

Perspective-taking as part of narrative comprehension: A functional MRI study

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ABSTRACT

During narrative comprehension, readers understand the emotions of the protagonist by taking the perspective of the character, which is an essential component of empathy. Spatial perspective-taking is crucial to understanding the standpoints and perceptions of others, and gives clues as to what the protagonist knows. As a default, a “here and now” point-of-view is adopted to make sense of the narrative. If the protagonist is in a different location while an event takes place (“there and now”), in order to comprehend the narrative the reader must take an allocentric perspective, which places greater demands on spatial perspective-taking. Utilizing this phenomenon, we evaluated the neural substrates of perspective-taking in emotional narrative comprehension using functional MRI in 18 normal adults. The subjects read short stories followed by a target sentence, which described an event that might evoke an emotional response in the protagonist if the character were present. The stories involved a scenario in which the character was either present at the same location (“here and now”) or at a distant location (“there and now”) during the event. The “there and now” scenario activated the posterior cingulate cortex and the right temporo-parietal junction more prominently than the “here and now” condition. In contrast to the control tasks, both scenarios activated the well-known mentalizing network including the dorsomedial prefrontal cortex, temporal pole, posterior cingulate cortex and temporo-parietal junction. Along with the mentalizing network, the posterior cingulate cortex and the right temporo-parietal junction are involved in spatial perspective-taking during emotional narrative comprehension.

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1. Introduction

A story is the depiction of events, which are driven by the intentional behaviours of agents with unique goals, in imagined settings that can parallel the real world (Mar, 2004). Understanding a narrative requires one to understand the intentions, goals, emotions and other mental states of the characters, which is known as mentalizing (Frith & Frith, 2003). Readers often understand stories by taking the perspective of a character and mentally representing his or her emotional state (de Vega, Leon, & Diaz, 1996; Gernsbacher, Goldsmith, & Robertson, 1992; Komeda & Kusumi, 2006), which is an important process in narrative comprehension. Perspective-taking, which is the ability to adopt and understand the perspective of others, is an essential component of empathy, or the reaction of one individual to the observed experiences of another (Blair, 2005; Davis, 1983). Perspective-taking involves two components: the information effect, which is related to the assessment of what

the interlocutor knows; and the weighting effect, which describes the need to assess how the interlocutor will weigh up the different information required to make a decision (Dixon & Moore, 1990).

Narrative comprehension involves the construction of a representation of the state of affairs described in the text (Zwaan & Radvansky, 1998). These representations of textual information are called situation models (e.g., see Gernsbacher, 1990; Kintsch, 1998; van Dijk & Kintsch, 1983; Zwaan & Radvansky, 1998). A situation model consists of several dimensions, such as time, space, intentionality and the protagonist, including his or her emotional state (Ferstl & von Cramon, 2007; Ferstl, Rinck, & von Cramon, 2005; Zwaan & Radvansky, 1998). Readers predict that changes in each dimension will occur in the text. Changes in any dimension require readers to update their situation models, in order to fill in the gaps left by deviations from the predicted changes. Thus, a change in any dimension leads to an increase in reading time (Zwaan, 1999).

Rall and Harris (2000) proposed that perspective-taking in story comprehension can be explained by a situation model. This model includes the selection of a particular location and timeframe within the imagined scene from which to clarify the setting and the action. In other words, a “here and now” point-of-view is adopted in order to make sense of the narrative. Information that is spatially close to the protagonist is more readily accessible than that which is spa-

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tially separate (Bower & Morrow, 1990), as reflected by elongated reading times for spatially separate information. This is particularly relevant if the protagonist in the story is in the same location as the reader's "here and now" perspective; in such a case, the information is shared by both the protagonist and the reader, and so narrative comprehension should be easier. If the protagonist is in a different location from the reader's perspective ("there and now"), in order to achieve emotional comprehension the reader has to take an allocentric perspective, which places a greater emphasis on spatial perspective-taking (Zwaan, 1999).

The neural substrates of emotional comprehension (i.e., the coordination of perspective-taking and emotional attribution) have been studied using functional neuroimaging techniques. To evaluate the interaction between perspective-taking and emotional attribution, Ruby and Decety (2004) used a factorial design, including emotional (emotional vs. non-emotional) and perspective-taking (third person vs. first person) factors. In their study, each subject was asked to adopt either their own first-person (egocentric) perspective or the third-person (allocentric) perspective of their mother in response to situations involving social emotions or neutral situations. The main effect of the third-person vs. first-person perspective resulted in hemodynamic increases in the medial part of the superior frontal gyrus, the left superior temporal sulcus (STS), the left temporal pole, the posterior cingulate gyrus and the right inferior parietal lobe. Their study was an important building block in our understanding of social emotion processing and human empathy. Specifically, Ruby and Decety (2004) evaluated the weighting effect by comparing the third-person and first-person perspectives. However, currently no research has evaluated the effect of perspective-taking in the emotional comprehension of narratives.

