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# Everyday conversation requires cognitive inference: Neural bases of comprehending implicated meanings in conversations

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ABSTRACT

In ordinary conversations, literal meanings of an utterance are often quite different from implicated meanings and the inference about implicated meanings is essentially required for successful comprehension of the speaker's utterances. Inference of finding implicated meanings is based on the listener's assumption that the conversational partner says only relevant matters according to the maxim of relevance in Grice's theory of conversational implicature. To investigate the neural correlates of comprehending implicated meanings under the maxim of relevance, a total of 23 participants underwent an fMRI task with a series of conversational pairs, each consisting of a question and an answer. The experimental paradigm was composed of three conditions: explicit answers, moderately implicit answers, and highly implicit answers. Participants were asked to decide whether the answer to the Yes/No question meant 'Yes' or 'No'. Longer reaction time was required for the highly implicit answers than for the moderately implicit answers without affecting the accuracy. The fMRI results show that the left anterior temporal lobe, left angular gyrus, and left posterior middle temporal gyrus had stronger activation in both moderately and highly implicit conditions than in the explicit condition. Comprehension of highly implicit answers had increased activations in additional regions including the left inferior frontal gyrus, left medial prefrontal cortex, left posterior cingulate cortex and right anterior temporal lobe. The activation results indicate involvement of these regions in the inference process to build coherence between literally irrelevant but pragmatically associated utterances under the maxim of relevance. Especially, the left anterior temporal lobe showed high sensitivity to the level of implicitness and showed increased activation for highly versus moderately implicit conditions, which imply its central role in inference such as semantic integration. The right hemisphere activation, uniquely found in the anterior temporal lobe for highly implicit utterances, suggests its competence for integrating distant concepts in implied utterances under the relevance principle.



## Introduction

Understanding the other's intentions is a prerequisite for human communication. To understand intended meanings of an utterance, however, one must be able to evaluate the whole meaning of the sentence within a given social context, which requires more than a simple linguistic capability; it requires pragmatic communicative competence. In order to be competent in verbal communication, one must understand not only syntactic and semantic aspects of an utterance, but also pragmatic aspects as well—the social settings, the characteristics of relationships between the speaker and the listener, and so on, or every arena of language use (Clark, 1993).

More often than not, the explicit meanings (or face values) of an utterance might be quite different from the implicated (or intended) meanings. This phenomenon is well explained by Grice's theory of conversational implicature (Grice, 1975). Grice first used the term *implicature* to indicate 'what is suggested or implicated' as opposed to 'what is said'. Consider the following example:

A: "Smith doesn't seem to have a girlfriend these days."

B: "He's been paying lots of visits to New York lately."

According to Grice, speakers and listeners rely on the four maxims of conversation: 'be informative (quantity), don't say what you believe to

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be false (quality), be relevant (relevance) and be brief and clear (manner)'. Under the basic premise that cooperative principles are observed, the listener understands the meaning that the speaker (B) has implicated by intentionally flouting a particular maxim. Since B does not make a direct reference to Smith's girlfriend, B's utterance seems to be violating the maxim of relevance – 'be relevant' – at least at its face value. But the listener assumes that B is cooperative; thus, A believes that B is observing the maxim of relevance. Based on this assumption, the listener infers that B's answer indicates that Smith may have, or has, a girlfriend in New York.

As the ability to properly comprehend implicated meanings is crucial for verbal communication, the present study was aimed at investigating functional neuroanatomy of comprehending conversational implicatures, specifically focusing on the implicature in which the maxim of relevance is violated, i.e., 'relevance implicature.'

In the field of pragmatics, relevance implicature has been distinguished from other types of conversational implicatures such as irony and metaphor. While relevance implicatures arise from flouting the maxim of relevance, i.e., 'be relevant', metaphor and irony occur by flouting the maxim of quality, i.e., 'be truthful' (Grice, 1975). In other words, the speaker does not believe that the literal meaning of metaphor or irony is true. For example, 'You are my sunshine' expressed metaphorically does not mean that 'you' is literally 'sunshine'. Likewise, when someone says sarcastically that 'his room is awfully clean', it means that the room is actually not clean at all.

There exist many neuroimaging studies on irony or metaphor (Eviatar and Just, 2006; Kircher et al., 2007; Mashal et al., 2005, 2007; Rapp et al., 2004, 2010; Schmidt and Seger, 2009; Shamay-Tsoory et al., 2005; Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006; Wakusawa et al., 2007; Wang et al., 2006). However, to our knowledge, there are no fMRI studies on the neural substrates associated with comprehension of relevance implicatures.

To investigate functional neuroanatomy for comprehending relevance implicature, we presented a series of conversational pairs (questions and answers) to the participants under fMRI scanning. For each of the questions, the following three types of answers were used as stimuli, depending on the level of implicitness: explicit answer, moderately implicit answer, and highly implicit answer. For example, the three answers that were presented for the question,

A: "Is Dr. Smith in his office now?"were:

(1) B: "Dr. Smith is in his office now" (explicit);
(2) B: "Dr. Smith's car is parked outside the building" (moderately implicit); and
(3) B: "The black car is parked outside the building" (highly implicit).

Answer (1) is conveying the information the questioner seeks, and no implicature is involved. For answers (2) and (3), the face values of the utterances are not directly related to the question. If the listener has no contrary evidence to assume that the speaker is observing the maxim of relevance, the listener may infer that *Dr. Smith* is in the office, thinking, 'If his car is outside the building, he must be in his office.' The bridging words, *Dr. Smith* in condition (2), help the participants generate inference more easily. The literal meaning of condition (3) is even less relevant to the question because there is no linguistic expression that directly links the answer sentence with the question, compared to condition (2). In this highly implicit condition (3), only pragmatic circumstance guides inference to establish coherence between the question and the answer. For successful comprehension of (3), the listener further infers that 'the black car' in the speaker's utterance must be associated with *Dr. Smith* in this pragmatic context and this generated inference bridges two utterances to be more coherent in the conversation.

As shown in the above example, the comprehension of implicated meanings requires an inference process to establish coherence between the question and the answer utterances. This inference differs from other types of inferences such as causal or logical inferences in that it is mainly guided by the maxim of relevance. To make what the speaker is saying consistent with the presumption that the speaker observes the relevance maxim, the listener must suppose that the speaker did not say that utterance otherwise the speaker believes 'what the speaker implicated' (i.e., Dr. Smith is in the office). The listener should also know that 'the speaker thinks (and expects the listener to think that the speaker thinks) that the listener is competent to figure out 'what the speaker implicated' (Grice, 1975). With these presumptions, listeners infer the underlying meanings of speakers' utterances based on information from the literal value of the linguistic expressions, shared knowledge, and discourse contexts. Information from mentalization, i.e., interpreting utterances from the perspective of the speaker's mental state according to the theory of mind (ToM) (Premack and Woodruff, 1978), is essentially needed to understand the implicated meaning (Sperber and Wilson, 1995). All accessible information both given and generated should be integrated to fill the semantic gap (i.e., coherence break) and to construct coherence between literally unrelated utterances. The process required to build coherence between sentences is called 'inference' (Ferstl and von Cramon, 2001), more specifically, 'binding inference' in the comprehension of relevance implicatures, and may be made automatically (Just et al., 1996). Therefore, inference by integrating irrelevant or broadly-related semantic cues would be particularly important in comprehending implicit answers in this study.

In this respect, neuroimaging studies on comprehending stories or discourses provide some insights into neurobiological bases for comprehension of relevance implicatures since successful comprehension in these domains essentially requires filling coherence breaks by inferring information that was not literally stated in a given utterance or text and mentalizing the speaker or protagonist (Graesser et al., 1994; Kintsch, 1998; van den Broek, 1994).

Reviews or meta-analysis of text and discourse comprehension studies have consistently reported co-involvement of the fronto-temporal semantic network including the anterior temporal lobe (ATL), angular gyrus (AG) and inferior frontal gyrus (IFG), and the extra-linguistic cognitive network, such as the superior medial prefrontal cortex (mPFC) (Binder et al., 2009; Ferstl et al., 2008; Jung-Beeman, 2005; Mason and Just, 2006).

