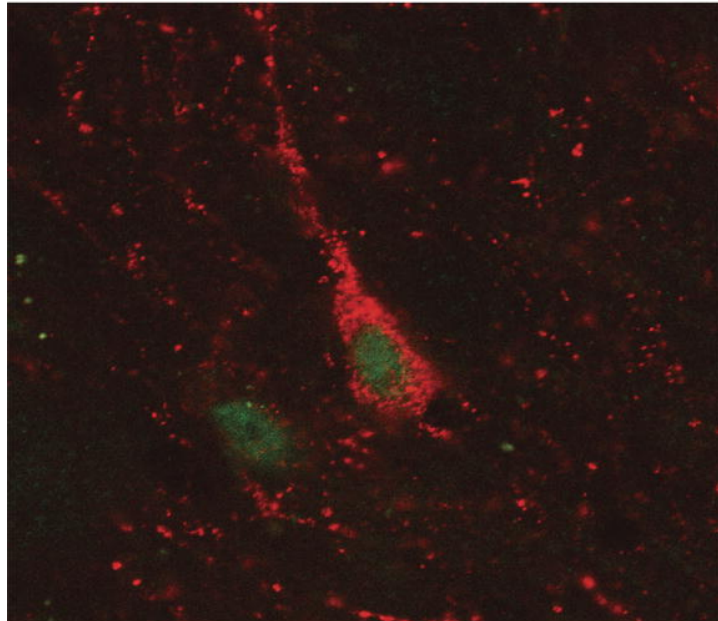


Brain Research



AUGUST 29, 2007 | VOLUME 1166
ISSN 0006-8959

This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Neural mechanisms involved in the comprehension of metaphoric and literal sentences: An fMRI study**Midori Shibata^{a,*}, Jun-ichi Abe^a, Atsushi Terao^a, Tamaki Miyamoto^b^aDepartment of Psychology, Hokkaido University, Kita 10, Nishi 7, Kita-ku, Sapporo, 060-0810, Japan^bBrain Function Research Laboratory, Hokkaido University Graduate School of Medicine, Sapporo 060-8698, Japan

ARTICLE INFO

Article history:

Accepted 15 June 2007

Available online 6 July 2007

Keywords:

Metaphor comprehension

Literal comprehension

Japanese

Left inferior frontal cortex

Medial frontal cortex

Functional magnetic
resonance imaging

ABSTRACT

In this study, we investigated the neural substrate involved in the comprehension of novel metaphoric sentences by comparing the findings to those obtained with literal and anomalous sentences using event-related functional magnetic resonance imaging (fMRI). Stimuli consisted of 63 copula sentences ("An A is a B") in Japanese with metaphorical, literal, or anomalous meanings. Thirteen normal participants read these sentences silently and responded as to whether or not they could understand the meaning of each sentence. When participants read metaphoric sentences in contrast to literal sentences, higher activation was seen in the left medial frontal cortex (MeFC: Brodmann's area (BA) 9/10), the left superior frontal cortex (SFC: BA 9), and the left inferior frontal cortex (IFC: BA 45). The opposite contrast (literal sentences in contrast to metaphoric sentences) gave higher activation in the precuneus (BA 7) and the right middle and SFC (BA 8/9). These findings suggest that metaphor comprehension is involved in specific neural mechanisms of semantic and pragmatic processing which differ from those in literal comprehension. Especially, our results suggest that activation in the left IFC reflects the semantic processing and that activation in the MeFC reflects the process of inference for metaphorical interpretation to establish semantic coherence.

© 2007 Elsevier B.V. All rights reserved.

1. Introduction

Metaphor comprehension is achieved by the complex interaction of topic and vehicle word meanings. Although a metaphor is literally a false statement, its meaning can be interpreted, and previous cognitive studies have investigated metaphor comprehension in comparison to literal comprehension (Blasko and Connine, 1993; Gibbs, 1990; Gildea and Glucksberg, 1983; Glucksberg, 2003; Glucksberg and Keysar, 1990; Glucksberg

et al., 1982; Grice, 1975; Searle, 1979). According to the standard pragmatic model (Grice, 1975; Searle, 1979), a hearer tries to determine the connotation of an utterance only after failing to find a literal meaning. This model implies that metaphor comprehension requires more steps and a longer duration of processing than literal comprehension. In contrast, according to the class-inclusion model (Gildea and Glucksberg, 1983; Glucksberg, 2003; Glucksberg and Keysar, 1990; Glucksberg et al., 1982), literal and metaphorical comprehension processes

* Corresponding author. Fax: +81 11 706 3033.

E-mail address: shibata@psych.let.hokudai.ac.jp (M. Shibata).

Abbreviations: BA, Brodmann's area; EEG, electroencephalogram; fMRI, functional magnetic resonance imaging; IFC, inferior frontal cortex; LH, left hemisphere; LHD, left hemisphere-damaged; MeFC, medial frontal cortex; MEG, magnetoencephalogram; MFC, middle frontal cortex; MNI, Montreal Neurological Institute; PET, positron emission tomography; RH, right hemisphere; RHD, right hemisphere-damaged; SFC, superior frontal cortex; SOA, stimulus-onset asynchrony; SPM, statistical parametric mapping

are basically identical. Thus, metaphors are understood directly as categorical assertions rather than through a property-matching comparison process. Indeed, these psychological studies have supported that metaphorical meanings are processed the same as literal counterparts using the metaphor interference task.

However, other studies using event-related potentials (ERPs) (Sotillo et al., 2005) and divided visual field paradigms (Anaki et al., 1998; Faust and Mashal, 2007) have shown that the neural substrate involved in metaphor comprehension differs from that involved in literal comprehension, and that the right hemisphere (RH) plays a crucial role in metaphor comprehension in addition to literal language processing in the left hemisphere (LH). For instance, Faust and Mashal (2007) investigated the role of the RH in the processing of novel metaphoric word meanings. Their stimuli consisted of pairs of words that formed four types of semantic relations (i.e., literal, conventional metaphoric, novel metaphoric and unrelated). The results showed that responses to target words presented to the LVF/RH were more accurate and faster than responses to those presented to the RVF/LH for novel metaphoric expressions, and supported a RH advantage for processing of novel metaphoric word meanings. On the other hand, Faust and Weisner (2000) investigated hemispheric asymmetries in comprehending metaphoric word meanings within a sentence context using the divided visual field paradigm. The results showed that both the LH and the RH play a role in processing non-literal language. Thus, there is still controversy regarding the role of the RH.

Behavioral studies with patients who suffer from brain lesions investigated whether the RH has a specific role for metaphor comprehension (Giora et al., 2000; Winner and Gardner, 1977; Zaidel et al., 2002). Winner and Gardner (1977) used a picture-matching task paradigm in which they orally presented metaphors. In this task, one type of picture portrayed the literal meaning, whereas the other type portrayed the metaphorical meaning of each metaphor. Right hemisphere-damaged (RHD) patients more often chose the literal-meaning pictures than left hemisphere-damaged (LHD) patients and participants in a non-neurological deficit group. However, in another task, RHD patients were able to offer verbal explications of the metaphors. Zaidel et al. (2002) investigated RH involvement in metaphor interpretation using the Right Hemisphere Communication Battery. The results showed that both groups performed significantly worse than normal controls, but there was no significant difference in test scores between LHD patients and RHD patients. Rinaldi et al. (2004) also reported that RHD patients tended to select the literal-meaning pictures in their picture-matching task but not in their verbal task, and that RHD patients might have preserved ability to understand metaphoric sentences. Thus, the results from these hemisphere-damaged patients indicate that the RH is not uniquely involved in processing metaphor comprehension.