The purpose of the present study was to depict the neural substrates of spatial perspective-taking in narrative emotional comprehension. Spatial perspective-taking is important in understanding another person's standpoint and perceptions, which provide clues as to what the character does or does not know. Our hypothesis was that spatial perspective-taking in the situation model formed during narrative comprehension is represented by the neural substrates of spatial perspective-taking during motor imagery (Ruby & Decety, 2001). This is because the major factor involved in constructing a situation model is the perspective from which the action of the narrative is imagined (Rall & Harris, 2000). Based on the situation model, "there and now" stories place a greater emphasis on spatial perspective-taking than "here and now" stories. A comparison of the two conditions should thus depict the neural substrates of emotional comprehension that are relevant for spatial perspective-taking.

Here we explicitly manipulated the spatial perspective of the protagonist during an emotional comprehension task (the scenario reading task). The first sentence (S1) described the location and behaviour of a protagonist. Subjects were then required to evaluate the emotional state of the protagonist portrayed in sentence 2 (S2), which was either the same protagonist as in S1 or a different person. Both S1 and S2 depicted phenomena that happened at the same time. By modifying S1 while keeping S2 constant, we modulated the emotional state of the protagonist in the scenario.

In the spatially coupled (SC) condition, S1 and S2 described events that occurred at the same place, and hence the protagonist would be aware of both events. For example,

S1: Kana is playing with her much-loved stuffed toy.
S2: Kana's stuffed toy was pecked and ripped by a bird in her room.

In the spatially decoupled (SD) condition, the events described in S1 and S2 were spatially separated, and hence the protagonist was not aware of the event described in S2. For example,

S1: Kana is watching her favourite comedy at the movie theatre.
S2: Kana's stuffed toy was pecked and ripped by a bird in her room.

In SC and SD, S1 and S2 are related to the same protagonist, and hence the context provided by S1 affects the inference evoked by S2 regarding the emotional state of the protagonist. Also, S2 provides the location of both the protagonist and the emotional event. Thus, S1 alone cannot cue the correct response. By contrast, in the unconnected (UC) condition, upon reading S2 it was clear to the subject that the event described in S1 involved a different person, and hence there was no information as to the involvement of the protagonist in the event described in S2. Thus, the S2 response during the UC condition controlled for the S2-related lexical processes during the SC and SD conditions. For example,

S1: Norio is watching his favourite comedy at the movie theatre.
S2: Kana's stuffed toy was pecked and ripped by a bird in her room.

Therefore, the difference in the response to S2 between the SD and UC conditions (and also between the SC and UC conditions) controls for the linguistic processing of S2, and thus represents spatial perspective-taking and the comprehension of the emotional state of the protagonist.

2. Materials and methods

2.1. Subjects

In total, 36 right-handed healthy volunteers took part in the study. Eighteen subjects (10 females and eight males; mean age $\pm$ standard deviation = 24.2 ± 5.3 years, range = 18–34 years; mean education¹ $\pm$ standard deviation = 16.6 ± 2.7 years, range = 13–21 years) participated in the preliminary psychological testing. Another 18 subjects took part in the functional MRI (fMRI) study (10 females and 8 males; mean age $\pm$ standard deviation = 25.2 ± 2.5 years, range = 21–30 years; mean education $\pm$ standard deviation = 17.6 ± 1.9 years, range = 15–21 years). Handedness was determined using the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were native Japanese speakers. No subject had a history of neurological or psychiatric disease, or drug or alcohol abuse. Written informed consent to take part in this study was obtained following procedures approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan.

2.2. Stimuli, task and preliminary psychological testing

We used an emotional comprehension task, which was a modified version of the task used in a previous study (Pons & Harris, 2004; Fig. 1). We prepared short passages composed of two Japanese sentences that would evoke an emotional response in the protagonist if he or she were present. Each trial involved two sentences (S1 and S2). We used an event-related design that consisted of three conditions: the SC condition ("here and now"), the SD condition ("there and now") and the UC condition. During all of the trials, the visual cue was either "P" (positive) or "N" (negative). The task design is represented schematically in Fig. 2.

In the SC condition, S1 and S2 were set in the same location, and hence the protagonist was aware of the event described in S2. In the SD condition, S1 and S2 took place in different locations, and hence the protagonist did not know about the episode described in S2. In the UC condition, the names of the characters were different in S1 and S2; the character shown in S1 was different from the protagonist in S2, and hence the story was irrelevant to the emotional state of the protagonist described in S1.

We used 24 S2 sentences and 72 S1 sentences (including three conditions for each S2 sentence) for the fMRI experiment. All test materials (translated into English) are shown in Appendix A. We initially generated 32 S2 sentences and 96 S1 sentences, and selected the fMRI experimental stimuli from among them. The remaining 24 stories were used for the pre-scanning training. The average length (mean $\pm$ standard deviation) of the S1 sentences was 26.8 ± 1.9 characters for the SC condition, 25.0 ± 1.6 for the SD condition and 25.1 ± 1.8 for the UC condition. There were no significant differences in the sentence lengths between the SC, SD and UC conditions. The mean length (mean $\pm$ standard deviation) of the S2 sentences was 27.0 ± 1.2 characters.