As a core part of the fronto-temporal semantic network, the ATL has been implicated in integrating semantic or conceptual information in various comprehension tasks (Ferstl and von Cramon, 2001; Fletcher et al., 1995; Humphries et al., 2006; Visser and Lambon Ralph, 2011; Xu et al., 2005). The AG, located among different sensory systems, is directly or indirectly associated with semantic system, such as lexical representation, memory retrieval and social cognition (Humphries et al., 2007; Obleser and Kotz, 2010; Price, 2010; Xu et al., 2005). The IFG subserves one of the important cores for semantic processing by retrieving semantic memory or by selecting plausible semantic inference (Bookheimer, 2002; Huang et al., 2012; Rapp et al., 2004; Thompson-Schill et al., 1997; Virtue et al., 2006a; Wagner et al., 2001; Zhu et al., 2012). The extra-linguistic cognitive network in the text or discourse comprehension has often been associated with social cognition. The mPFC was consistently activated in tasks involving text or discourse comprehension (Ferstl and von Cramon, 2001; Maguire et al., 1999; Xu et al., 2005), mediating ToM processes (Mar, 2011; Saxe, 2006) or/and mediating self-initiated coherence building to establish meaningful stories (Ferstl and von Cramon, 2001, 2002; Kuperberg et al., 2006; Siebörger et al., 2007), often with co-involvement of the posterior cingulate cortex (PCC) in establishing a situation model (Maguire et al., 1999; Mano et al., 2009). These previous findings suggest that multiple brain regions, if not all, in both the fronto-temporal semantic network and extra-linguistic cognitive network would mediate the comprehension of literally irrelevant but pragmatically relevant utterances in conversation.

We further questioned the involvement of the right hemisphere in the relevance implicature comprehension, especially at the right region homologues to the left language areas. The specialized role of the right hemisphere has been an important issue in the text and discourse comprehension. The prevailing idea is that the left language area is responsible for literal language processing but the right hemisphere mediates complex and non-literal language processing such as comprehension of texts, figurative languages and social concepts (Ferstl et al., 2008; Jung-Beeman, 2005; Mason and Just, 2006; Prat et al., 2011; Virtue et al., 2006a). However, a considerable number of studies have shown the involvement of the left hemisphere in text or discourse comprehension (Chow et al., 2008; Ferstl and von Cramon, 2001, 2002; Rapp et al., 2004; Scott et al., 2000; Spitsyna et al., 2006). These controversial results may be attributable not only to the difference in the task complexity or task types but also to the gap between the linguistic categorization and the neural characterization of stimuli, for example, literal/non-literal versus fine/coarse in the fine–coarse coding model (Beeman, 1993, 1997) or salient/less-salient in the graded salience hypothesis (Giora, 2007; Giora et al., 2000). According to the fine–coarse coding theory (Beeman, 1997), the right hemisphere activates a broad spectrum of meanings and generates weak but distributed semantic fields, which allows an efficient integration of overlapped meanings. In contrast, the left hemisphere conducts fine semantic coding and selects only a small number of relevant meanings rapidly. According to this theory, the right hemisphere would be efficient in integrating semantically distant stimuli, for example, relevance implicatures with highly implicitness.

In this study, we used simple question and answer dialogues with explicit, moderately implicit and highly implicit answers. No contexts for conversations were given to participants in order to make implicature comprehension be guided mainly by the maxim of relevance. To focus on cognitions other than basic language processes, we contrasted two implicit conditions with the explicit condition. From two different levels of implicit conditions and a correlation analysis with implicitness rating scores, we expected to obtain some evidences about the right hemisphere's functional properties suggested in previous studies as well as information about the regional sensitivity to the implicitness level.

We expected that the stronger effort for inference would be needed for more implicit answers and would be reflected in the longer reaction time. We predicted that the fronto-temporal semantic network would be essential and would show increased activations at both implicit conditions. We also predicted increased activation in the extra-linguistic cognitive network in comprehending highly implicit utterances, which demands stronger inference for active coherence building via situation modeling and/or mentalization. We further anticipated the involvement of the right hemisphere for comprehending literally unrelated but highly implicated dialogues according to the coarse coding theory of the right hemisphere.

## Methods

### *Participants*

Twenty-four native Korean speakers (14 males and 10 females) participated in this study. The ages of the participants ranged from 19 to 30 years (mean age = 22.67, standard deviation (SD) = 2.81). All of the participants had no history of neurological illness and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). One participant was excluded from the data analysis due to low task accuracy (<50%) across all of the conditions, leaving 23 participants (14 males and 9 females; mean age = 22.61, SD = 2.86). This study was carried out under the guidelines established by the Severance Hospital Institutional Review Board, and all participants provided written informed consent before participating.

### *Stimuli preparation*

The stimulus materials consisted of 60 pairs of written Korean utterances between two hypothetical speakers A and B in which A asks a question and B responds to that question. All are Yes/No questions, but the responses are not explicit Yes/No answers.

We divided B's answers into three conditions: explicit answer, moderately implicit answer, or highly implicit answer. The sentences assigned to the explicit answer condition were almost repetitions of the previous question sentences with slight variations; omitting subjective, adverb, or adjective words or replacing some words with synonyms. Only five stimuli were strict reiteration of questions as answers. These explicit answers were used as the control condition. For the moderately implicit condition, we used binding words that directly or indirectly link the question and the answer sentences. Binding words were not necessarily the same words listed in the question sentence but words having similar meaning related to the question. Table 1 presents some examples of stimuli used in the current experiment.

Each experimental condition consisted of 20 conversational pairs derived from the 20 basic sets of conversation topics. Although conversations for the three conditions originated from same topics, we slightly varied them by using a different subject or object, thereby keeping the syntactic structure and the conversational situation identical while minimizing repetition effect from presenting the same stimulus. The different nouns used as a subject or object belonged to the same semantic field and they were exchangeable in the aspect of lexical meaning; for example, 'professor', 'teacher' and 'doctor'. However, if a changed noun could alter the context of the conversation, question sentences in a set were kept the same for all conditions as in the set no. 2 and no.5 in Table 1. Four of twenty sets have the same question sentences across different conditions.

In addition to matching conversational contexts across conditions, we balanced basic linguistic properties across conditions. All question and answer pairs were composed of simple sentences of 8–12 Korean syllables with similar level of syntactic complexity and without syntactic violations. One-way ANOVAs showed no significant differences among conditions in sentence length ($F_{2,54} = 1.65$, $p = 0.20$) and frequency for words (according to "The Research for Frequency of Modern Korean Use", National Korean Research Institution, 2003) ($F_{2,54} = 0.22$, $p = 0.81$). In the Yes/No questions, only three 'No' answers (out of nineteen answers) were presented in each condition to ensure that subjects were paying attention to the stimuli. Stimuli with 'No' answers were presented in random order within and between subjects.

The level of implicitness of the dialogues was assessed through a rating test with 16 participants (10 males and 6 females; mean age = 27.19, SD = 1.71) who did not participate in the subsequent fMRI study. They were asked to rate each dialogue on a five-point scale in terms of how directly (explicitly) B answered to the question of A. More indirect and implicit answers were given lower scores.

Finally, we determined stimulus sets for three conditions based on their explicitness rating scores. We divided all stimuli into three conditions according to the explicitness rating scores; scores from 5.0 to 4.5 to the explicit condition; scores from 4.5 to 3.0 to the moderately-implicit condition; and scores from 3.0 to 1.0 to the highly-implicit condition. We excluded a set from experimental material, where mean scores of all conditions were above 4.0 (unspecific to conditions), and consequently nineteen sets (57 dialogues, i.e., total 19 sets and 3 variants per set) were used in the fMRI experiment. The mean rating scores were 4.79 (SD = 0.36) for explicit answers, 3.45 (SD = 0.61) for moderately implicit answers, and 2.71 (SD = 0.52) for highly implicit answers. We regarded the implicitness rating scores as the minus explicitness rating scores throughout the paper.