There are other studies with patients who fail to understand the figurative language (schizophrenia: De Bonnis et al., 1997; Kircher et al., 2007, high-functioning children with autism: Dennis et al., 2001, Alzheimer's disease: Papagno, 2001). For example, Kircher et al. (2007) investigated processing of metaphoric sentences with fMRI in 12 patients with

schizophrenia and 12 control subjects using the same paradigm in Rapp et al. (2004) (cf., next paragraph). The results showed that metaphoric sentences in contrast to literal sentences elicited strongest activation in the left lateral inferior frontal cortex (IFC: BA 45/47) in the control subjects. Reading metaphoric sentences in contrast to literal sentences also elicited activation in the left inferior frontal cortex (IFC: BA 45/47) in patients with schizophrenia, but the exact location of peak activation was more dorsal. According to Kircher et al. (2007), numerous studies have shown altered lateral frontal lobe structure and function in schizophrenia, and changes in frontal lobe structure might affect an altered activation pattern during reading of metaphors. Thus, all the behavioral and imaging studies with patients have suggested that the RH is not selectively involved in processing metaphor comprehension. These studies also have suggested that finer-scale investigation is needed for identifying neural substrate for metaphor comprehension.

Recently, many researchers have investigated the neural basis of metaphor processing with normal participants (Ahrens et al., 2007; Bottini et al., 1994; Eviatar and Just, 2006; Giora et al., 2000; Lee and Dapretto, 2006; Mashal et al., 2005, 2007; Pynte et al., 1996; Rapp et al., 2004, 2007; Stringaris et al., 2006, 2007). In the first neuroimaging study on metaphor processing, Bottini et al. (1994) investigated cerebral activity with positron emission tomography (PET) in six healthy participants, and they concluded that the RH has a specific role in the appreciation of metaphors. Rapp et al. (2004) conducted another imaging study using event-related functional magnetic resonance imaging (fMRI) of healthy participants. Their stimuli consisted of 60 novel short German sentence pairs with either a metaphorical or literal meaning. The participants read the literal and metaphorical sentences and judged whether the sentences had positive or negative connotations. Their results showed that metaphorical sentences elicited greater activation than literal sentences in the left lateral inferior frontal cortex (IFC: BA 45/47), inferior temporal cortex (BA 20), and posterior middle/inferior temporal (BA 37) cortex. They concluded that particular activation in the left IFC may reflect semantic inferencing processes during the understanding of a metaphor. Even though both of the studies by Bottini et al. (1994) and Rapp et al. (2004) had the same goal (i.e., to identify the neural mechanism of metaphor comprehension), there are some differences between the results. Several studies (Eviatar and Just, 2006; Rapp et al., 2004; Stringaris et al., 2007) argued the possibility that the activation in the RH in Bottini et al. (1994) was affected by their task (i.e., judging the plausibility of the metaphors) and the higher complexity of their stimuli.

Following these pioneering works, studies that have investigated the neural substrate for metaphor comprehension have grown in number over the past few years. Some studies investigated the neural substrate associated with processing metaphoric word meaning (e.g., Lee and Dapretto, 2006; Mashal et al., 2005, 2007), and other studies have investigated the neural substrate associated with processing metaphoric sentences (e.g., Ahrens et al., 2007; Eviatar and Just, 2006; Rapp et al., 2007; Stringaris et al., 2006, 2007). Regarding the latter studies in detail, the studies by Rapp et al. (2004, 2007), Kircher et al. (2007) and Stringaris et al. (2006, 2007) used novel metaphors for their experiments, whereas

Eviatar and Just (2006) used conventional metaphors. Ahrens et al. (2007) used both anomalous (novel) and conventional metaphors. The results in Rapp et al. (2004, 2007) and Kircher et al. (2007) showed that metaphorical sentences elicited greater activation than literal sentences in the left lateral inferior frontal cortex (IFC: BA 45/47), inferior temporal cortex (BA 20), and posterior middle/inferior temporal (BA 37) cortex. In the studies by Stringaris et al. (2007), participants read metaphoric, literal, or nonsense sentences and decided whether or not the sentences made sense. The results showed that metaphoric sentences elicited greater activation than literal sentences in the left IFC (BA 47), the left precentral gyrus (BA 6) and the left inferior parietal lobe (BA 40/19). Ahrens et al. (2007) investigated cerebral activity using conventional metaphors, anomalous metaphors, and literal sentences within unmediated responses (their participants did not perform a sentence verification task). Their results showed that conventional metaphors induced activation in the right inferior temporal gyrus almost the same as literal sentences, but anomalous metaphors (compared to literal sentences) induced activation bilaterally in the frontal and temporal gyrus. Eviatar and Just (2006) also used conventional metaphoric utterances in brief three-sentence stories in contrast to ironic and literal utterances, and the conventional metaphoric utterances resulted in significantly higher levels of activation in the left IFC and in the bilateral inferior temporal cortex than the literal and ironic utterances. These results mainly showed the LH involvement in novel phrasal metaphor comprehension, but it has not arrived at the consensus for the activation patterns. This implies that the results of these studies described above are probably affected by various factors, i.e., novel or conventional metaphor, metaphoric words or phrasal metaphors, and different judgment processes (cf., Giora, 2007).

Although a number of experimental studies have been performed on the neural substrate involved in metaphor comprehension as described thus far, unfortunately, at the present time we were not able to arrive at any conclusion of this issue, i.e., the issue whether metaphor comprehension differs from literal comprehension or not is still controversial. In light of various results in the literature, the present study aims at identifying the neural substrate involved in the comprehension of novel metaphoric sentences by comparing literal and anomalous sentences using the sentence comprehension task. Especially, the present study aims at evaluating the involvement of the RH in the comprehension of novel phrasal metaphors. In addition, the present study intends to obtain the data of Japanese language. In recent neuroimaging studies, the results of English (Stringaris et al., 2007), German (Rapp et al., 2004, 2007), and Mandarin Chinese (Ahrens et al., 2007) have revealed the activation pattern involved in novel metaphoric sentence comprehension. The present study evaluates whether the activation pattern is affected by differences in languages.

2. Results

2.1. Behavioral results

Reaction time was defined as the time between the onset of the sentence presentation and the button press by the

participant. The mean reaction time for each type of sentence was 1326.8 ms for the literal sentence condition, 1771.4 ms for the metaphoric sentence condition, and 1503.8 ms for the anomalous sentence condition (Fig. 1). A one-way ANOVA for the reaction time of sentence type revealed a significant main effect ($F(2,62)=67.78$, $p<0.001$), and Tukey–Kramer post-hoc tests yielded significant differences in the reaction time between the three types of sentences (HSD (2)=2.40, $p<0.01$). The mean rate of “Yes” responses was 97.3% for literal sentences and 67.5% for metaphoric sentences. The mean rate of “No” responses for anomalous sentences was 92.5%. Although the mean rate of “Yes” responses for metaphoric sentences did not exceed 90%, it seems that participants were engaged in metaphor comprehension processing. We analyzed the image data based on the three sentence conditions that we first set up rather than on how the participants actually responded.

Behavioral data suggest that the process of metaphorical sentence comprehension differs from that of literal sentence comprehension. Based on the results of previous behavioral and imaging studies, conventional metaphors are mostly processed like a literal sentence with regard to reaction time and activation pattern (Ahrens et al., 2007; Eviatar and Just, 2006), but the process of novel metaphor comprehension is different from that of literal sentence comprehension (Ahrens et al., 2007). In the present study, we used novel metaphors as materials for the metaphoric sentence condition; our behavioral results revealed differences among the three sentence conditions.