¹ Japanese education involves: 6 years in elementary school, 3 years in junior high school, 3 years in high school, 4 years in college or university, 2 years in master's courses, and 3 or 4 years in doctoral courses.

Experimental design (example of a trial)

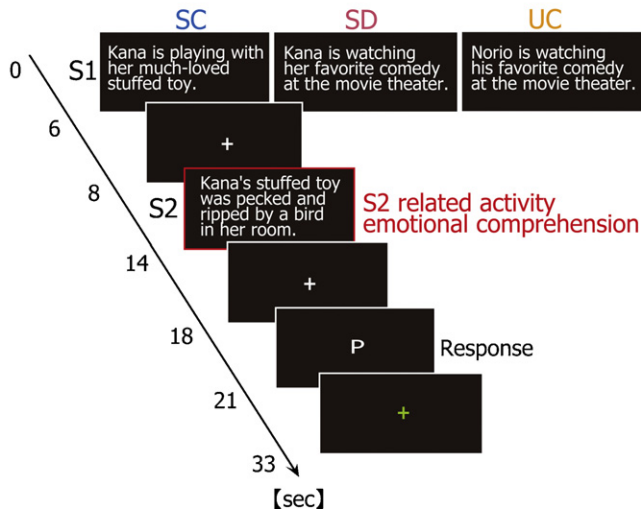


Fig. 1. Examples of stimuli and the time course of the experiment. S1 and S2 each explained the situation of a character. They described episodes that happened at the same time, but that might have occurred in different places. By modifying S1 while keeping S2 constant, the whole scenario represented either the “here and now” SC condition (i.e., S1 and S2 took place in the same location, and hence the character was aware of the episode described in S2), the “there and now” SD condition (i.e., S1 and S2 took place in different locations, and hence the character would not be aware of the episode described in S2) or the UC condition (i.e., the character shown in S1 was different from the character shown in S2, and hence the story was irrelevant and the answer was always “No”).

In the preliminary psychological testing, all of the stimuli were presented using Presentation software (Neurobehavioral Systems, CA, USA) on a personal computer (Dimension 9100, Dell Computer Co., TX, USA). All of the sentence stimuli for the tasks were written in Japanese and presented as white letters against a black background. The maximum visual angle was 7.3° (width) by 1.3° (height). Subjects underwent three sessions, each of which contained 24 trials (eight SC trials, eight SD trials and eight UC trials) and the order of the trials was counterbalanced for each subject. Throughout the three sessions, the subjects were asked to fixate a small cross-hair at the centre of the screen. Initially, S1 was presented. After reading S1 at their own pace, subjects pressed a button with their right thumb that prompted the replacement of S1 with S2. After reading S2, the subjects once again pressed the button, which triggered the disappearance of S2 and the appearance of the visual cue “P/N”. During the SC and SD trials, the subjects were asked to push a button with their right index or right middle finger to signal whether the emotion shown in the presented cue was correct. When the sign was correct, subjects were required to press the right index-finger button as soon as possible, in order to measure the reading time. Subjects pressed the right middle-finger button when the sign was incorrect. Subject’s responses were considered correct when the participant selected the cue (Positive or Negative) that accurately matched the protagonist’s emotional state coherent to the situation. During the UC trials, the subjects were not required

to deduce the protagonist’s emotions and beliefs, because the protagonists differed in S1 and S2; therefore, the subjects were asked to push the right middle-finger button, as the answer was always “No”. There is a possibility that the valence of S2 could affect the participant’s emotional state (affective empathy), even in the UC condition. However, in the case of the UC condition, comprehension of the protagonist’s emotional status (cognitive empathy) was unlikely, because the characters differed between S1 and S2, and subjects were instructed to “not make a decision”.

Statistical analysis was carried out using SPSS version 10.0J software (SPSS Japan Inc., Tokyo, Japan). To compare the mean percentage of correct responses and the mean reaction time to the question cue for the SC, SD and UC conditions, a one-way repeated measures analysis of variance (ANOVA) was performed. We tested the predefined contrast of (SC, SD, UC) = (−1, 1, 0) to confirm the notion that the SD condition was more difficult than the SC condition in terms of reaction time, and the contrast (1, −1, 0) was used for the percentage correct response data. The results were considered statistically significant at $p < 0.05$.

2.3. fMRI study

In the fMRI study, we used the same materials as in the preliminary behavioural study. Using a liquid crystal display (LCD) projector (DLA-M200L, Victor, Yokohama, Japan), the visual stimuli were projected onto a half-transparent screen. The subjects viewed the stimuli through a mirror attached to the head coil of the scanner. All of the sentence stimuli for the tasks were written in Japanese and presented as white letters against a black background. The maximum visual angle was 7.3° (width) by 1.3° (height).