**Table 1**
Examples of stimuli (translated from Korean).

| No. | Condition | Question | Answer | Expected response |
|---|---|---|---|---|
| 1 | Explicit | Is the doctor in his office now? | The doctor is in his office now. | Yes |
| | Moderately implicit | Is the teacher in his office now? | The teacher's car is outside the office. | Yes |
| | Highly implicit | Is the professor in his office now? | No black car is outside the office. | No |
| 2 | Explicit | Have gas prices gone up a lot? | Prices have gone up a lot. | Yes |
| | Moderately implicit | Have gas prices gone up a lot? | I am saving gas nowadays. | Yes |
| | Highly implicit | Have gas prices gone up a lot? | My dad takes the bus these days. | Yes |
| 3 | Explicit | Has my uncle already left? | (Your uncle) has left. | Yes |
| | Moderately implicit | Has my brother already left? | Your brother's bike is not here. | Yes |
| | Highly implicit | Has my brother already left? | There is no black bike here. | Yes |
| 4 | Explicit | Can I get loan counseling now? | You cannot get counseling right now. | No |
| | Moderately implicit | Can I get investment counseling now? | The person in charge is not here. | No |
| | Highly implicit | Can I get loan counseling now? | Manager Kim is not in the office. | No |
| 5 | Explicit | Is today holiday? | Today is not holiday. | Yes |
| | Moderately implicit | Is today holiday? | (It) is in red in calendar[a]. | Yes |
| | Highly implicit | Is today holiday? | The street is empty. | Yes |

() indicates omission. Note that no significant differences existed in sentence length, word frequency and syntactic structures across conditions in Korean. See the text.
[a] In Korea, holidays are usually marked on the calendar in red.

The one-way ANOVA of rating scores showed that there were significant differences among conditions ($F_{2,57} = 84.73$, $p < 0.0001$). The Tukey's honestly significant difference (HSD) test as a post hoc test revealed that the explicit answers had higher scores than the moderately implicit answers ($p < 0.001$) and the moderately implicit answers had higher scores than highly implicit answers ($p < 0.001$).

*Task procedure*

Participants were presented with the 57 pairs of dialogue in a random order using E-Prime software (Psychology Software Tools, USA) during MRI scanning. In the first part of each trial, A's question was presented for 2000 ms, and then B's answer was presented for 9000 ms. A cross-fixation point followed and lasted for 500 to 1500 ms as jitter (see Fig. 1). Therefore, the average intertrial interval for the task of interest was 12 s.

Participants were asked to press the left button on a mouse if they thought that B's answer meant "Yes" and the right button if they thought that it meant "No" immediately after viewing B's answer. Because implicature is based on subjective judgment of possible relevance between two facts, there may be individual differences with respect to the extent of relevance that has been comprehended. As such, it is possible for a subject to regard an implicit answer as unrelated to the question at hand. In order to minimize this problem, the task directions were such that the participants were forced to select one of two answers. We acquired reaction time and task accuracy while the participants were performing the task in the scanner. Implicature is not a logical conclusion without error, but an inference based on probability, i.e., 'stereotyped expectations of what would, more often than not, be the case' (Allan, 2001). Because there is no indisputably correct answer to an implicit message, task accuracy was determined as the percentage of the responder's conformity to what

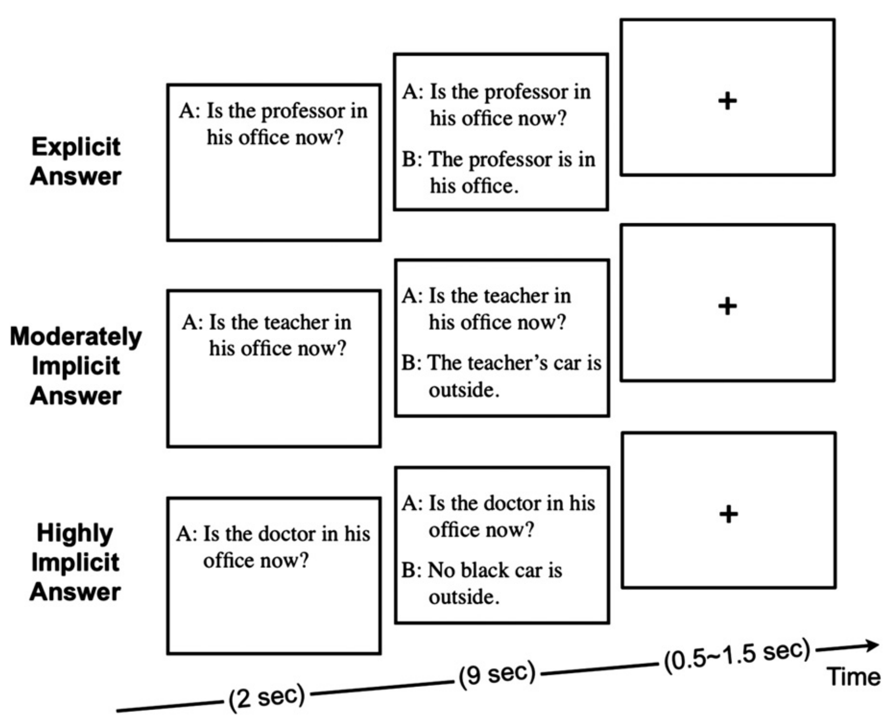


**Fig. 1.** Paradigm for the fMRI experiment. A trial consisted of three slides: question (2 s), question and answer (9 s), and cross-fixation (0.5–1.5 s). There were 20 trials per experimental condition. A total of 60 trials were presented in random order in the same session.

was expected by the researchers. Reaction time was defined as the amount of time it took for the participants to respond after the answer sentence was presented.

### *Data acquisition, processing, and statistical analysis*

Brain activity was measured using a Philips 3 T MRI system (Achieva; Philips Medical System, Best, The Netherlands) with T2* weighted single shot echo planar imaging (EPI). For each task, fMRI images with four dummy scans were acquired axially with the following parameters: 30 ms TE, 2000 ms TR, 90° flip angle, 3.5 mm slice thickness, 0.5 mm slice gap, 34 slices acquired in an ascending interleaved sequence, 128 × 128 recon matrix, 220 × 220 mm field of view, and a 1.719 × 1.719 × 4.0 mm voxel unit. Head movement was limited by foam padding within the head coil and a restraining band across the forehead. To facilitate later spatial normalization, we also obtained a high-resolution T1-weighted MRI volume dataset for each subject with a SENSE head coil using a 3D T1-TFE sequence configured with the following acquisition parameters: axial acquisition with a 224 × 224 matrix, 220 mm field of view, 0.98 × 0.98 × 1.2 mm voxel unit, 4.6 ms TE, 9.6 ms TR, 8° flip angle, and 0 mm slice gap.

Image preprocessing was carried out by statistical parametric mapping (SPM8, http://fil.ion.ucl.ac.uk/spm, Wellcome Department of Cognitive Neurology, London, UK) (Friston et al., 1995). The procedure included slice time correction for the interleaved sequence, and motion correction by realigning all the images to the first image. To spatially normalize the fMRI, we derived bias-corrected, skull-stripped, and CSF-suppressed images from T1-weighted images using unified segmentation (Ashburner and Friston, 2005) available in the DARTEL toolbox in the SPM8. These skull-stripped and CSF-suppressed images were co-registered to the mean fMRI data for each individual and then were used to achieve nonlinear transformation to the skull stripped T1-template in the normalized space. The spatially normalized functional data were smoothed with a 6-mm full-width-at-half-maximum Gaussian filter. Low-frequency drifts were removed using a high-pass filter with a cut-off frequency of 128 s.

Only data for the correct responses were analyzed. As a slow event-related design, regional hemodynamic activities for conditions were estimated using a generalized linear model at every voxel with respect to the canonical hemodynamic response function. To model hemodynamic responses of the task performance during variable reaction time periods, the event duration was set to be 3.21 s, the average plus two standard deviation of reaction times across conditions and subjects, which covered most reaction time ranges. The onset time in the model was set to the presentation time of each B's answer stimulus. To reduce compound effects reflected in the different reaction times other than comprehension processes within each condition, we added reaction times to the model as a covariate of no interest for each condition using parametric modulation analysis in SPM8. We assumed that these compound effects would be similar across conditions and thus similarly regressed out in each condition. Group-level activation for each condition was compared using a random effect model for the effect of interest. Statistical difference in activation and deactivation for the group during the moderately implicit answer vs. explicit answer and highly implicit answer vs. moderately implicit answer was estimated using paired *t*-tests.