2.2. Imaging results

In the activation of the literal sentence condition, the bilateral superior parietal lobules (BA 7), the right precuneus, the left SFC (BA 6), and the bilateral IFC (BA 9/45) were activated as well as the anterior cingulate cortex (BA 32) and the thalamus. In the activation of the metaphoric sentence condition the right SFC (BA 8), the left MeFC (BA 10), the bilateral middle frontal cortex (MFC: BA 46), the right IFC (BA 46/13), the left precentral (BA 44), the left insula, the anterior cingulate cortex (BA 24/32), and the thalamus were activated. In the activation of the anomalous sentence condition, the left SFC (BA 6), the left MeFC (BA 6), the bilateral IFC (BA 44/45), the right MFC (BA 9/46),

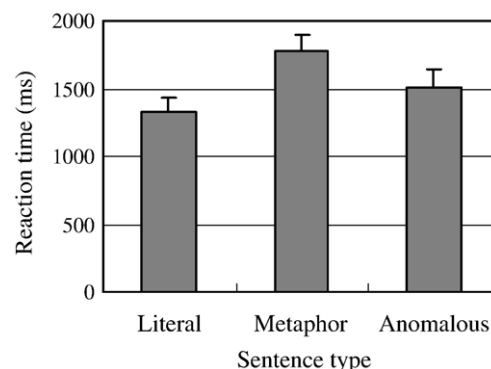


Fig. 1 – Mean reaction times for literal, metaphoric, and anomalous sentence conditions.

the bilateral superior temporal cortex (BA 22), the right cingulate cortex (BA 23/24/32), the thalamus, and the insula were activated (Fig. 2; Table 1).

As shown in Fig. 2 and Table 1, in both the literal sentence condition and the anomalous sentence condition, the left IFC (BA 9/44/45: Broca's area) showed a strong activation, whereas the right IFC showed relatively weak activation. In the metaphoric sentence condition, the left MFC (BA 46) was strongly activated, whereas the right middle and inferior frontal cortices were slightly activated.

The main goal of this study was to identify the neural substrate involved in metaphor interpretation compared to literal and anomalous interpretation. We analyzed differential contrast in the metaphoric sentence condition versus the literal sentence condition. As shown in Fig. 3 and Table 2, this contrast revealed higher activation in the inferior parietal lobule (BA 40), the left SFC (BA 9), the left MeFC (BA 9/10), and the left IFC (BA 45). This activation is significant at the cluster level. The opposite contrast (the literal sentence condition versus the metaphoric sentence condition) revealed higher activation in the right superior parietal cortex (BA 7), the bilateral precuneus (BA 7), the right SFC (BA 9), and the right MFC (BA 8). Differential contrast in the metaphoric sentence condition versus the anomalous sentence condition revealed

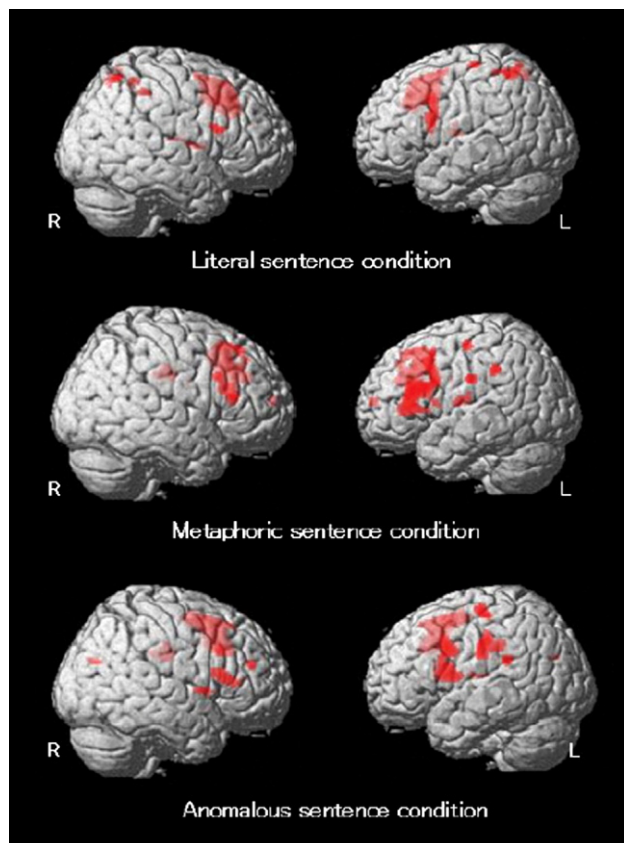


Fig. 2 – Regions exhibiting significant activation in the literal sentence condition (top row), the metaphoric sentence condition (middle row) and the anomalous sentence condition (bottom row). A random effects analysis was performed and activations are rendered onto a lateral view of a standard brain ($p < 0.001$, uncorrected).

Table 1 – Cerebral regions showing significant BOLD signal increases of each sentence condition

Region of activation	Left/ right	Brodmann area	Talairach coordinates			t value
			X	Y	Z	
<i>Literald sentence</i>						
Superior parietal	L	7	−32	−51	58	7.29
Superior parietal	R	7	34	−59	56	5.69
Inferior parietal	L	40	−36	−38	57	4.29
Precuneus	R	7	12	−44	54	5.57
Superior frontal	L	6	0	7	55	6.68
Inferior frontal	L	9/44/45	−55	11	20	6.61
Inferior frontal	R	9/44/45	53	14	18	5.10
Anterior cingulate		32	0	23	36	6.68
Thalamus	R		20	−9	12	4.64
Thalamus	L		−2	−7	17	4.59
<i>Metaphoric sentence</i>						
Superior frontal	R	8	2	28	47	7.30
Medial frontal	L	10	−8	57	8	5.99
Middle frontal	L	46	−44	28	17	7.22
Middle frontal	R	46	44	24	17	4.71
Inferior frontal	R	46/13	51	26	12	4.32
Precentral	L	44	−51	8	9	4.39
Anterior cingulate	R	24	4	−22	34	8.00
Anterior cingulate	L	24/32	−2	23	32	6.94
Insula	L		−42	−9	15	5.33
Thalamus	L		−4	−11	13	4.60
<i>Anomalous sentence</i>						
Precuneus	R		10	−71	26	4.94
Superior frontal	L	6	−2	8	49	8.75
Medial frontal	L	6	−2	−1	52	7.10
Middle frontal	R	9/46	55	21	32	4.99
Inferior frontal	L	9/44/45	−53	5	29	6.77
Inferior frontal	R	9/44/45	50	18	14	5.26
Superior temporal	L	22	−50	4	7	7.92
Superior temporal	R	22	51	8	1	6.64
Anterior cingulate	R	32/23/24	4	23	30	7.11
Thalamus	L		−6	−23	12	4.91
Random effects model, $P<0.001$ (uncorrected), extent threshold 10 voxels.						

Random effects model, $P < 0.001$ (uncorrected), extent threshold 10 voxels.

higher activation in the right SFC (BA 9/10), the left MeFC (BA 10), the left MFC (BA 46), and the left middle temporal cortex (BA 39). The opposite contrast (the anomalous sentence condition versus the metaphoric sentence condition) revealed higher activation in the right posterior cingulate cortex (BA 31) (Table 2).

