)	-30	10	-14	8.04	552
F conj. Rest					
Posterior LvIFG (47)	-30	10	-14	10.12	1216
FT conj. Rest					
Posterior LvIFG (47)	-30	10	-14	8.41	712

BA, Brodmann area; T, text meaning comprehension; F, figure meaning comprehension; FT, figure+text meaning comprehension; LvIFG, left ventral inferior frontal gyrus;

^a The talairach coordinates of the centroid and associated maximum(Peak) T value within contiguous regions are reported.

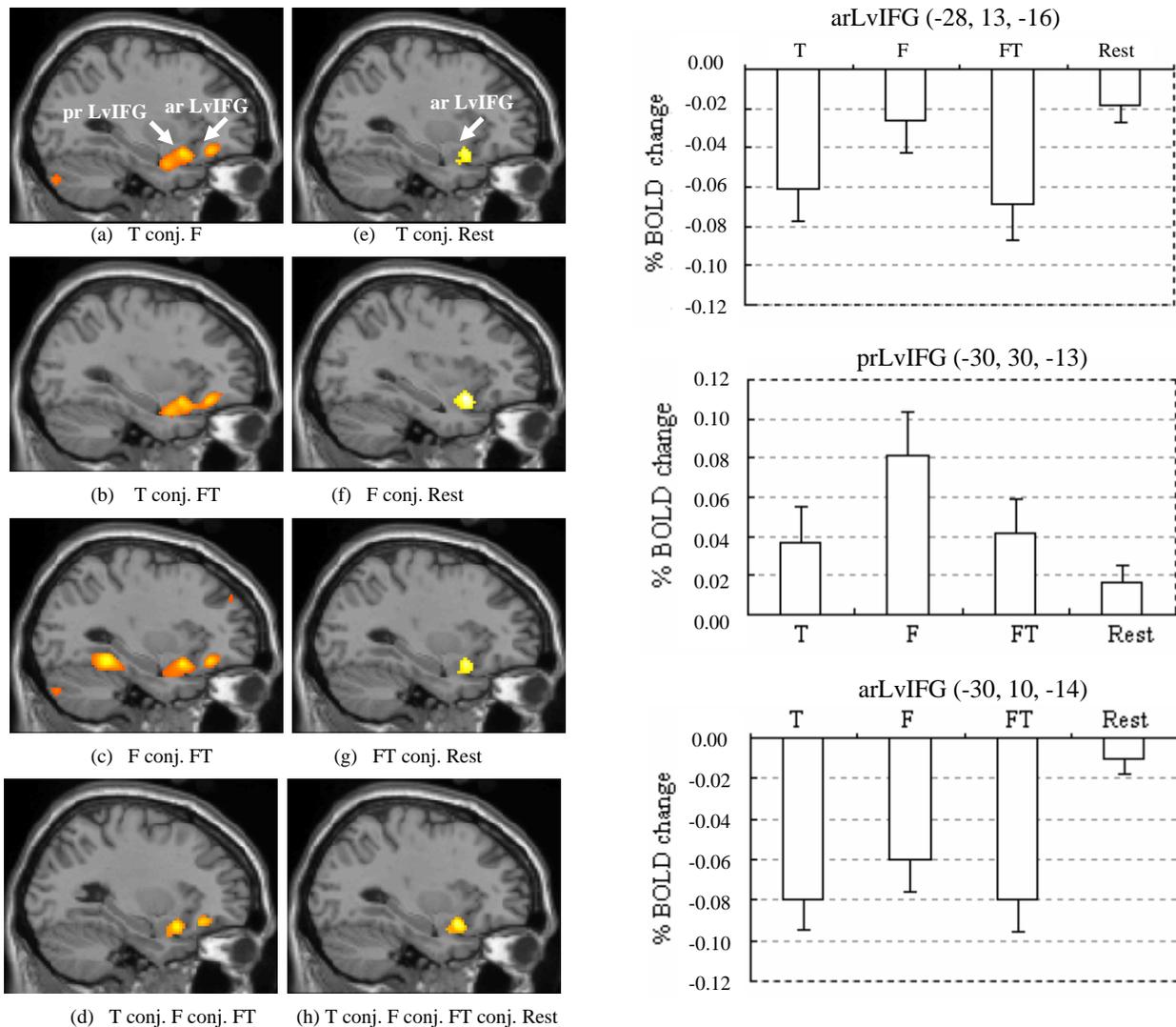


Figure 2 Regions of significant activation in the left ventral inferior frontal cortex. (a-d) Results with respect to the conjunction analysis between task and task: (a) T conj. F, (b) T conj. FT, and (c) F conj. FT, (d) T conj. F conj. FT. All of (a-d) showed that two distinct segregated areas activated in the left ventral inferior frontal gyrus (LvIFG) involving an anterior portion (BA47/11) and a posterior portion (BA47). (e-h) Results with respect to the conjunction analysis between task and rest: (e) T conj. Rest, (f) F conj. Rest, (g) FT conj. Rest, and (h) T conj. F conj. FT conj. Rest. All of (e-h) show that the consistent activation in the posterior portion (BA47) with (a-d) during resting state, whereas the anterior portion (BA47/11) of (a-d) has not activated in resting state. The results have implicated the posterior portion (BA47) related to semantic memory and the anterior portion (BA47/11) is not. The bar graph right shows the BOLD signal change percentages at the activated clusters in the anterior portion and posterior portion of the LvIFG. The statistical parametric map T of all were presented a threshold of 5.05 ($P < 0.05$, corrected for multiple comparisons) and a 400 mm³ cluster size. arLvIFG: anterior portion of LvIFG; prLvIFG: posterior portion of LvIFG.

IV. DISCUSSION

The goal of the present study was to examine the neural mechanism of the LvIFG related to semantic processing and semantic memory during reading comprehension of text, figure and figure+text. The three type tasks commonly activated the LvIFG involving an anterior portion and a posterior portion. The increase in BOLD signal of anterior portion showed the semantic processing characteristics, whereas the decrease in BOLD signal of posterior portion showed the semantic memory characteristics. In order to

further verify this result, we also do the further analysis about the conjunction between task and rest. If the posterior portion of LvIFG was related to the semantic memory, there would be only this region activated during rest state, and the BOLD signal of this region would be negative. Consistent with this hypothesis, the results of conjunction between task and rest showed that only the posterior portion of LvIFG was decreased activated and the BOLD signal was indeed decreased, whereas the anterior portion was not activated. Thus, the present findings reveal dissociation between semantic processing and semantic memory within the LvIFG.

A. Anterior portion of the LvIFG and semantic processing

This study showed that the activation of the anterior portion of the LvIFG was more related to the semantic processing regardless of text, figure and figure+text. Many previous neuroimaging studies using Positron emission tomographic (PET) and fMRI have consistently demonstrated that the anterior extent of the LIFG, corresponding to BA45/47, plays a crucial role in semantic processing of verbal and nonverbal tasks [1-10]. Petersen et al. (1988) with PET firstly reported that the left inferior frontal gyrus (LIFG) was identified in