In the fMRI study, the inter-trial interval (ITI) was fixed at 12 s. We ran three fMRI sessions, each of which contained 24 trials (eight SC trials, eight SD trials, and eight UC trials), the order of which was counterbalanced for each subject. Throughout the three sessions, the subjects were asked to fixate a small cross-hair at the centre of the screen. Initially, S1 was presented on the screen for 6 s, followed by a cross-hair for 2 s. The S2 then appeared for 6 s, followed by the cross-hair for 4 s. A visual cue “P/N” was then presented for 3 s (Figs. 1 and 2). This delayed cued response was introduced to separate out the neural responses related to the S2 presentation and the button press. As in the preliminary psychological testing, when the presented sign was correct, the subject was required to press the button with the right index finger, and the subject pressed the right middle finger button when the sign was incorrect. During the UC trials, the subjects were asked to push the button with their right middle finger, as the answer was always “No”. In the present study, we delayed the response timing following S2 presentation by 4 s. The accuracy and reaction times in response to the question cue between the SC, SD and UC conditions were assessed statistically in the same way as in the preliminary psychological data.

2.4. Imaging data acquisition and analysis

Images were acquired using a 3 T MR imager (Allegra, Siemens, Erlangen, Germany). For functional imaging, interleaved T2*-weighted gradient-echo echo-planar imaging (EPI) sequences were used to produce 44 continuous 3-mm-thick trans-axial slices covering the entire cerebrum and cerebellum (repetition time = 3000 ms; echo time = 30 ms; flip angle = 85° ; field of view = 192 mm; 64×64 matrix; voxel dimension = $3.0 \text{ mm} \times 3.0 \text{ mm}$).

After discarding the first three volumes, the remaining 264 volumes per session (a total of 792 volumes per subject for three sessions) were used for analysis. The data were analyzed using Statistical Parametric Mapping 5 software (SPM5, Wellcome Department of Imaging Neuroscience, London, UK; Friston, Ashburner, Kiebel, Nichols, & Penny, 2007) implemented in Matlab 7.1 (Mathworks, Sherborn, MA, USA). After correcting for differences in slice timing within each image volume (Buckner & Friston, 1997), head motion was corrected using the SPM5 realignment

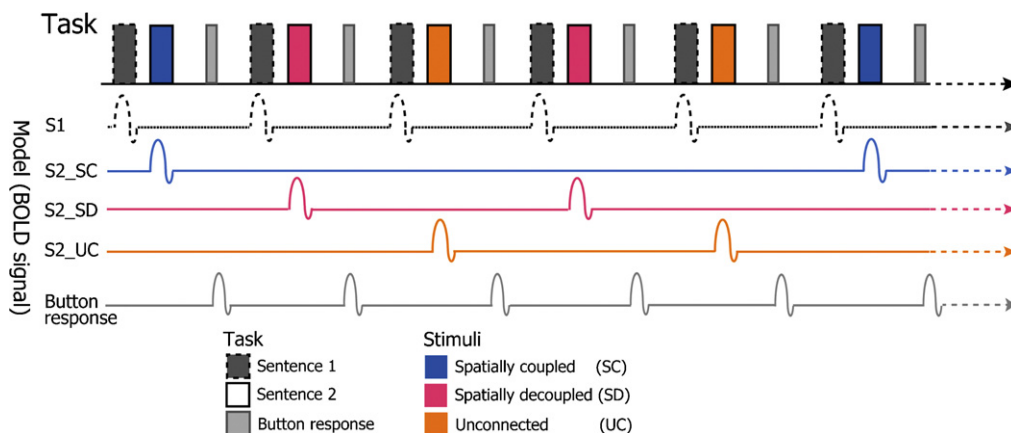


Fig. 2. Task design and models for analyses. The time course of the tasks is presented schematically at the top of the figure. The model of the expected blood oxygen level-dependent (BOLD) signal change is presented for the event-related paradigms.

program. Following realignment, the volumes were normalized to Montreal Neurological Institute (MNI) space (Evans, Kamber, Collins, & MacDonald, 1994) using a transformation matrix obtained from the normalization process of the first EPI image of each individual subject to the EPI template. The normalized fMRI data were spatially smoothed with a Gaussian kernel of 8 mm (full width at half maximum) in the *x*, *y* and *z* axes.

2.5. Statistical analysis

Statistical analysis was conducted at two levels. First, the individual task-related activation was evaluated (Friston et al., 1995). Second, the summary data of all subjects were analyzed using a random-effect model (Friston, Holmes, & Worsley, 1999), in order to make inferences at a population level.