We conducted a time-course analysis of the percent signal change of MR signals to examine the activation patterns in five regions using Marsbar (<http://marsbar.sourceforge.net/>). Mean percent signal changes were taken from the raw data of the relative fitted responses obtained by an analysis of the local maximum voxel (BA 9: (0, 52, 21), $t = 6.29$, BA 10: (0, 61, 14), $t = 5.56$, BA 9: (–4, 50, 29), $t = 4.58$, BA 45: (–42, 24, 14), $t = 5.16$, for the metaphoric sentence condition versus the literal sentence condition; BA 7: (10, –46, 50), $t = 6.95$, for the literal sentence condition versus the metaphoric sentence condition) (in Talairach's coordinates). The five locations and their coordinates are shown in Fig. 3 and Table 2. The percent signal change was averaged separately for each participant

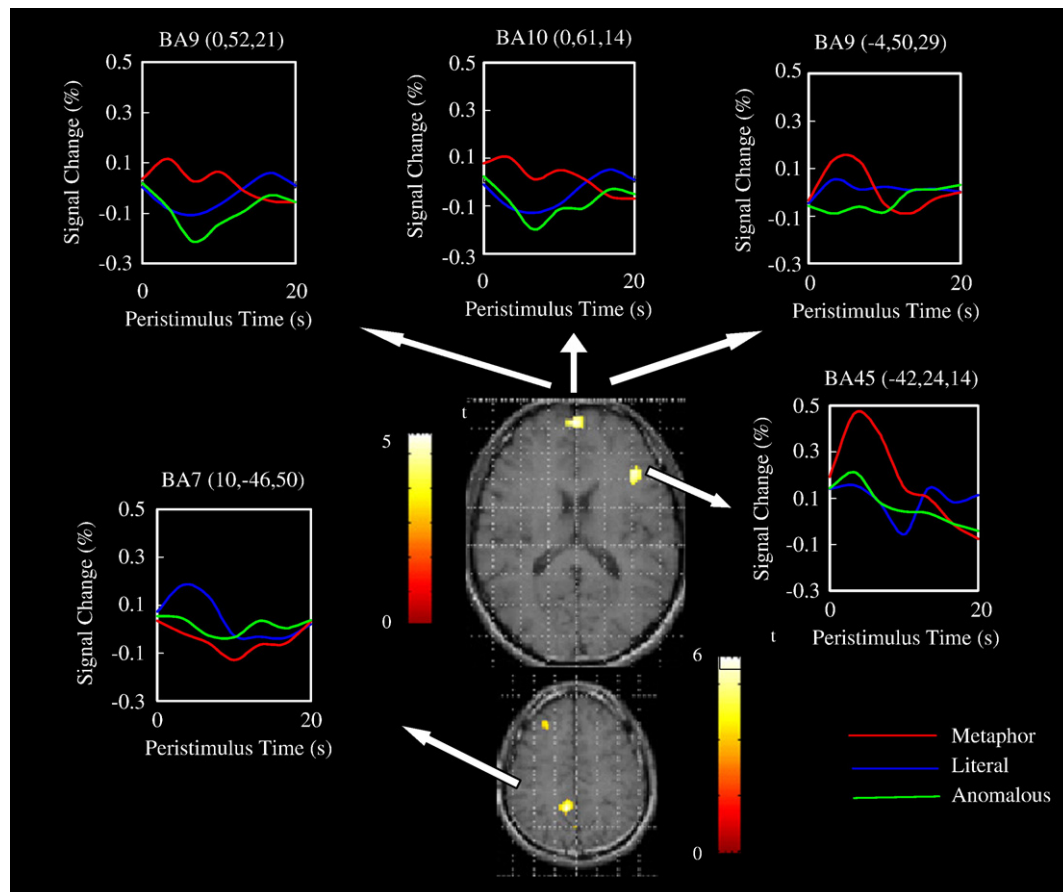


Fig. 3 – Time-course of signal changes for metaphoric, literal, and anomalous sentences in five regions. The regions were collected according to the highest *t* value for each type of response. Time curves were drawn based on the relative fitted responses from the local maximum voxel obtained in the analysis. The top panel shows the activation of differential contrast for the metaphoric sentence condition versus the literal sentence condition (BA 9: 0, 52, 21; BA 10: 0, 61, 14; BA 9: -4, 50, 29; BA 45: -42, 24, 14). The bottom panel shows the activation of differential contrast for the literal sentence condition versus the metaphoric sentence condition (BA 7: 10, -46, 50).

and each condition. As shown in Fig. 3, the percent signal change has a different pattern among the three sentences conditions. Fig. 3 shows that metaphoric sentences elicited a positive-going curve at four points (BA 9: (0, 52, 21), BA 10: (0, 61, 14), BA 9: (-4, 50, 29), BA 45: (-42, 24, 14)), while literal and anomalous sentences elicited negative-going curves in the SFC and the MeFC. In contrast, literal sentences elicited a positive-going curve in the BA 7: (10, -46, 50), while metaphoric and anomalous sentences elicited negative-going curves at that point.

In light of the behavioral result that the mean rate of “Yes” responses was 67.5% and that of “No” responses was 32.5%, we conducted an additional time-course analysis of the percent signal change of MR signals to examine the activation patterns of “Yes” or “No” judgments separately. As shown in Fig. 4, both “Yes” and “No” responses to metaphoric sentences elicited a positive-going curve in the BA 45: (-42, 24, 14). While “Yes” responses to metaphoric sentences elicited a positive-going curve at two points (BA 9: (0, 52, 21), BA 10: (0, 61, 14)), “No” responses to metaphoric sentences elicited negative-going curves in the same regions. In contrast, while “No” responses to metaphoric sentences elicited a positive-going curve at a

point (BA 9: (-4, 50, 29)), “Yes” responses to metaphoric sentences elicited negative-going curves at that point. In the BA 45, Figs. 3 and 4 showed that the activation patterns of “No” judgments were the same as those for metaphoric sentences, and differed from those for anomalous sentences. This indicates that despite their “No” judgments, the participants were also engaged in metaphor comprehension processing.

3. Discussion

The purpose of the present study was to identify the neural substrate involved in understanding novel metaphoric sentences in comparison to literal sentences. We used 63 Japanese copula sentences (“An A is a B”) as stimuli and all of the stimulus sentences were matched for syntax structure, word length, word familiarity, and tense. The sentences were simple statements, so the load of processing the sentence can be considered small. The mean reaction time differed among the three types of sentences. The mean reaction time for metaphoric sentences was significantly longer than those for literal and anomalous sentences. This result indicated that the

Table 2 – Cerebral regions showing significant BOLD signal increases in the metaphoric sentence condition versus the literal sentence condition, the metaphoric sentence condition versus the anomalous sentence condition, and each opposite contrast

Region of activation	Left/ right	Brodmann area	Talairach coordinates			t value
			X	Y	Z	
Metaphoric sentence condition vs. Literal sentence condition						
Inferior parietal lobule	L	40	−46	−50	39	4.40
Superior frontal	L	9	−4	50	29	4.58
Medial frontal	L	9	0	52	21	6.29
Medial frontal	L	10	0	61	14	5.56
Inferior frontal	L	45	−42	24	14	5.16
Literal sentence condition vs. Metaphoric sentence condition						
Superior parietal	R	7	10	−63	58	4.58
Precuneus	R	7	10	−46	50	6.95
Precuneus	L	7	−8	−53	58	4.56
Postcentral	L	7	−16	−51	65	5.94
Superior frontal	R	9	22	48	34	4.24
Middle frontal	R	8	26	35	41	4.78
Metaphoric sentence condition vs. Anomalous sentence condition						
Superior frontal	R	9/10	2	54	23	8.95
Medial frontal	L	10	0	61	12	5.71
Middle frontal	L	46	−40	26	15	5.25
Middle temporal	L	39	−34	−61	25	6.12
Anomalous sentence condition vs. Metaphoric sentence condition						
Cingulate	R	31	12	−37	44	4.60

Random effects model, $P < 0.001$ (uncorrected), extent threshold 10 voxels.

processing of novel metaphoric sentences required more time to attain a coherent semantic interpretation.