processing for semantic association [1]. Other functional neuroimaging studies have implicated that the LIFG is involved in semantic processing, such as semantic judgement [1-6], the control of semantic retrieval [4,7], and the selection of semantic information [8]. Moreover, this region is also related to the processing the nonverbal [9, 10]. Further studies that the LIFG was separated into two functional areas, including the dorsal (near the inferior frontal sulcus involving BA44/45) and ventral parts (BA45/47), and the posterior and dorsal aspect of the left IFG related to phonological processing and the anterior and ventral aspect involved selectively in semantic processing [11-13]. Additionally, many prior studies about sentence comprehension were also found the activation in LIPG [19-24]. The cognitive process at the sentence level is not only the semantic processing of words alone, but also refers to syntactic processing [19, 20], semantic working memory [21], and the integration of world knowledge [22,23]. Furthermore, the higher level about the discourse comprehension also found that the LIPG is activated [27,28].

In our study, subjects were instructed to read and comprehend the information presented by the text, figure or figure+text, which involves many cognitive processes such as semantic processing of words, phrases or graph and using world knowledge to construct the whole meaning. Thus, our finding suggests that the activation in the anterior portion of LvIFG contributes to the semantic processing and the integration of semantic and world knowledge.

B. Posterior portion of the LvIFG and semantic memory

In the present study, the posterior portion of the LvIFG (BA47) was decreased activated by the conjunction of task and task, and the conjunction of task and rest, suggesting this region might be more closely related to the semantic memory. This is consistent with previous studies [4][24-26]. Gabrieli et al. found that, when making semantic decisions about words, the repeated semantic processing is decreased activation in LIPG relative to initial semantic processing. This decrease in activation represents a semantic repetition priming effect that occurs under implicit test instruction [25]. Further, such repetition-induced decreases in LIPG activation appear specific to semantic processing: Repeated nonsemantic processing of words does not reduce LIPG activation [4]. Another study about the semantic repetition

priming examined the stimulus generality of LIPG function during repeated relative to initial semantic processing of words and of pictures. Their results suggested that the LIPG area (approximately to BA45/47 posteriorly) is decreased activation with repetition regardless of perceptual form [26]. Semantic memory refers to persons' general world knowledge [29,30], involving a wide range of information including facts, concepts and vocabulary [31]. Retrieval from semantic memory occurs during performance many cognitive tasks such as reading and making semantic decision. Other studies about the sentence comprehension have also reported that the LvIFG is activated and this region might be involved in verbal working memory during on-line sentence comprehension [20, 32]. In our study, the complex reading tasks require to repeated retrieval of semantic knowledge to comprehend the whole meaning. Together with the results during rest state, therefore, this study suggests that the decreased activation of the posterior portion of the LvIFG was more involved in semantic memory.