To identify the brain regions showing a monotonic increase or decrease according to implicitness rating scores, we further conducted a trial-by-trial correlation analysis between implicitness rating scores of stimuli and their hemodynamic responses. After mean-centering both rating scorings and reaction times, we orthogonalized reaction times with respect to rating scores using recursive Gram–Schmidt orthogonalization algorithm (spm_orth.m function in SPM8). These orthogonalized rating scores and reaction times were included in a parametric modulation analysis on a trial-by-trial basis throughout all conditions using the amplitude-modulation method implemented in SPM8. This correlation analysis after regressing out partial reaction time components orthogonal to rating scores was expected to confirm that the results of the paired *t*-tests might not be derived by compounding factors other than components for implicature comprehension embedded in different reaction times across conditions.

For the group level inference, we set a cluster level criterion with a voxel level threshold, $p < 0 .005$, and with an extent threshold of 73 contiguous voxels. This criteria is equivalent to $p < 0.05$ corrected by cluster level for multiple comparisons as estimated by 10,000 Monte Carlo simulations (Gao et al., 1995) using the AlphaSim program (Ward, 2000) implemented in the REST toolbox (http://restfmri.net/).

As a post-hoc analysis, the percent signal changes for significantly detected clusters were calculated by counting 3 mm-diameter sphere regions around the peak of the cluster using MarsBaR software (Brett et al., 2002).

## Results

### *Behavioral results*

Repeated-measures ANOVA of task accuracy showed that the main effect for accuracy was significant across the conditions ($F_{2,44} = 4.61$, $p = 0.015$), as shown in Fig. 2A. Participants showed high accuracy across all the dialogue types (explicit answers: M = 98.63%, SD = 2.36%, moderately implicit answers: M = 95.19%, SD = 4.74%, highly implicit answers: M = 94.74% SD = 6.92%), which means that participants had no difficulties in successfully understanding the meanings of the messages. Task accuracy was, as expected, significantly higher in explicit answers than in moderately implicit answers ($t_{22} = 2.92$, $p = 0.008$) or highly implicit answers ($t_{22} = 2.68$, $p = 0.014$), but there was no significant difference in accuracy between moderately implicit and highly implicit answers ($t_{22} = 0.30$, $p = 0.770$).

The results of repeated measures ANOVA revealed a significant effect on reaction time ($F_{2,44} = 71.79$, $p < 0.0001$) (Fig. 2B). Paired

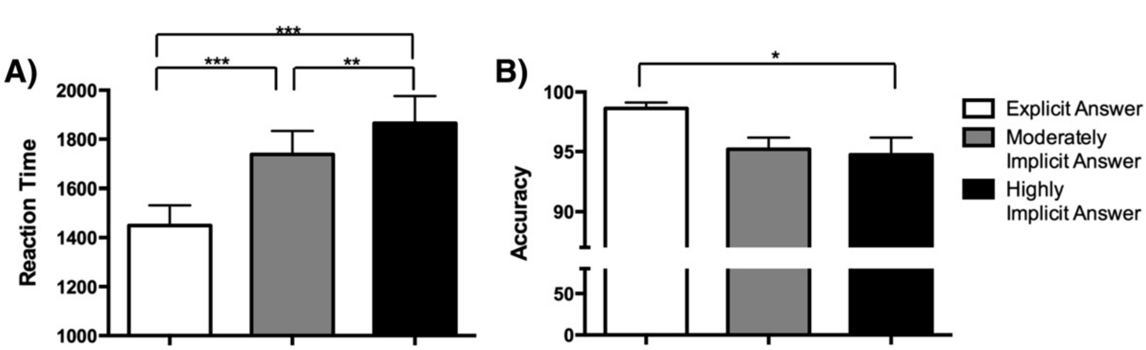


**Fig. 2.** (A) Reaction time and (B) task accuracy. Means and standard errors are shown. Repeated-measures ANOVA of reaction time and task accuracy revealed significant main effects between answer conditions ($p < 0.0001$ and $p = 0.015$). (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

$t$-tests showed that the reaction to explicit answers was faster than that to moderately implicit answers ($t_{22} = 8.57$, $p < 0.0001$) and, in turn, the reaction to moderately implicit answers was faster than that to highly implicit answers ($t_{22} = 4.96$, $p < 0.0001$).

### fMRI results

Table 2 summarizes the results for all contrasts between conditions. The results for correlation analysis between activations and implicitness rating scores are listed in Table 3.

Moderately implicit answers showed higher activity than explicit answers in the ATL, middle temporal gyrus (MTG), and AG in the left hemisphere. In contrast, moderately implicit answers showed lower activity than explicit answers in a larger set of regions including the bilateral anterior cingulate cortex, bilateral superior and middle occipital lobe, right inferior parietal lobule, right postcentral gyrus, right middle frontal gyrus, right middle temporal lobe and left posterior cingulate cortex (see Fig. 3A).

When results from highly implicit answers were compared to those from explicit answers, highly implicit answers showed stronger activation in the ATL, AG, PCC, mPFC, and IFG in the left hemisphere and the anterior middle temporal gyrus (aMTG)/ATL in both hemispheres (Fig. 3B). Highly implicit answers showed lower activation than explicit answers in other regions, including the bilateral inferior parietal lobule, bilateral middle occipital gyrus, bilateral postcentral gyrus, left superior temporal gyrus, left posterior cingulate cortex, and the right inferior frontal gyrus. The left aMTG showed higher activity for highly implicit answers than for moderately implicit answers (Fig. 3C).

Brain regions of which activity showed significant positive correlations with implicitness rating scores were highly correspondent to

**Table 3**
Brain activation correlated with implicitness rating scores.

| Region | BA | Coordinates | | | $Z_{max}$ | Cluster size |
|---|---|---|---|---|---|---|
| | | x | y | z | | |
| R middle temporal gyrus | 21 | 50 | 2 | −24 | 5.06 | 437 |
| R superior temporal gyrus | 38 | 40 | 14 | −28 | 4.03 | – |
| L superior temporal gyrus | 38 | −48 | 10 | −22 | 4.93 | 2109 |
| L middle temporal gyrus | 21 | −52 | 2 | −26 | 4.37 | – |
| L inferior frontal gyrus (tri) | 45 | −50 | 22 | 10 | 3.65 | – |
| L inferior frontal gyrus (tri) | 47 | −50 | 26 | 2 | 3.38 | – |
| L angular gyrus | 39 | −50 | −66 | 30 | 4.31 | 544 |
| L superior temporal gyrus | 39 | −42 | −58 | 26 | 3.77 | – |
| L putamen | | −18 | 6 | 4 | 4.15 | 81 |
| L superior frontal gyrus | 10 | −16 | 60 | 22 | 3.72 | 171 |
| L medial frontal gyrus | 10 | −14 | 68 | 10 | 3.49 | – |
| L posterior cingulate | 23 | −4 | −56 | 16 | 3.37 | 91 |
| R superior frontal gyrus | 9 | 10 | 50 | 24 | 3.25 | 126 |
| L superior frontal gyrus | 9 | −12 | 54 | 38 | 3 | – |
| L superior frontal gyrus | 6 | −4 | 12 | 58 | 2.98 | 74 |
| R inferior parietal lobule | 40 | 40 | −54 | 50 | −4.76 | 9599 |
| L precuneus | 19 | −18 | −82 | 40 | −4.68 | – |
| L inferior parietal lobule | 40 | −52 | −36 | 48 | −4.62 | 1571 |
| R fusiform gyrus | 37 | 32 | −48 | −12 | −4.61 | 1058 |
| R inferior frontal gyrus | 44 | 48 | 6 | 22 | −4.31 | 356 |
| L parahippocampal gyrus | 37 | −22 | −48 | −12 | −4.24 | 531 |
| L cingulate gyrus | 23 | −4 | −22 | 32 | −4.01 | 340 |
| R cingulate gyrus | 31 | 6 | −38 | 26 | −3.87 | – |
| R middle frontal gyrus | 46 | 46 | 46 | 8 | −3.96 | 169 |
| R precentral gyrus | 4 | 54 | −6 | 46 | −3.15 | 106 |

$p < 0.005$, cluster size > 73, BA: Brodmann area, coordinates: Montreal Neurological Institute coordinate, $Z_{max}$: Z maximum within a cluster, positive Z indicates positive correlation while negative Z indicates negative correlation. "–" in the cluster size indicates that this coordinate is a peak location that belongs to the cluster listed immediately above. L: left, R: right.