In the individual analyses, the signal intensity from the images was proportionally scaled by setting the whole-brain mean value to 100 arbitrary units. We adopted proportional scaling to adjust for the scanner gain, which is a factor that scales the whole image, and is known to vary slowly during a session. Proportional scaling is most appropriate for data for which there is a gain factor that varies over scans, with an assumption that global cerebral blood flow (gCBF) is independent of condition (Kiebel & Holmes, 2007). As “deactivation” was not a major concern of the present study, the use of proportional scaling is justified. The signal time-course for each subject was modelled with a general linear model. Regressors of interest (condition effects) were generated using a box-car function convolved with a hemodynamic-response function. Specifically, S1 responses were modelled as one regressor for all three conditions. The S1s provided different contexts for identical S2 sentences. Thus, the difference between the S2 sentences preceded by different S1s represents the context effect. In this task design, the difference in response to S1 was of no interest, and thus we adopted a single regressor. The S2 responses of each condition (SC, SD and UC) were modelled separately. Button-press responses were modelled as one regressor for all three conditions. Regressors of no interest, such as the session effect and high-pass filtering (128 s), were also included. To test hypotheses about regionally specific effects, the estimates for each model parameter were compared using the following predefined linear contrasts: (SC–UC), (SD–UC), (SC–SD), (SD–SC), and (SC–UC) + (SD–UC).

The weighted sum of the parameter estimates in the individual analyses constituted “contrast” images, which were used for the second-level group analyses (Friston et al., 1999). The contrast images obtained by the individual analyses represent the normalized task-related increment of the MR signal of each subject. One-sample *t*-tests were conducted on a voxel-by-voxel basis. The resulting set of voxel values for each contrast constituted an SPM(*t*). The threshold for the SPM(*t*) was set at $t > 3.65$ (corresponding to uncorrected $p < 0.001$) and cluster size larger than 10 voxels. The activation foci depicted by this height and extent threshold were then tested by their spatial extent as well as the false discovery rate (FDR) at voxel level. The spatial extent test was based on the theory of Gaussian random fields, which considers clusters as “rare events” that occur in a whole brain according to the Poisson distribution (Friston, Holmes, Poline, Price, & Frith, 1996). The FDR is the proportion of false positives (incorrect rejections of the null hypothesis) among multiple voxel-wise tests for which the null hypothesis is rejected, and hence the procedure controls the family-wise error rate (Genovese, Lazar, & Nichols, 2002). The *p*-values for both spatial extent test and FDR were reported.

Here, the difference in context effects reflects the difference in perspective-taking – that is, “here and now” for (SC–UC) vs. “there and now” for (SD–UC). Thus, (SD–SC) should depict the neural substrates of spatial perspective-taking. We searched the effect of (SD–SC) within the areas that showed the effect of (SD–UC) + (SC–UC) that represents the emotional comprehension of the protagonist (who was referred to in both S1 and S2) in either SD or SC conditions.

The areas activated by both (SC–UC) and (SD–UC) should highlight the neural substrates of the common psychological construct, that is, the judgment of the protagonist’s emotional state. The areas commonly activated by (SC–UC) and (SD–UC) were depicted by the intersection of the areas defined by each contrast, expressed as (SD–UC) & (SC–UC), where “&” indicates the intersection. Similarly, the areas commonly activated by the (SD–SC), (SD–UC), and (SC–UC) contrasts were depicted as (SD–SC) & (SD–UC) & (SC–UC). These were characterized as the neural representation of the emotional comprehension process, with perspective-taking as a specific component of this process.

The percent signal changes in the regions of interest (ROI) adjacent to the precuneus/posterior cingulate cortex and right TPJ, which were depicted by (SD–SC) contrast, were calculated. First, the local maximum highlighted by (SD–SC) was located. Within the areas defined by (SD–UC) & (SC–UC), the local maximum depicted by (SD–UC) + (SC–UC) was identified adjacent to the (SD–SC) areas. The linear contrasts of the parameter estimates of the regressors of interest [(SD–UC) and (SC–UC)] of each ROI corresponded to the percent signal change relative to the mean global activity, which was scaled to 100 (Kiebel & Holmes, 2007).

3. Results

3.1. Preliminary psychological testing

The mean ($\pm$ standard deviation) percentages of correct responses were $90.0 \pm 5.3\%$ for the SC condition, $87.8 \pm 9.4\%$ for the

SD condition and $99.1 \pm 2.3\%$ for the UC condition. With the predefined contrast of (1, –1, 0), there were no significant differences in the accuracy of performance between the SC and SD conditions ($F(1, 17) = 0.18$, $p = 0.68$). The mean ($\pm$ standard deviation) reaction times were 1273.4 ± 376.6 ms for the SC condition, 1522.6 ± 494.4 ms for the SD condition and 690.1 ± 396.6 ms for the UC condition. The predefined contrast of (–1, 1, 0) was significant ($F(1, 17) = 5.5$, $p = 0.031$), indicating that the reaction times during the SD condition were significantly slower than those during the SC condition.