To summarize the imaging results of this experiment, Fig. 2 indicates that in addition to LH language processing the RH homologues also contributes to language comprehension. The results concerning literal sentence processing showed that the bilateral superior parietal lobules (BA 7), the right precuneus, the left SFC (BA 6) and the bilateral IFC (BA 9/45) were activated as well as the anterior cingulate cortex (BA 32) and the thalamus. On the other hand, in the activation of the metaphoric sentence condition, the results showed that the right SFC (BA 8), the left MeFC (BA 10), the bilateral middle frontal cortex (MFC: BA 46), the right IFC (BA 46/13), the left precentral (BA 44), the left insula, the anterior cingulate cortex (BA 24/32) and the thalamus were activated. These findings suggest the different processing pathway for literal and metaphoric sentences.

In the activation of the anomalous sentence condition, the results showed that the left SFC (BA 6), the left MeFC (BA 6), the bilateral IFC (BA 44/45), the right MFC (BA 9/46), the bilateral superior temporal cortex (BA 22), the right cingulate cortex (BA 23/24/32), the thalamus, and the insula were activated. Anomalous sentences contained a semantic violation, and could not be comprehended. Some studies (Arcuri et al., 2000; Baumgärtner et al., 2002; Hagoort et al., 2004; Kiehl et al., 2002) investigated the neural mechanism of semantic violation using fMRI. For example, Arcuri et al. (2000) presented sentences such as “the man is a baker” (semantically congruent) and “the man is a guitar” (semantically incongruent), and examined the processing of semantic properties. In the study by Kiehl et al. (2002), the

participants read sentences with endings that were either congruent (e.g., the dog caught the ball in his MOUTH) or incongruent (e.g., they called the police to stop the SOUP) to the sentence context. Incongruent sentence endings, like the anomalous sentences in our study, induced a strongly left-lateralized activation in the IFC. Arcuri et al. (2000) and Baumgärtner et al. (2002) investigated the neural correlates of integrating words into a sentence context and obtained similar results. Thus, these studies showed that the less congruent a particular sentence completion fits into a local context, the more signal changes there will be in the frontal and temporal language areas. Previous studies have indicated activation in the superior temporal cortex bilaterally for semantically anomalous sentences (Friederici et al., 2000, 2003; Kaan and Swaab, 2002; Newman et al., 2001). Our results in the activation of the anomalous sentence condition are basically consistent with those of previous studies.

We examined the differential contrasts in our results in more detail. As shown in Fig. 3, the point to observe is the activation in the left IFC (BA 45) and MeFC (BA 9/10). The opposite contrast revealed higher activation in the right precuneus (BA 7). Before discussing the roles of the left IFC and MeFC, we will discuss the role of the precuneus. Regarding activation in the precuneus (BA 7), some studies (Fletcher et al., 1995; Kircher et al., 2007) indicated that these areas have been implicated in processing of imaginable vs. abstract words. As shown in the Appendix, our stimulus sentences in the literal sentence condition consisted of more concrete and imaginable words than in metaphoric sentence condition. The activation in the precuneus might be affected by the imaginability of the stimulus sentences.

In this study, we sought to identify the neural substrate involved in novel Japanese phrasal metaphor comprehension as compared with literal and anomalous comprehension. We will now discuss the roles of the regions that showed significant activation in the metaphoric sentence condition versus the literal sentence condition. As shown in Fig. 3, there were mainly two regions; the left IFC (BA 45, Tal X Y Z: -42, 24, 14) and the MeFC (BA 9/10). First, the left IFC (BA 45) showed a greater signal change for metaphoric sentences than for anomalous and literal sentences. The difference in signal change in this region might reflect a difference in processing load between the three types of sentences. In line with our results, some studies have shown activation in the left IFG (Ahrens et al., 2007 (BA 9/13/44/45/47, Tal X Y Z: -50,20,26); Eviatar and Just, 2006 (BA 46, Tal X Y Z: -43,17,19); Kircher et al., 2007 (BA 45/47, Tal X Y Z: -44.5,40, -10); Rapp et al., 2004 (BA 45/47, Tal X Y Z: -39,35,1); Stringaris et al., 2007 (BA 47, Tal X Y Z: -43,29, -2)). Kircher et al. (2007), Rapp et al. (2004) and Stringaris et al. (2007) used simple novel sentences similar to our stimuli. The participants in the study by Rapp et al. (2004) and Kircher et al. (2007) had to judge whether or not the sentences had a positive or negative connotation. In our study and Stringaris et al. (2007), the participants were required to judge whether or not the sentence was understandable. Ahrens et al. (2007) used conventional and anomalous

(novel) metaphors and literal sentence as their stimuli with silent reading task and their findings showed the activation in LIFG in their anomalous metaphor vs. conventional metaphor condition. Eviatar and Just (2006) also used conventional metaphoric utterances in brief three-sentence stories in contrast to ironic and literal utterances, and the conventional metaphoric utterances resulted in significantly higher levels of activation in the left IFC and in the bilateral inferior temporal cortex than the literal and ironic utterances. In light of all these previous and present results, activation in the left IFC might play a key role in the process of metaphor comprehension. Our results also support that the RH is not selectively involved in processing metaphor comprehension.

Secondly, our results showed that the MeFC was involved in metaphor comprehension. As shown in Fig. 3, metaphoric sentences increased signal change in the MeFC. In contrast, literal and anomalous sentences decreased signal change in the MeFC. These results indicate that the MeFC might be specifically involved in metaphor processing. Moreover, Fig. 4 indicates that the “Yes” and “No” responses in the metaphoric sentences elicited a positive-going curve in the BA 45: (-42, 24, 14). In the MeFC regions, the “Yes” responses in the metaphoric sentences elicited a positive-going curve in two points (BA 9: (0, 52, 21), BA 10: (0, 61, 14)), but the “No” responses in the metaphoric sentences elicited negative-going curves in the same regions. In