**Table 2**
Brain activation corresponding to the main effect of answer type and all contrasts between conditions.

| Highly implicit–explicit | | | | Moderately implicit–explicit | | | |
|---|---|---|---|---|---|---|---|
| Region | Coordinate x, y, z | $Z_{max}$ | Cluster size | Region | Coordinate x, y, z | $Z_{max}$ | Cluster size |
| Highly implicit > explicit | | | | Moderately implicit > explicit | | | |
| L superior temporal gyrus (BA 38)[a] | −50, 8, −24 | 4.8 | 1721 | L superior temporal gyrus (BA 38) | −48, 8, −26 | 3.19 | 110 |
| L middle temporal gyrus (BA 21) | −52, −6, −16 | 4.42 | – | L middle temporal gyrus (BA 22) | −56, −36, 0 | 3.83 | 107 |
| L fusiform gyrus (BA 20) | −52, −2, −28 | 4.64 | – | | | | |
| L inferior frontal gyrus (BA47, tri)[a] | −50, 26, 0 | 3.47 | – | | | | |
| L posterior cingulate (BA 30) | −6, −56, 18 | 4.43 | 219 | | | | |
| L superior temporal gyrus (BA 39) | −44, −62, 28 | 4.2 | 569 | L superior temporal gyrus (BA 39) | −44, −58, 28 | 3.02 | 96 |
| L angular gyrus (BA 39) | −46, −74, 36 | 4.2 | – | L angular gyrus (BA 39) | −48, −74, 34 | 2.98 | – |
| L precuneus (BA 19) | −38, −78, 42 | 3.24 | – | | | | |
| R middle temporal gyrus (BA 21)[a] | 54, 0, −20 | 3.76 | 143 | | | | |
| L superior frontal gyrus (BA 10)[a] | −14, 60, 22 | 3.56 | 104 | | | | |
| L superior frontal gyrus (BA 9) | −4, 58, 32 | 3.08 | 143 | | | | |
| Highly implicit > moderately implicit | | | | | | | |
| L middle temporal gyrus (BA 21) | −54, −2, −12 | 3.12 | 104 | | | | |
| Highly implicit < explicit | | | | Moderately implicit < explicit | | | |
| L inferior parietal lobule (BA 40) | −44, −56, 56 | 4.95 | 9266 | | | | |
| L middle occipital gyrus (BA 19) | −42, −84, 12 | 4.85 | – | L middle occipital gyrus (BA 19) | −38, −86, 10 | 4.23 | 176 |
| R inferior parietal lobule (BA 40) | 40, −52, 48 | 4.81 | – | R inferior parietal lobule (BA 40) | 42, −38, 46 | 4.4 | 3917 |
| | | | | R superior occipital gyrus (BA 19) | 34, −82,26 | 4.4 | – |
| L inferior parietal lobule (BA 40) | −66, −30, 28 | 4.04 | 355 | | | | |
| L superior temporal gyrus (BA 41) | −56, −20, 6 | 4.01 | 224 | | | | |
| R inferior frontal gyrus (BA 44) | 50, 6, 24 | 3.92 | 119 | R inferior frontal gyrus (BA 44) | 50, 6, 22 | 4.1 | 146 |
| R inferior frontal gyrus (BA 46) | 46, 44, 8 | 3.44 | 172 | | | | |
| R sub-gyral | 32, 44, 4 | 4.95 | – | R sub-gyral (BA 37) | 52, −42, −8 | 3.62 | 142 |
| | | | | R anterior cingulate (BA 32) | 20, 34, 10 | 3.49 | 115 |
| L cingulate gyrus (BA 23) | −4, −18, 30 | 3.69 | 190 | | | | |
| R insula (BA 13) | 30, −18, 24 | 3.19 | 74 | | | | |
| | | | | L caudate | −36, −44, 0 | 3.14 | 107 |
| L fusiform gyrus (BA 19) | −24, −60, −12 | 4.59 | 99 | L parahippocampal gyrus (BA 19) | −28, −56, −10 | 3.11 | 115 |
| | | | | R parahippocampal gyrus (BA 19) | 30, −48, −10 | 4.12 | 260 |
| R declive | 28, −54, −16 | 4.92 | 570 | R declive | 28, −68, −18 | 3.03 | – |

$p < 0.005$, cluster size > 73, BA: Brodmann area, coordinate: Montreal Neurological Institute coordinate, $Z_{max}$: Z maximum within a cluster, L: left, R: right. "–" in the cluster size indicates that this coordinate is a peak location that belongs to the cluster listed immediately above.

[a] Indicates regions displayed in Fig. 4.

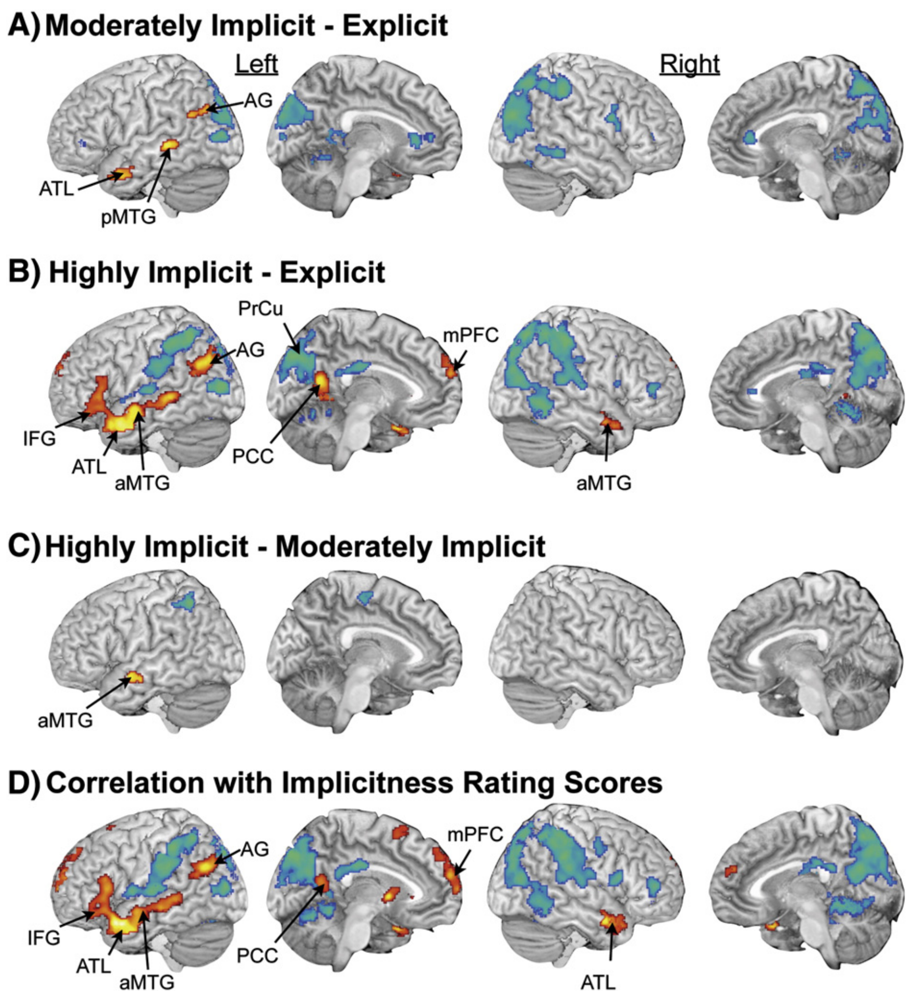


**Fig. 3.** Activation maps for all contrasts and correlation analysis results. The clusters with a threshold $p < 0.005$ and cluster size $k > 73$ are displayed (red: positive activation, blue: negative activation, AG: angular gyrus, ATL: anterior temporal lobe, IFG: inferior frontal gyrus, aMTG: anterior middle temporal gyrus, pMTG: posterior middle temporal gyrus, PCC: posterior cingulate cortex, PrCu: precuneus, mPFC: medial prefrontal cortex).

regions found in the highly implicit versus explicit conditions (Fig. 3D). Significant positive correlations were found in the left ATL, aMTG, AG, IFG, mPFC, PCC, superior frontal gyrus, and putamen in the left hemisphere and the ATL in the right hemisphere. This result confirms that the results of paired *t*-tests in Figs. 3A–C were mainly derived from differences in implicature comprehension rather than other compounding factors that partly affected reaction times.