3.2. fMRI study

3.2.1. Behavioural data

The mean ($\pm$ standard deviation) percentages of correct responses were $90.7 \pm 7.6\%$ for the SC condition, $85.2 \pm 13.9\%$ for the SD condition and $97.5 \pm 5.6\%$ for the UC condition. With the predefined contrast of (1, –1, 0), there were no significant differences in the percentage of correct responses between the SC and SD conditions ($F(1, 17) = 2.3$, $p = 0.15$). The mean ($\pm$ standard deviation) reaction times were 1189.8 ± 655.3 ms for the SC condition, 1293.4 ± 683.3 ms for the SD condition and 859.0 ± 626.9 ms for the UC condition. The predefined contrast of (–1, 1, 0) was significant ($F(1, 17) = 5.8$, $p = 0.028$), indicating that the reaction times during the SD condition were significantly slower than those during the SC condition. These data replicated the results from the preliminary psychological testing.

3.3. Imaging data

The activation patterns of (SC–UC) and (SD–UC) were almost identical (Fig. 3a and b). The areas showing common activation during emotional comprehension were highlighted by the intersection of the (SC–UC) and (SD–UC) contrasts. The commonly activated areas included bilateral dorsal premotor cortex (PMd), dorsolateral prefrontal cortex (DLPFC), inferior frontal gyrus (IFG), medial and lateral orbitofrontal cortex (OFC), the medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), temporal pole (TP), middle temporal gyrus (MTG), inferior temporal gyrus (ITG), temporo-parietal junction (TPJ), superior parietal lobule (SPL), precuneus (PCu), lingual gyrus (LG), parahippocampal gyrus (HG), cerebellum, and thalamus (Table 1 and Fig. 4). There was no significant activation for the (SC–SD) contrast (Fig. 3c).

The areas involved in perspective-taking, as depicted by the (SD–SC) contrast, were the precuneus extending to PCC, and right TPJ (Table 2 and Fig. 3d). These foci overlapped with the areas involved in emotional comprehension (Fig. 4). The anterior portion of the PCC/precuneus was mainly activated by emotional comprehension, whereas the posterior portion showed a more prominent effect for perspective-taking. We undertook an additional analysis incorporating gender and RT scores as covariates. There was no significant gender effect or correlation with RT across the whole brain. No significant activation was found for the (SC–SD) contrast.

4. Discussion

4.1. Performance of emotional comprehension

The data of the preliminary testing confirm that the “there and now” condition required a higher workload than the “here and now” condition. The present study is based on previous studies investigating reading stories in which the situation model was implemented with perspective-taking (Rall & Harris, 2000): when the story is being read, information that is spatially close to the protagonist is more readily accessible than information which is spatially separate (Bower & Morrow, 1990). This is reflected in the elongated reading times for spatially separate information.