V. CONCLUSION AND FUTURE WORK

In summary, this study investigated whether the functional segregation of LvIFG in the semantic processing and semantic memory. The present findings indicated that distinct subregions in the LvIFG support the functional segregation of semantic processing and semantic memory. Our results suggest that the anterior portion of the LvIFG is more related to semantic processing, whereas the posterior portion of the LvIFG is more related to semantic memory. We look forward to future studies that further detail these complementary functions and the cooperative work between the anterior and posterior LvIFG play in the reading comprehension.

ACKNOWLEDGMENTS

This work is partially supported by the National Science Foundation of China (No. 60775039 and No. 60905027), the 8th Graduate Science and Technology Foundation of Beijing University of Technology (No. ykj-2010-3409) and the grant-in-aid for the grant-in-aid for scientific research (No.18300053) from the Japanese Ministry of Education, Culture, Sport, Science and Technology, and the Open Foundation of Key Laboratory of Multimedia and Intelligent Software Technology (Beijing University of Technology) Beijing.

REFERENCES

- [1] S. E. Petersen, P. T. Fox, M. I. Posner, M. Mintun, and M. E. Raichle, "Positron emission tomographic studies of the cortical anatomy of single-word processing," *Nature*, vol. 331, pp. 585-589, 1988.

- [2] R. Vandenberghe, C. Price, R. Wise, O. Josephs, and R. Frackowiak, "Functional anatomy of a common semantic system for words and pictures," *Nature*, vol. 383, pp. 254-256, 1996.
- [3] X. Wu, J. Lu, K. W. Chen, Z. Y. Long, X. Y. Wang, H. Shu, K. C. Li, Y. J. Liu, and L. Yao, "Multiple neural networks supporting a semantic task: An fMRI study using independent component analysis," *Neuroimage*, vol. 45, pp. 1347-1358, 2009.
- [4] J. B. Demb, J. E. Desmond, A. D. Wagner, C. J. Vaidya, G. H. Glover, and J. Gabrieli, "Semantic encoding and retrieval in the left inferior prefrontal cortex- a functional MRI study of task-difficulty and process specificity," *Journal of neuroscience*, vol. 15, pp. 5870-5878, 1995.
- [5] J. X. Zhang, J. Zhuang, L. F. Ma, W. Yu, D. L. Peng, G. S. Ding, Z. Q. Zhang, and X. C. Weng, "Semantic processing of Chinese in left inferior prefrontal cortex studied with reversible words," *Neuroimage*, vol. 23, pp. 975-982, 2004.
- [6] J. L. Wu, C. Cai, T. Kochiyama, and K. Osaka, "Function segregation in the left inferior frontal gyrus: a listening functional magnetic resonance imaging study," *Neuroreport*, vol. 18, pp. 127-131, 2007.
- [7] A. D. Wagner, E. J. Pare-Blagoev, J. Clark, and R. A. Poldrack, "Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval," *Neuron*, vol. 31, pp. 329-338, 2001.
- [8] S. L. Thompson-Schill, M. D'Esposito, G. K. Aguirre, and M. J. Farah, "Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation," *Proc. Natl. Acad. Sci. USA*, vol. 94, pp. 14792-14797, 1997.
- [9] M. Chee, B. Weekes, K. M. Lee, C. S. Soon, A. Schreiber, J. J. Hoon, and M. Chee, "Overlap and dissociation of semantic processing of Chinese characters, English words, and pictures: Evidence from fMRI," *Neuroimage*, vol. 12, pp. 392-403, 2000.
- [10] J. V. Haxby, L. G. Ungerleider, B. Horwitz, J. M. Maisog, S. I. Rapoport, and C. L. Grady, "Face encoding and recognition in the human brain," *Proc. Natl. Acad. Sci. U S A*, vol. 93, pp. 922-927, 1996.
- [11] R. A. Poldrack, A. D. Wagner, M. W. Prull, J. E. Desmond, G. H. Glover, and J. Gabrieli, "Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex," *Neuroimage*, vol. 10, pp. 15-35, 1999.
- [12] J. A. Fiez, "Phonology, semantics, and the role of the left inferior prefrontal cortex," *Human brain mapping*, vol. 5, pp. 79-83, 1997.
- [13] K. B. McDermott, S. E. Petersen, J. M. Watson, and J. G. Ojemann, "A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging," *Neuropsychologia*, vol. 41, pp. 293-303, 2003.