Fig. 4 displays hemodynamic response curves estimated for three conditions in the left ATL (Montreal Neurological Institute coordinate, −50/8/−24), right ATL (54/0/−20), left IFG (−50/26/0) and left mPFC (−14/60/22). These regions of interest were defined based on peak coordinates of activated clusters for the highly implicit versus the explicit conditions in Table 2. As the regions of interest were defined from the SPM results, we did not attempt to make any double-dipping inferences from those hemodynamic response curves (Kriegeskorte et al., 2009). Instead, from those curves, we tried to visualize the signal change differences among conditions and thus to show plausibility of hemodynamic response curves in this study, as discussed in Poldrack and Mumford (2010).

## Discussion

The fMRI experiment in this study was aimed at identifying the neural correlates of relevance implicature comprehension by comparing brain responses of highly implicit and moderately implicit dialogues with explicit dialogues and by correlating brain responses with implicitness rating scores. When we contrasted implicit conditions with the explicit condition, we found increased hemodynamic responses for implicature processing at regions known to be involved in text or discourse comprehension, such as the ATL, AG, IFG, PCC and mPFC. Activations in these regions were monotonically increased with increasing implicitness rating scores. Among them, the bilateral ATL activation was most sensitive to implicitness. The increased activation in the right ATL compared to the explicit condition was significant only for highly implicit implicature comprehension.

Communicative competence for comprehending relevance implicature is essential in everyday conversation. In successful conversation, a speaker and a listener contribute to each other's utterances to achieve the purpose of conversation, that is, they adhere to the ‘cooperative principle’ (Grice, 1975). According to this cooperative principle, the listener expects the speaker to observe the maxim of relevance and to say only matters relevant to the conversational purpose. Occasionally, intended meanings are delivered to the listener via implicated expression by the speaker and thus literal meanings (or face values) of an utterance may be different from implicated meanings. In this case, the premise about observance of the maxim of relevance leads the listener not to simply disregard implicated expressions as being unrelated to the context but to generate inference for building coherence between utterances.

In the “Yes/No” tasks with implicit conversations, the participants as a third-person observing the conversations needed to infer implicated meanings of the answer sentences in the perspective of the listener assuming that the conversational partners observed the maxim of

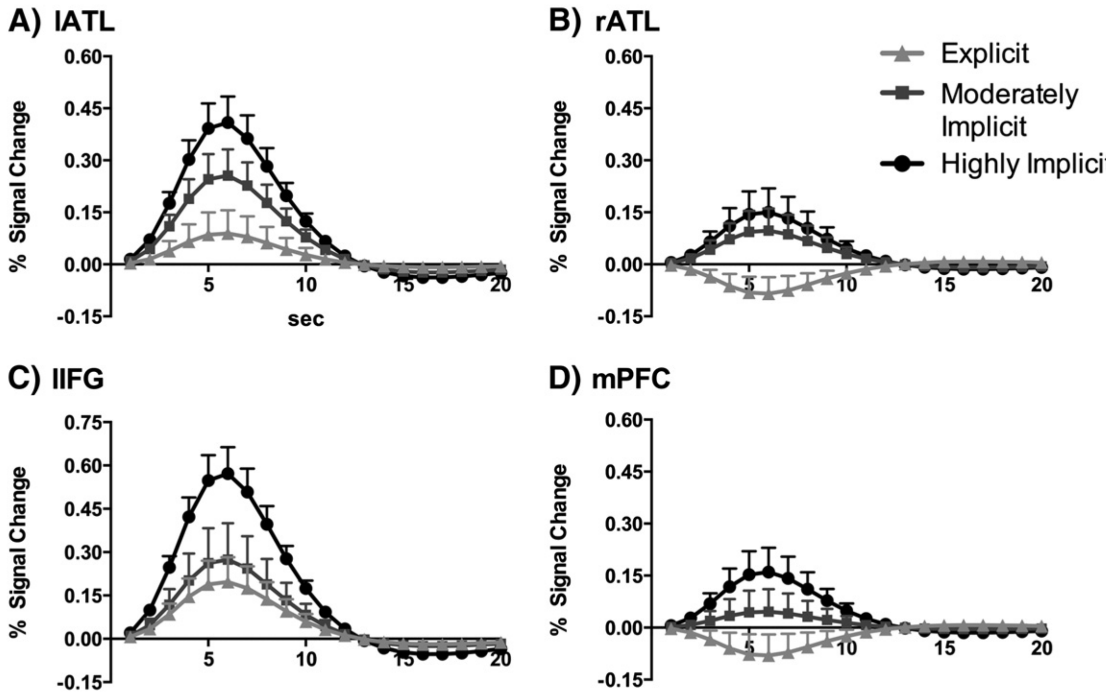


**Fig. 4.** Percent signal changes in brain regions. The brain regions are (A) the left anterior temporal lobe (lATL: Montreal Neurological Institute coordinate −50/8/−24), (B) right anterior temporal lobe (rATL: 54/0/−20), (C) left inferior frontal gyrus (LIFG: −50/26/0), and (D) left medial prefrontal cortex (mPFC: −10/66/10).

relevance. Explicit answers in this experiment did not require high level of inference to comprehend them. The semantic incoherence between utterances in the implicit conditions would initiate inference process under the assumption that the speaker had no reason to say irrelevant matters. The participants would attempt to retrieve background knowledge associated with information given by utterances. They would also make efforts to establish a coherent situation model (Van Dijk and Kintsch, 1983) by integrating what is retrieved with what is heard from the conversation and by inferring the missing link between the question and answer. Based on the established situation model, the participants might recognize the meaning implicated in the utterance and would make a decision required from the experimental task. In the highly implicit condition, the inference processes to build coherence were presumed to be more complex due to the absence of direct link between the question and the answer utterances. The increased complexity of inference process with increased implicitness was evident in the longer reaction time to the highly implicit answers than to the moderately implicit answers without affecting the accuracy (Fig. 2).

According to previous literatures, we expected that regions in the fronto-temporal and extra-linguistic networks would be differentially involved in the comprehension of implicated meanings depending on the implicitness level. The current fMRI results by and large were consistent with our expectations; stronger involvement of the left ATL and left AG in the fronto-temporal network for both the implicit conditions and the PCC and mPFC in the extra-linguistic network for the highly implicit condition than for the explicit condition.

In the following sections, we will discuss specific regional involvements for implicature comprehension in terms of the fronto-temporal semantic network and the extra-linguistic cognitive network (cf. the left fronto-temporal text integration network vs. the medial frontal protagonist/agent interpreter network in Mason and Just (2006)).

*Fronto-temporal semantic network*

Increased activations in the ATL, posterior MTG, and AG in the left hemisphere were detected for both moderately and highly implicit conditions compared to the explicit discourse condition. The right ATL (anterior MTG) and the left IFG showed increased activations only when question and answer pairs were highly irrelevant. These regions were generally found to be involved in diverse inference settings in previous studies (Ferstl and von Cramon, 2001; Friese et al., 2008; Kuperberg et al., 2006; Prat et al., 2011; Siebörger et al., 2007; Virtue et al., 2008). It should be noted that all conditions had no significant differences in basic linguistic factors such as word frequency, sentence length and syntactic complexity. Therefore, the regions detected after contrasting with the explicit condition may well be interpreted as a part of semantic network. The increased activations may also reflect the differential involvement for word and sentence level processes but may also reflect results of sub-modules of the semantic system.

The ATL, AG and IFG have been implicated as main parts of the fronto-temporal semantic network. The ATL is generally considered as an amodal semantic hub involved in sentence comprehension (Visser and Lambon Ralph, 2011; Xu et al., 2005), inference in text or narrative comprehension (Ferstl and von Cramon, 2001; Fletcher et al., 1995; Xu et al., 2005) and comprehension of social interactions (Ross and Olson, 2010; Zahn et al., 2007). As expected, the increased activation in the right ATL was detected for the highly implicit condition compared to the explicit condition.