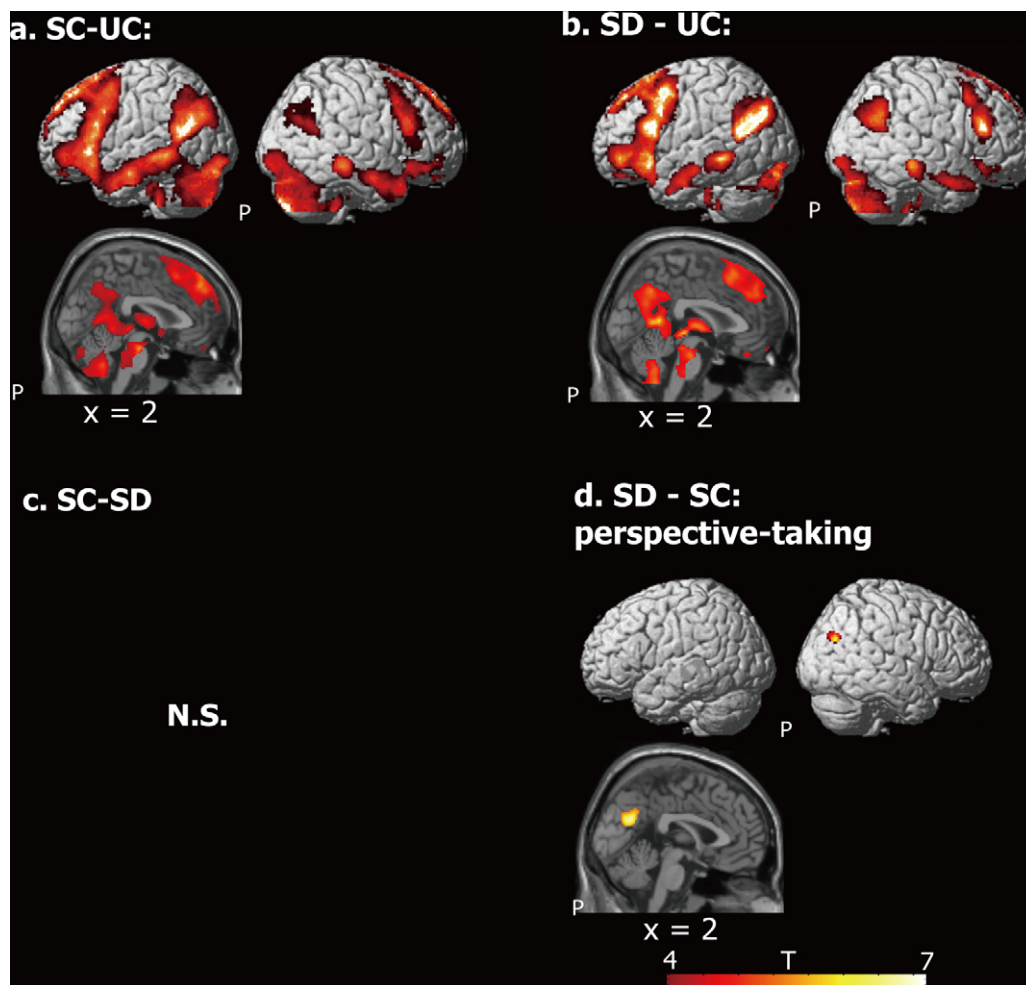


Fig. 3. Activation patterns. (a) Areas associated with the (SC–UC) contrast. The activated areas are projected onto a surface-rendered high-resolution magnetic-resonance image. The colour scale (red) indicates the t -value, which is superimposed onto the sagittal plane ($x = 2$) of an anatomically normalized magnetic-resonance image (MNI template). Height threshold of $t > 3.65$ with $p < 0.05$ corrected for multiple comparisons at cluster level, with the search volume of the entire brain are shown. (b) Areas associated with the (SD–UC) contrast. The activated areas were shown with the same threshold as (a). (c) The (SC–SD) contrast. There were no significant regions of activation. (d) Areas associated with perspective-taking based on the (SD–SC) contrast. Height threshold was set at $t > 3.65$ with clusters larger than 10 voxels.

Perspective-taking is an essential component of cognitive empathy, in addition to being important to story comprehension. As the task entailed inferring the emotional state of the protagonist, in both the SD and SC conditions the participants were required to take the perspective of the protagonist. Upon the presentation of S2, the location of both the protagonist and the emotional event became evident. In the SD condition, the spatial location of the event occurring in S1 was different from that in S2, whereas the location of the S1 and S2 events was the same in the SC condition. Thus, the more prominent S2-related workload during the SD compared to the SC condition represents the greater workload required to update the situation model based on the information provided by S2, due to the distance between the protagonist's point-of-view and the location of the event.

In the present study, the preliminary psychological testing confirmed this finding. There was no statistical difference in accuracy between the SC and SD conditions. Thus, it is unlikely that generic task difficulty is the cause of the longer RTs in the SD condition.

The purpose of the preliminary psychological examination was to confirm the findings of previous studies regarding reading times, and thus it was essential to measure the reading times in a self-paced manner. On the other hand, during the fMRI study, in order to depict the neural response to the S2 presentation, it was neces-

sary to separate the neural activity related to the button response. Thus, we temporally segregated the button response from S2 presentation by a 4-s time interval.

Reaction times during fMRI scanning were shorter when compared to those obtained during the psychological testing. This could be due to several reasons. First, different subjects participated in the preliminary psychological study and the fMRI experiment. Second, the experimental environment was different: one group performed the task in the magnet and other group completed the task outside of the magnet. Third, the task setting was different: in the preliminary psychological study, S1 and S2 were presented in a self-paced manner, immediately followed by the response cue. This was designed to correspond with previous psychological studies investigating the updating of the situation model by measuring reading time. On the other hand, in the fMRI study, S1 and S2 were presented at predefined time intervals, and the response cue did not immediately follow S2 presentation. We did this so that we could model out the response-related activity, because we were specifically interested in the S2-related activity.

4.2. Neural substrates of emotional comprehension

In the SC and SD conditions, the subjects were required to comprehend the emotional state of the protagonist during the pre-

Table 1

Activation in the (SD–UC)+(SC–UC) contrast within the areas of (SD–UC) & (SC–UC) (emotion comprehension).