- [14] J. F. Demonet, F. Chollet, S. Ramsay, D. Cardebat, J. L. Nespoulous, R. Wise, A. Rascol, and R. Frackowiak, "The anatomy of phonological and semantic processing in normal subjects," *Brain*, vol. 115, pp. 1753-1768, 1992.
- [15] R. J. Zatorre, A. C. Evans, E. Meyer, and A. Gjedde, "Lateralization of phonetic and pitch discrimination in speech processing," *Science*, vol. 256, pp. 846-849, 1992.
- [16] J. A. Fiez, M. E. Raichle, F. M. Miezin, S. E. Petersen, P. Tallal, and W. F. Katz, "PET studies of auditory and phonological processing - effects of stimulus characteristics and task demands," *Journal of cognitive neuroscience*, vol. 7, pp. 357-375, 1995.
- [17] S. Kapur, F. Craik, E. Tulving, A. A. Wilson, S. Houle, and G. M. Brown, "Neuroanatomical correlates of encoding in episodic memory - levels of processing effect," *Proc. Natl. Acad. Sci. USA*, vol. 91, pp. 2008-2011, 1994.
- [18] S. E. Petersen, P. T. Fox, M. I. Posner, M. Mintun, and M. E. Raichle, "Positron emission tomographic studies of the processing of single words," *Journal of cognitive neuroscience*, vol. 1, pp. 153-170, 1989.
- [19] M. Dapretto and S. Y. Bookheimer, "Form and content: Dissociating syntax and semantics in sentence comprehension," *Neuron*, vol. 24, pp. 427-432, 1999.
- [20] Y. Uchiyama, H. Toyoda, M. Honda, H. Yoshida, T. Kochiyama, K. Ebe, and N. Sadato, "Functional segregation of the inferior frontal gyrus for syntactic processes: A functional magnetic-resonance imaging study," *Neuroscience research*, vol. 61, pp. 309-318, 2008.
- [21] D. Caplan and G. S. Waters, "Verbal working memory and sentence comprehension," *Behavioral and brain sciences*, vol. 22, p. 77-94, 1999.
- [22] P. Hagoort, L. Hald, M. Bastiaansen, and K. M. Petersson, "Integration of word meaning and world knowledge in language comprehension," *Science*, vol. 304, pp. 438-441, 2004.
- [23] G. R. Kuperberg, T. Sitnikova and B. M. Lakshmanan, "Neuroanatomical distinctions within the semantic system during sentence comprehension: Evidence from functional magnetic resonance imaging," *Neuroimage*, vol. 40, pp. 367-388, 2008.
- [24] J. Gabrieli, R. A. Poldrack and J. E. Desmond, "The role of left prefrontal cortex in language and memory," *Proc. Natl. Acad. Sci. U S A*, vol. 95, pp. 906-913, 1998.
- [25] J. Gabrieli, J. E. Desmond, J. B. Demb, A. D. Wagner, M. V. Stone, C. J. Vaidya, and G. H. Glover, "Functional magnetic resonance imaging of semantic memory processes in the frontal lobes," *Psychological science*, vol. 7, pp. 278-283, 1996.
- [26] A. D. Wagner, J. E. Desmond, J. B. Demb, G. H. Glover, and J. Gabrieli, "Semantic repetition priming for verbal and pictorial knowledge: A functional MRI study of left inferior prefrontal cortex," *Journal of cognitive neuroscience*, vol. 9, pp. 714-726, 1997.
- [27] M. St George, M. Kutas, A. Martinez, and M. I. Sereno, "Semantic integration in reading: engagement of the right hemisphere during discourse processing," *Brain*, vol. 122, pp. 1317-1325, 1999.
- [28] J. Xu, S. Kemeny, G. Park, C. Frattali, and A. Braun, "Language in context: emergent features of word, sentence, and narrative comprehension," *Neuroimage*, vol. 25, pp. 1002-1015, 2005.
- [29] E. Tulving, "Episodic and semantic memory", In E. Tulving & W. Donaldson (Eds.), *Organization of memory*, New York: Academic Press, pp. 381- 403, 1972.
- [30] E. Tulving, "Elements of Episodic Memory", Oxford: Clarendon Press, 1983.
- [31] L. R. Squire, "Memory and brain", Oxford Eng.: Oxford University Press, 1987.
- [32] F. Dick, E. Bates, B. Wulfeck, J. A. Utman, N. Dronkers, and M. A. Gernsbacher, "Language deficits, localization, and grammar: Evidence for a distributive model of language breakdown in aphasic patients and neurologically intact individuals," *Psychological review*, vol. 108, pp. 759-788, 2001.