The AG is activated in sentences with comprehensible meanings and coherent narratives (Humphries et al., 2007; Obleser and Kotz, 2010; Price, 2010; Xu et al., 2005). A major role for the AG may be to process semantic information in a context-dependent fashion by integrating input information with prior knowledge into linguistic context (Humphries et al., 2006; Lau et al., 2008; Seghier, 2013).

In contrast to our expectation that the IFG would be involved in basic implicature processing as a basic fronto-temporal semantic network, no significant increase was found in the activation of the IFG in the moderately implicit condition compared to the explicit condition. The increased activation in the left IFG for the highly implicit but not for moderately implicit conditions may be associated with its higher-level role in the hierarchical fronto-temporal network. The left IFG was recruited in the inference generation for implicit events in the coherence break during story comprehension (Virtue et al., 2006a), comprehending irony (Rapp et al., 2010) and metaphor (Rapp et al., 2004). At the semantic level, the left IFG mediates the controlled semantic retrieval of semantic information (Wagner et al., 2001), semantic integration of explicit and implicit sentences (Huang et al., 2012; Zhu et al., 2012), semantic selection of inferential information (Kan and Thompson-Schill, 2004; Thompson-Schill et al., 1997), and semantic decision-making (Bookheimer, 2002).

Although the bilateral ATL, left AG and left IFG were co-activated in many previous studies of complex language processing, the specialized role of each region is not clearly understood. In a semantic processing model, Jung-Beeman (2005) attributed semantic activation (related to input word, generating semantic field) to the posterior MTG and potentially the AG, semantic integration (message-level interpretation by calculating semantic overlaps among multiple fields) to the bilateral ATL, and semantic selection (inhibiting competing concepts while selecting most appropriate concept) to the left IFG. In this model, semantic selection process modulates both word-level semantic activation and message-level semantic integration. Lau et al. (2008) suggested a semantic model in which the posterior MTG stores and activates amodal lexical representations that are accessed by the ATL, AG and IFG. Especially, the IFG may be involved in top-down semantic retrieval of lexical representations (anteriorly) and/or selection among highly activated lexical representation (posteriorly) (Lau et al., 2008). In a model of Patterson et al. (2007), the ATL may function as a semantic generalization hub in the semantic network with the AG, posterior MTG, and IFG. They related the functional property of the ATL with its neuroanatomical proximity to the anterior parts of the medial temporal memory system that is responsible for rapid learning of new episodic information and new conceptual knowledge (Patterson et al., 2007).

These theories consistently implied the importance of the ATL in the hierarchical semantic system. In the current study, the left ATL was highly sensitive to the implicature processing, responding to even moderately implicit condition and showing significant increases according to implicitness level. The left ATL activation in the implicit conditions may be attributable to the semantic integration of syntactic, semantic or conceptual information required for inference to resolve coherence breaks between irrelevant utterances (Binder et al., 2011; Jung-Beeman, 2005). There exist many evidences showing the left ATL involved in semantic or conceptual combinations in the text and discourse (Humphries et al., 2006; Scott et al., 2000; Spitsyna et al., 2006; Stowe et al., 2005). Semantic integration in moderately implicit answers is essential but is relatively easy because the bridging words help to link between the question and the answer. As evidenced in the increased reaction time in the highly implicit condition, comprehending conversation with high implicitness requires more strained efforts at semantic integration to achieve coherence in the conversation. This explanation may account for the higher activation in the left ATL for highly implicit conversations compared to moderately implicit conversations. For the highly implicit condition, the left ATL may be supported by the coarse-coding capability of the right ATL (Beeman, 1993, 1997), which will be discussed in the Hemispheric specialization for relevance implicature comprehension section below.

As discussed before, there were no significant differences across conditions in the word frequency, sentence length, and syntactic complexity. Therefore, it may be unlikely that the increased ATL activation resulted from increased syntactic processing (Friederici and Kotz, 2003; Humphries et al., 2006). One may attribute the increased ATL activation in the implicit conditions to the similarity between the question and the answer sentences in the explicit condition, since consecutive presentations of same sentences or same syntactic structures led to suppressions in the left ATL because of easier comprehension due to repetitions (Hasson et al., 2006; Noppeney and Price, 2004). Since there were no significant syntactic differences across conditions, the syntactic adaptation, if present, might affect all the conditions similarly. Although we cannot rule out adaptation effects due to sentence repetitions in the explicit condition, the adaptation by sentence repetition might not affect the current results as high as was found in Hasson et al. (2006) since only five out of nineteen answers were reiterations of the previous questions in the explicit condition and they were presented with a different syntactic structure, i.e., question versus answer.

### *Extra-linguistic cognitive network*

In addition to the general linguistic network, the increased involvement of the mPFC and the PCC for highly implicit condition were consistently observed in text and discourse comprehension tasks (Ferstl and von Cramon, 2001; Maguire et al., 1999; Xu et al., 2005).

The significant involvement of the mPFC and PCC for highly implicit utterances can be attributed to the ToM processes. It is obvious that mentalization is a basic process for comprehending implicatures, as presented in the format of reasoning process of Grice (1975), for example, "… he could not be doing this unless he thought that *q* (i.e., his belief); he knows (and knows that I know that he knows) that I can see that the supposition that he thinks that *q* is required; … he intends me to think, or is at least willing to allow me to think, that *q*; …". Accordingly, comprehending implicit answers in this study requires the listener to infer something about the speaker's beliefs and intentions, which can be utilized to interpret the implicated meaning.

Among many types of conversational implicatures, irony comprehension relies highly on ToM processes to understand relevant but untruthful utterances. Accordingly, the comprehension of irony was mediated by the bilateral temporal-parietal junction and mPFC (Spotorno et al., 2012). In this study of relevance implicature comprehension, however, the mPFC involvement was not significantly high especially at the moderately implicit condition and no significantly increased activation was detected in the right temporal–parietal junction, one of central regions for ToM (Saxe, 2006). It may be because no specific context about the speaker's intention was provided in the task and the stimuli were too short and simple to elicit a high-level ToM process, as noted in reviews of irony processes (Spotorno et al., 2012). Unless information from mentalization is critical, inference process may be automatic, utilizing a basic but strong pragmatic premise that 'the speaker is trying to deliver relevant message.'

Although ToM is considered as a basis for every conversation, the activation in the mPFC and PCC can be attributed to a more general process commonly recruited in diverse tasks (including ToM tasks). For example, although the mPFC is one of central regions of ToM (Mar, 2011; Saxe, 2006), the mPFC was involved in coherence process whether it is in the ToM-related tasks or ToM-unrelated tasks (Ferstl and von Cramon, 2002). In this respect, the role of the mPFC in text or discourse comprehension is often interpreted in terms of self-initiated coherence building of implicitly related sentences (for reviews see Ferstl et al., 2008; Mason and Just, 2006). This process at mPFC may be intentional, controlled, strategic, higher-order inferential process that actively builds coherence between successive sentences in a discourse (Ferstl and von Cramon, 2001; Kuperberg et al., 2006; Siebörger et al., 2007). This role of the mPFC explains the lack of significantly increased activation in the mPFC for the moderately implicit implicatures, where coherence can be built relatively easily as compared to the highly implicit conversations. This is consistent with a study showing that inference of coherent but highly related sentences showed reduced activation in the mPFC compared to the moderately related ones (Kuperberg et al., 2006).

The PCC activation was also observed in story comprehension studies (Ferstl and von Cramon, 2001; Maguire et al., 1999; Whitney et al., 2009), in which the PCC may play a role in forming a situation model by linking the text with prior knowledge of real world (Maguire et al., 1999) or by spatial perspective-taking (Mano et al., 2009).

Although the mPFC and the PCC may cooperatively be involved in establishing coherence within a story (Fletcher et al., 1995; Maguire et al., 1999), these regions may be differently specialized for understanding implicated meanings in conversation. Ferstl and von Cramon (2001) suggested that the PCC contributes to the establishment of a new situation model of the story by integrating new information and prior knowledge or the previously established situation model proposed by Fletcher et al. (1995), while the mPFC contributes to the self-initiation of a cognitive process for coherence building in the context of tasks. In this perspective, the increased activity in the PCC and mPFC during highly implicit condition may be explained by increased efforts to establish a situation model and to build coherence between conversational utterances.