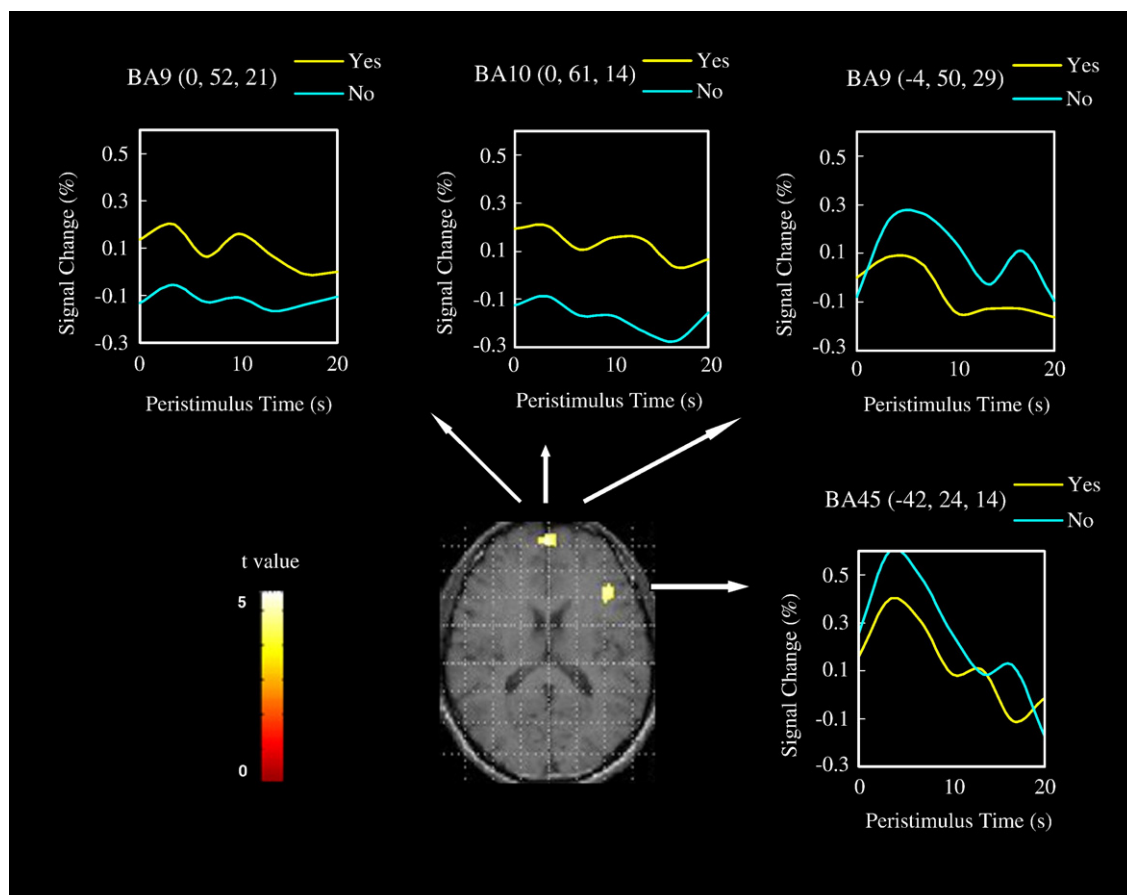


Fig. 4 – Time-course of signal changes for metaphoric sentences in four regions shown the activation patterns of “Yes” or “No” judgments separately. Time curves were drawn based on the relative fitted responses from the local maximum voxel obtained in the analysis. The panel shows the activation of differential contrast for the metaphoric sentence condition versus the literal sentence condition (BA 9: 0, 52, 21; BA 10: 0, 61, 14; BA 9: -4, 50, 29; BA 45: -42, 24, 14).

contrast, the “No” responses in the metaphoric sentences elicited a positive-going curve in the point (BA 9: (–4, 50, 29)), but the “Yes” responses in the metaphoric sentences elicited negative-going curves in that point. These results suggest that the MeFC activation reflects the judgment process of metaphorical interpretation to establish the semantic coherence. Recently, many studies have reported that the MeFC plays a crucial role in mentalizing, self-knowledge, person-knowledge, action monitoring, and outcome monitoring (Amodio and Frith, 2006; Frith and Frith, 1999; Frith, 2001; Gallagher and Frith, 2003). Several neuroimaging studies have implicated the medial frontal region as playing a role in comprehending stories with a Theory of Mind component (Bird et al., 2004; Ferstl and Cramon, 2001, 2002; Fletcher et al., 1995). Ferstl and Cramon (2002) showed that the medial frontal region is important for coherence processes in language comprehension for establishing the pragmatic connection between presented sentences. Other studies have indicated that the MeFC is involved in higher-level language comprehension. MeFC activation has been found in the context of pragmatic comprehension, i.e., plausibility judgment (Bottini et al., 1994), reasoning (Goel et al., 1997), coherence judgment (Ferstl and Cramon, 2002), and self-referential processing (Gusnard et al., 2001). In light of these previous studies, Jung-Beeman (2005) suggested the role of the MeFC in detecting, maintaining, or building coherent natural language representations. Our finding of a signal change in the medial frontal region for metaphoric sentences might suggest the role in detecting or failing to detect semantic coherence.

We evaluated whether the activation pattern is affected by differences in languages. The results in studies in English (Stringaris et al., 2007), German (Rapp et al., 2004, 2007), and Mandarin Chinese (Ahrens et al., 2007), and in Japanese in our study revealed that the left IFC is involved in metaphoric sentence comprehension. This suggests that the left IFC is involved in the comprehension of novel metaphoric sentences in all languages.

In summary, we found that differential contrast in the metaphoric sentence condition versus the literal sentence condition mainly showed higher activation in the left IFC (BA 45), and the MeFC (BA 9/10). We interpreted these results as indicating that different neural networks are involved in processing in metaphorical and literal interpretation. This also suggests that the left IFC is involved in semantic processing and that the MeFC is involved in the inference process of metaphoric interpretation to establish semantic coherence. However, due to the temporal resolution problem with fMRI, it is still not clear whether metaphor processing begins with a verification of semantic deviation and then semantic coherence is established, or if these processes are executed in parallel. Further research on temporal processes will be needed to clarify the relations in metaphor processing.

4. Experimental procedures

4.1. Participants

Thirteen normal graduate and undergraduate students (eight males and five females; mean age 23.8 years, range 21–29) participated in this experiment. They were all native Japanese

speakers. Handedness was assessed by the Edinburgh Handedness Survey (Oldfield, 1971), and all participants were right-handed. This experiment was conducted under a protocol approved by the Ethics Committee of Hokkaido University Graduate School of Medicine. All participants gave their written informed consent prior to participation in this experiment.

4.2. Materials

The experimental design used 3 conditions of sentence type (literal, metaphor and anomalous sentence conditions). We used 63 copula sentences for the materials. These materials consisted of 21 literal sentences (e.g., “A dolphin is an animal.”), 21 novel metaphoric sentences (e.g., “An education is stairs.”), and 21 anomalous sentences (e.g., “Scissors are dogs.”). Our stimuli were simple and short Japanese copula sentences of the form “An A is a B” without any contextual information. We chose this form to minimize the effects of complex syntax structures and complex contextual information. Prior to this experiment, 100 metaphoric sentences were extracted from Nakamoto and Kusumi (2004) or Shibata and Abe (2005) and another 20 participants rated the comprehensibility of each sentence as a metaphor on a scale of 1 to 9. The 21 metaphoric sentences with the highest comprehensibility were selected for this experiment (mean comprehensibility: 7.04, SD=1.17). In addition to these metaphoric sentences, 21 literal meaning sentences (category inclusion statements) and 21 anomalous sentences (semantic violation statements) were created for this experiment. These literal sentences and anomalous sentences were also rated for comprehensibility on a scale of 1 to 9 by another 20 participants who did not participate in this fMRI experiment (mean comprehensibility of literal sentences: 8.95, SD=1.60, mean comprehensibility of anomalous sentences: 1.22, SD=1.17). Based on these mean comprehensibility ratings, there were obviously qualitative differences among the three sentence conditions. All of the words of these sentences were selected from the NTT database: the lexical properties of Japanese such as familiarity, frequency and accent (Amano and Kondo, 2000); and were matched by word length and the familiarity rate of each word using this database. A one-way ANOVA was performed and the results showed that there were no significant differences in word familiarity ($F(2,125)=2.52$, $p=0.084$), or word length ($F(2,125)=0.32$, $p=0.725$). All sentences followed the standard Japanese writing style.

4.3. Procedure

The MRI scanning phase consisted of three sessions (150 functional image volumes per session with 5 initial volumes to avoid transient non-saturation effects) with 21 sentences (7 literal sentences, 7 metaphoric sentences, and 7 anomalous sentences) per session. The trials were pseudo-randomly ordered so that there were never more than three trials of the same sentence type in a row. Each stimulus sentence was displayed at the center of a rear projection screen. The participants viewed the screen comfortably through a mirror system mounted at the head coil. The participants were asked to read each sentence carefully to understand the content of the sentences and to press one of two buttons with their right

index finger if they understood the meaning of the sentence and with their middle finger if they did not, regardless of whether the meaning was literal or metaphorical. They literally determined the meaning of the literal sentence and metaphorically determined the meaning of the metaphoric sentence. They were tested individually, and their comprehension time (reaction time) and Yes/No judgments were recorded. Each sentence was presented for 3 s and immediately followed by the presentation of a cross-hair with a stimulus-onset asynchrony (SOA) of 20 s. The experimental stimuli and the recording of the participants' responses were controlled by E-prime (Psychology Software Tools, Inc.). All of the participants completed each test within 22 min.

4.4. fMRI data acquisition

A whole-body 1.5-T Signa Echo-Speed scanner (General Electric, Inc.) was used to acquire high-resolution T1-weighted anatomical images and gradient echo echo-planar T2*-weighted images with blood oxygenation level-dependent (BOLD) contrast of 16 axial slices. The parameters of the sequence were set as follows: TR=2800 ms, TE=40 ms, flip angle=90°, FOV=240×240 mm, matrix=64×64, slice thickness=4 mm, slice gap=0.8 mm. A total of 450 scans per participant were acquired (150 volumes×3 sessions).

4.5. fMRI data analysis

The data were analyzed by statistical parametric mapping (SPM2, Wellcome Department of Cognitive Neurology, London, UK: <http://www.fil.ion.ucl.ac.uk/spm/>) (Friston et al., 1995a,b). All functional volumes were realigned to the first volume of each participant to correct for head motion, spatially normalized to the Montreal Neurological Institute (MNI) brain template and smoothed using an 8-mm full-width-at-half-maximum Gaussian kernel. Functional data were analyzed in an event-related design, and the reaction time that was collected while the participants performed the task in the scanner was entered in these analyses as a regressor. For the group analysis, random effect analysis was conducted, based on the general linear model, with each of the three conditions modeled by the canonical hemodynamic response function and its temporal and dispersion derivatives. A high-pass filter with a cutoff period of 80 s was used to remove low-frequency noise. Global scaling was not applied. Statistical parametric maps were generated for each contrast of the *t* statistic on a voxel-by-voxel basis. The resulting statistical maps were height-thresholded at $p < 0.001$ uncorrected for multiple comparisons, and clusters of 10 or more contiguous voxels were reported. The complete data set was transformed into Talairach space (Talairach and Tournoux, 1988).

Acknowledgments

This research was supported in part by a Grant-in-Aid for Scientific Research (A: 15200019) from the Japan Society for the Promotion of Science. We are grateful to everyone who participated in our study.

Appendix A

–Literal sentence condition

The dolphin is an animal.
The chair is a piece of furniture.
The plate is a piece of tableware.
Rice is a plant.
Iron is a mineral.
Soybean paste (*miso*) is food.
A cherry (*sakura*) is a tree.
A piano is a musical instrument.
The flying dragon is an insect.
The saury is a fish.
The bus is a vehicle.
Wine is an alcoholic beverage.
Kelp is seaweed.
The Earth is a planet.
Tennis is a ball game.
The mandarin orange is a fruit.
The crow is a bird.
Cosmos are flowering grasses.
Cheese is a dairy product.
Copper is a metal.
The stomach is an internal organ.

–Metaphor sentence condition

An education is stairs.
Truth is a labyrinth.
Therapy is repair.
The child is an angel.
Loneliness is a cold wintry wind.
Life is a voyage.
Impact is electricity.
Judgment is a scale balance.
Rage is an eruption.
Smile is a flower.
Memory is a warehouse.
Love is a febrile disease.
Difficulty is a wall.
Research is a climbing.
The Earth is a mother.
Uneasiness is a dense fog.
Discussion is war.
An Age (or epoch; period) is a tide.
Zeal is lava.

Power is a drug.

Charm is a magnet.

–Anomalous sentence condition

Scissors are dogs.
Time is a strawberry.
The castle is an injection.
Seaweed is a small bird.
The star is curry.
Crystal is a pizza.
Chewing gum is baseball.
The dinosaur is tea.
The key is a green caterpillar.
The crab is a plum tree.
The eel is a station.
The string is a greenhouse.

The book is a marriage.
Milk is pajamas.
The typhoon is yogurt.
The house is ramen.
The hot spring is English.
The duck is a horse.
The taxi is a draft beer.
The desk is a swim.
The mantis is a chestnut.