### *Hemispheric specialization for relevance implicature comprehension*

It has generally been accepted that bilateral extra-language areas are involved in complex literal and non-literal processes and right hemisphere is strongly recruited for highly complex or special language processing (for meta-analysis and reviews, see Binder et al., 2009; Ferstl et al., 2008; Jung-Beeman, 2005). However, it is not clearly understood as to how the right hemisphere contributes to the processing of complex language stimuli. The fine–coarse coding hypothesis (Beeman, 1993, 1997) suggests that wide semantic field activation in the right hemisphere is efficient for overlapping distantly related concepts. A growing number of evidences support this perspective; some examples include involvement of the right hemisphere for weakly constrained text but involvement of the left hemisphere for strongly constrained text (Virtue et al., 2006b), and consistent information processing in the left hemisphere but inconsistent information processing in the right hemisphere (Virtue and Motyka Joss, 2012).

In this study, most brain regions involved in understanding relevance implicature were located in the left hemisphere, except the right ATL (the anterior MTG) that showed increased activations only for the highly implicit answers. The current result is consistent with a meta-analysis of Ferstl et al. (2008) that showed left-dominancy for coherence building, with an engagement of the right ATL. The increased activation in the right ATL at highly implicit condition may be associated with high demand to integrate distant semantic relationships. In this respect, the current finding can be explained by the fine–coarse coding hypothesis in that the moderately related utterances are processed dominantly in the left hemisphere while highly irrelevant utterances, thus requiring pragmatic context for decision, recruit the right hemisphere. The right hemisphere is considered to be much more efficient in combining literal values of the utterances with the contextual and pragmatic information.

Despite the significant involvement of the right ATL, the activation in the left ATL also showed further increase for the highly implicit condition (Fig. 3C). This finding suggests that the right ATL may process stimuli in parallel and does not simply wait for the left ATL to reach its maximal capacity. In the contrast analysis between conditions, however, it was not clear whether the insignificant increase of activation in the right ATL for moderately implicit condition implies no involvement of the right ATL in processing moderately implicit implicatures. The correlation analysis (Fig. 3D) suggests that the right ATL might also be involved in processing implicatures in the moderately implicit condition but the signal was not sufficiently high enough for detection due to the weak activation property of the right hemisphere (Fig. 4B) as suggested in the fine–coarse coding hypothesis (Beeman, 1993, 1997). Further study is needed to resolve this issue.

### *Decreased activation*

We found decreased activations for implicit conditions compared to the explicit condition in the precuneus, postcentral gyrus, middle occipital gyrus, cuneus and superior and inferior parietal lobes. The decreased activation in these regions was unexpected except for the precuneus that may be associated with the default mode network (Gusnard et al., 2001). A growing number of studies have recently suggested that regions showing a task-load or level of attention dependent deactivation overlap with default mode networks (Harrison et al., 2011; McKiernan et al., 2003).

However, it is not clear to explain the cognitive mechanism of decreased activations in the sensory and association cortices in the implicit conditions compared to the explicit condition. It may be associated with increased activations in those regions to generate rapid responses for the explicit stimuli in the explicit condition. Participants waiting for complex stimuli may realize that the explicit dialogues are unexpectedly simple to comprehend and may automatically shift attention to generating rapid motor responses, which may lead to increased involvement of sensory, motor and association areas. Similar to this interpretation, Mohamed et al. (2004) showed that rapid reaction to a simple visual cue leads to increased amplitudes in the bilateral occipital and left sensorimotor area.

In line with this explanation, a causal inference study by Kuperberg et al. (2006) showed a very similar deactivation in regions found in the current study. In that study, the neural responses to intermediately-related discourse scenarios requiring causal inference, compared to highly-related ones, led to decreased activation in primary sensory and motor cortices as well as default mode networks, similar to the current result. They interpreted such deactivation as redirection of processing resources not only from the default mode network but also from the sensory–motor region when multiple cognitive processes were involved (Kuperberg et al., 2006). This interpretation may be used to explain the decreased activations in the implicit conditions compared to the explicit condition. However, this is a speculation and further studies are needed to identify the cause for the reduced activations in these regions in relation to implicitness.

### *Comprehension of relevance implicature and other related cognitive tasks*

Although there have been multiple studies investigating neural bases of text or discourse comprehension (i.e. irony, metaphor) in terms of inference (Ahrens et al., 2007; Bambini et al., 2011; Eviatar and Just, 2006; Ferstl and von Cramon, 2001, 2002; Filippova and Astington, 2010; Friese et al., 2008), this study is unique in that it investigated comprehension of conversations without any prior explicit context but with only pragmatic principle, i.e., the maxim of relevance. Although comprehending relevance implicatures may recruit cognitive processes involved in causal or logical inferences in previous literatures (Evans et al., 2010; Kuperberg et al., 2006), inference in the relevance implicature comprehension occurs easily and rapidly while logical inferences need deliberation (Ferstl and von Cramon, 2001). Inference in comprehending relevance implicatures may work even for the highly unrelated sentences in which logical or causal inference stops. For example, in the causal inference, the unrelated sentences elicit reduced activations compared to moderately related sentences (Kuperberg et al., 2006), and incoherent and incohesive sentences showed shorter reaction times than coherent and incohesive sentences (Ferstl and von Cramon, 2001). This was not the case in the current study with relevance implicature. When consecutive sentences are unrelated in the conversational circumstances, more elaboration is needed to link two sentences, rather than stopping the inference process. This was evident in the significantly increased activations in the highly implicit condition and significantly correlated activations with implicitness rating scores in the brain regions associated with inference processes (Chow et al., 2008; Ferstl and von Cramon, 2001; Friese et al., 2008; Kuperberg et al., 2006; Siebörger et al., 2007).

Although comprehension of irony and relevance implicatures may share cognitive modules such as coherence building and mentalization, the cognitive focus would differ between them. While the irony can be detected by inconsistency between the utterance and the situation, the relevance implicatures can be recognized by irrelevance between utterances. While inferring speaker's intention plays a critical role in comprehending ironic speech, intended meaning in relevance implicature may be derived mainly by integrating or bridging information into discourse representation under the guidance of the maxim of relevance. There are diverse regional involvement for irony processing depending on stimulus type and controls. Those regions included the bilateral temporal–parietal junction, left or bilateral temporal lobe, right temporal pole and IFG (Eviatar and Just, 2006; Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006; Wakusawa et al., 2007; Wang et al., 2006). As expected, one of regions repeatedly found to be involved in irony comprehension was the mPFC (Shibata et al., 2010; Spotorno et al., 2012; Uchiyama et al., 2006, 2012; Wang et al., 2006), which was consistently interpreted as mentalization process. These regions were not only found in the studies of the text comprehension but also were recruited in this study of the relevance implicature comprehension. Further studies with a direct comparison of irony and relevance implicature would clarify neural correlates specific to the relevance implicature comprehension. As there exist neural differences between metaphor and irony comprehensions (Eviatar and Just, 2006), and even among different types of metaphor comprehensions (for review see Giora, 2007), we can expect differential neural bases between the relevance implicature and other types of implicature processing. The difference may not necessarily lie in the specific locus but it may be in the differential integration of common cognitive modules (cf. Friston, 1994; Horwitz et al., 1999) for various types of implicature processing.

## Conclusion

We performed an event-related fMRI study of the inference processing in understanding literally irrelevant but pragmatically implicated meanings in conversation. With lower implicitness, the activation was detected in the left ATL, left posterior MTG and left AG, which may mediate semantic integration of the literal and contextual information. With higher levels of implicitness, brain involvement expanded to the left IFG and right ATL as a semantic language network and the mPFC and PCC as an extra-linguistic cognitive network, which may mediate bridging inference with semantic retrieval, semantic integration, and active coherence building in a generated situation model. The ATL activation irrespective of inference load suggests that the ATL is one of core regions for implicature processing. Furthermore, comprehension of highly implicit implicatures additionally activated the ATL in the right hemisphere, which is efficient for integrating distant concepts according to the coarse coding hypothesis of the right hemisphere. The significance of the present study is that it expands the range of neuroimaging approaches to include the theory of conversational implicature at the discourse level. Future studies are needed to identify and verify more detailed functions of each of the regions involved in conversational implicature.

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## Conflict of interest

There are no conflict of interests from all the authors.

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