REFERENCES

- Ahrens, K., Liu, H.L., Lee, C.Y., Gong, S.P., Fang, S.Y., Hsu, Y.Y., 2007. Functional MRI of conventional and anomalous metaphors in Mandarin Chinese. *Brain Lang.* 100, 163–171.
- Amano, S., Kondo, T., 2000. *Lexical Properties of Japanese*. NTT Database Series. Sanseido, Tokyo.
- Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. *Nat. Rev. Neurosci.* 7, 268–277.
- Anaki, D., Faust, M., Kravetz, S., 1998. Cerebral hemispheric asymmetries in processing lexical metaphors. *Neuropsychologia* 36, 691–700.
- Arcuri, S., Amaro, E., Kircher, T.T., Andrew, C., Brammer, M., Williams, S., Giampetro, V., McGuire, P.K., 2000. Neural correlates of the semantic processing of sentences: effects of close probability in an event-related fMRI study [Abstract]. *NeuroImage* 11, S333.
- Baumgaertner, A., Weiller, C., Buchel, C., 2002. Event-related fMRI reveals cortical sites involved in contextual sentence integration. *NeuroImage* 16, 736–745.
- Bird, C.M., Castelli, F., Malik, O., Frith, U., Husain, M., 2004. The impact of extensive medial frontal lobe damage on 'Theory of Mind' and cognition. *Brain* 127, 914–928.
- Blasko, D., Connine, C.M., 1993. Effects of familiarity and aptness on metaphor processing. *J. Exper. Psychol. Learn., Mem., Cogn.* 19, 295–308.
- Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., Frackowiak, R.S., Frith, C.D., 1994. The role of the right hemisphere in the interpretation of figurative aspects of language: a positron emission tomography activation study. *Brain* 117, 1241–1253.
- De Bonnis, M., Epelbaum, C., Deffez, V., Feline, A., 1997. The comprehension of metaphors in schizophrenia. *Psychopathology* 30, 149–154.
- Dennis, M.A., Lazenby, L., Lockyer, L., 2001. Inferential language in high-function children with autism. *J. Autism Dev. Disord.* 31, 47–54.
- Eviatar, Z., Just, M.A., 2006. Brain correlates of discourse processing: an fMRI investigation of irony and conventional metaphor comprehension. *Neuropsychologia* 44, 2348–2359.
- Faust, M., Mashal, N., 2007. The role of the right cerebral hemisphere in processing novel metaphoric expressions taken from poetry: a divided visual field study. *Neuropsychologia* 45, 860–870.
- Faust, M., Weisper, S., 2000. Understanding metaphoric sentences in the two cerebral hemispheres. *Brain Cogn.* 43, 186–191.
- Ferstl, E.C., Cramon, Y.V., 2001. The role of coherence and cohesion in text comprehension: an event-related fMRI study. *Cogn. Brain Res.* 11, 325–340.
- Ferstl, E.C., Cramon, Y.V., 2002. What does the front median cortex contribute to language processing: coherence or theory of mind? *NeuroImage* 17, 1599–1612.
- Fletcher, P.C., Happé, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S., Frith, C.D., 1995. Other minds in brain: a functional imaging study of "theory of mind" in story comprehension. *Cognition* 57, 109–128.
- Friederici, A.D., Wang, Y., Herrmann, C.S., Maess, B., Oertel, U., 2000. Localization of early syntactic processes in frontal and temporal cortical area: a magnetoencephalographic study. *Hum. Brain Mapp.* 11, 1–11.
- Friederici, A.D., Ruschemeyer, S.A., Hahne, A., Fiebach, C.J., 2003. The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cereb. Cortex* 13, 170–177.
- Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C., Frackowiak, R.S., Turner, R., 1995a. Analysis of fMRI time-series revisited. *NeuroImage* 2, 45–53.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.B., Frith, C.D., Frackowiak, R.S.J., 1995b. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- Frith, C.D., Frith, U., 1999. Interacting minds – a biological basis. *Science* 286, 1692–1695.
- Frith, U., 2001. Mind blindness and the brain in autism. *Neuron* 32, 969–979.
- Gallagher, H.L., Frith, C.D., 2003. Functional imaging of "theory of mind". *Trends Cogn. Sci.* 7, 77–83.
- Gibbs, R.W., 1990. Comprehending figurative referential descriptions. *J. Exper. Psychol. Learn., Mem., Cogn.* 16, 56–66.
- Gildea, P., Glucksberg, S., 1983. On understanding metaphor: the role of context. *J. Verbal Learn. Verbal Behav.* 22, 577–590.
- Giora, R., 2007. Is metaphor special? *Brain Lang.* 100, 111–114.
- Giora, R., Zaidel, E., Soroker, N., Batori, G., Kashner, A., 2000. Differential effect of right- and left-hemisphere damage on understanding sarcasm and metaphor. *Metaphor Symb.* 15, 63–83.
- Glucksberg, S., 2003. The psycholinguistics of metaphor. *Trends Cogn. Sci.* 7, 92–96.
- Glucksberg, S., Keysar, B., 1990. Understanding metaphorical comparisons: beyond similarity. *Psychol. Rev.* 97, 3–18.
- Glucksberg, S., Gildea, P., Bookin, H.B., 1982. On understanding nonliteral speech: can people ignore metaphors? *J. Verbal Learn. Verbal Behav.* 21, 85–98.
- Goel, V., Gold, B., Kapur, S., Houle, S., 1997. The seats of reason? An imaging study of deductive and inductive reasoning. *NeuroReport* 8, 1305–1310.
- Grice, H.P., 1975. Logic and conversation. In: Cole, P., Morgan, J. (Eds.), *Syntax and Semantics: Speech Acts*, vol. 3. Academic Press, New York.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* 98, 4259–4264.
- Hagoort, P., Hald, L., Bastiaansen, M., Petersson, K.M., 2004. Integration of word meaning and world knowledge in language comprehension. *Science* 304, 438–441.
- Jung-Beeman, M., 2005. Bilateral brain processes for comprehending natural language. *Trends Cogn. Sci.* 9, 512–518.
- Kaan, E., Swaab, T., 2002. The brain circuitry of syntactic comprehension. *Trends Cogn. Sci.* 6, 350–356.
- Kiehl, K., Laurens, K., Liddle, P., 2002. Reading anomalous sentences: an event-related fMRI study of semantic processing. *NeuroImage* 17, 842–850.
- Kircher, T.T., Leube, D.T., Erb, M., Grodd, W., Rapp, A.M., 2007. Neural correlates of metaphor processing in schizophrenia. *NeuroImage* 34, 281–289.
- Lee, S.S., Dapretto, M., 2006. Metaphorical vs. literal word meanings: fMRI evidence against a selective role of the right hemisphere. *NeuroImage* 29, 536–544.
- Mashal, N., Faust, M., Hendler, T., 2005. The role of the right hemisphere in processing nonsalient metaphorical meanings: application of principal components analysis to fMRI data. *Neuropsychologia* 43, 2084–2100.

- Mashal, N., Faust, M., Hendler, T., Jung-Beeman, M., 2007. An fMRI investigation of the neural correlates underlying the processing of novel metaphoric expressions. *Brain Lang.* 100, 115–126.
- Nakamoto, K., Kusumi, T., 2004. A classification of 120 Japanese metaphorical expressions on the basis of four psychological dimensions. *The Science of Reading* 48, 1–10.
- Newman, A.J., Pancheva, R., Ozawa, K., Neville, H.J., Ullmann, M.T., 2001. An event-related fMRI study of syntactic and semantic violations. *J. Psycholinguist. Res.* 30, 339–364.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9, 97–113.
- Papagno, C., 2001. Comprehension of metaphors and idioms in patients with Alzheimer's disease: a longitudinal study. *Brain* 124, 1450–1460.
- Pynte, J., Besson, M., Robichon, F.H., Poli, J., 1996. The time-course of metaphor comprehension: an event-related potential study. *Brain Lang.* 55, 293–316.
- Rapp, A.M., Leube, D.T., Erb, M., Grodd, W., Kircher, T.T., 2004. Neural correlates of metaphor processing. *Cogn. Brain Res.* 20, 392–402.
- Rapp, A.M., Leube, D.T., Erb, M., Grodd, W., Kircher, T.T., 2007. Laterality in metaphor processing: lack of evidence from functional magnetic resonance imaging for the right hemisphere theory. *Brain Lang.* 100, 142–149.
- Rinaldi, M.C., Marangolo, P., Baldassarri, F., 2004. Metaphor comprehension in right brain-damaged patients with visuo-verbal and verbal material: a dissociation (re)considered. *Cortex* 40, 479–490.
- Searle, J., 1979. Metaphor. In: Ortony, A. (Ed.), *Metaphor and Thought*. Cambridge University Press, pp. 92–123.
- Shibata, M., Abe, J., 2005. The comprehension process of copula sentence. *Proceedings of the Annuals of the Hokkaido Psychological Society*, vol. 28, p. 83.
- Sotillo, M., Carretie, L., Hinojosa, J.A., Tapia, M., Mercado, F., Lopez-Martin, S., Albert, J., 2005. Neural activity associated with metaphor comprehension: spatial analysis. *Neurosci. Lett.* 373, 5–9.
- Stringaris, A.K., Medford, N.C., Giora, R., Giampietro, V., Brammer, M.J., David, A.S., 2006. How metaphors influence semantic relatedness judgments: the role of the right frontal cortex. *NeuroImage* 33, 784–793.
- Stringaris, A.K., Medford, N.C., Giampietro, V., Brammer, M.J., David, A.S., 2007. Deriving meaning: distinct neural mechanisms for metaphoric, literal, and non-meaningful sentences. *Brain Lang.* 100, 150–162.
- Talairach, J., Tournoux, P., 1988. *A Co-Planner Stereotaxic Atlas of a Human Brain: A 3-Dimensional Proportional system. An Approach to Cerebral Imaging*. Thieme Medical Publishers, New York.
- Winner, E., Gardner, H., 1977. The comprehension of metaphor in brain-damaged patients. *Brain* 100, 717–729.
- Zaidel, E., Kasher, A., Soroker, N., Batori, G., 2002. Effects of right and left hemisphere damage on performance of the “Right Hemisphere Communication Battery”. *Brain Lang.* 80, 510–535.