Cluster size	MNI coordinates (mm)			t-Value	FDR corrected <i>p</i>	Location		
	x	y	z			Side	Area	BA
15,126	–38	8	58	12.22	<0.001	Lt	PMd	6
	–44	10	36	9.16	<0.001	Lt	DLPFC	9
	–42	24	20	7.90	<0.001	Lt	DLPFC	46
	–50	20	42	7.64	<0.001	Lt	DLPFC	8
	–54	28	2	12.70	<0.001	Lt	IFG	45
	–50	20	24	11.15	<0.001	Lt	IFG	44
	–40	24	–14	10.50	<0.001	Lt	IFG	47
	–46	40	0	8.07	<0.001	Lt	IFG	10
	–44	48	–12	14.65	<0.001	Lt	Lateral OFC	11
	–4	20	54	11.68	<0.001	Lt	mPFC	8
	–6	54	40	10.84	<0.001	Lt	mPFC	8
	–36	28	–22	9.00	<0.001	Lt	TP	38
	–52	–12	–22	7.93	<0.001	Lt	ITG	20
	–66	–34	–8	10.70	<0.001	Lt	MTG	21
	–56	–58	16	9.92	<0.001	Lt	TPJ	22/39
	–30	–78	40	8.29	<0.001	Lt	SPL	7
151	–28	12	–30	6.55	<0.001	Lt	TP	38
219	–6	52	–20	5.69	<0.001	Lt	Medial OFC	11
	10	36	–24	4.52	<0.001	Rt	Medial OFC	11
19,327	–22	–22	–14	5.57	<0.001	Lt	HG	36
	22	–22	–14	5.29	<0.001	Rt	HG	36
	–2	–58	8	10.33	<0.001	Lt	PCC	30
	–4	–62	38	7.81	<0.001	Lt	PCu	7
	0	–60	32	5.29	<0.001		PCu	31
	0	–52	36	5.19	<0.001		PCu	31
	10	–58	36	6.81	<0.001	Rt	PCu	7
	–28	–94	–10	5.08	<0.001	Lt	LG	18
	28	–94	–6	6.40	<0.001	Rt	LG	18
	–4	–14	6	9.68	<0.001	Lt	Thalamus	
	12	6	2	8.64	<0.001	Rt	Thalamus	
	–18	–38	–48	8.98	<0.001	Lt	Cerebellum	
	12	–84	–36	9.37	<0.001	Rt	Cerebellum	
1354	48	12	52	6.47	<0.001	Rt	PMd	6
	54	26	28	9.07	<0.001	Rt	DLPFC	46
	50	28	22	8.00	<0.001	Rt	IFG	45
1,286	54	14	–26	7.15	<0.001	Rt	TP	38
	54	–4	–22	8.08	<0.001	Rt	MTG	21
	44	40	–16	6.03	<0.001	Rt	Lateral OFC	11
577	68	–30	–14	6.31	<0.001	Rt	ITG	20
929	56	–64	26	8.35	<0.001	Rt	TPJ	39
	46	–72	28	5.98	<0.001	Rt	TPJ	39
	56	–62	28	6.90	<0.001	Rt	TPJ	39
	52	–64	44	5.88	<0.001	Rt	TPJ	40
	44	–76	40	5.31	<0.001	Rt	SPL	7

The local maxima of the *t*-values for the (SD–UC)+(SC–UC) contrast are shown. *p*-Values were corrected for multiple comparisons with FDR through the search volume defined by the intersection of the activated areas by (SC–UC) and those by (SD–UC), all of which survived the statistical threshold of $p < 0.05$ corrected at cluster level. The areas listed here are corresponding to those indicated by blue colour in Fig. 4. BA, Brodmann area; DLPFC, dorsolateral prefrontal cortex; HG, parahippocampal gyrus; IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; LG, lingual gyrus; mPFC, medial prefrontal cortex; MTG, middle temporal gyrus; OFC, orbitofrontal cortex; PCC, posterior cingulate cortex; PCu, precuneus; PMd, dorsal premotor cortex; SPL, superior parietal lobule; STS, superior temporal sulcus; TP, temporal pole; TPJ, temporo-parietal junction. Lt, left; Rt, right.

sensation of S2 based on the information provided by S1 about the involvement of the protagonist in the situation. In the UC condition, no such information was provided, and hence the subjects did not evaluate the emotional state of the protagonist (this was explicitly explained to the subjects before the experiment). Therefore, the areas that were commonly activated by the contrasts of (SC–UC) and (SD–UC) depicted the neural substrates of the comprehension of the emotion of others. The areas highlighted by the (SC–UC) contrast were among the areas highlighted by the (SD–UC) contrast, and hence the intersection of the (SC–UC) and (SD–UC) contrasts coincides with the areas depicted by the (SC–UC) contrast.

Among the commonly activated areas, it has been suggested that the mPFC, the temporal poles, the posterior STS located in

the TPJ, and the precuneus are the neural correlates of “mentalizing”, or thinking about the mental state of another person (Frith & Frith, 2003, 2006). These areas have been involved consistently in mentalizing tasks associated with stories (Ferstl & von Cramon, 2002; Fletcher & Happe, et al., 1995; Gallagher et al., 2000; Happe et al., 1996; Vogeley et al., 2001) as well as cartoons (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Gallagher et al., 2000). Moll, de Oliveira-Souza, and Eslinger (2003) proposed that the mPFC and frontopolar cortex are responsible for more conscious and effortful reasoning processes, including mentalizing and social judgment. The parahippocampal gyrus and the PCC are related to understanding spatial information during narrative comprehension (Ferstl & von Cramon, 2007). The lateral orbitofrontal cortex (Brodmann’s area 11 and 47) plays an important role in evaluating emotional

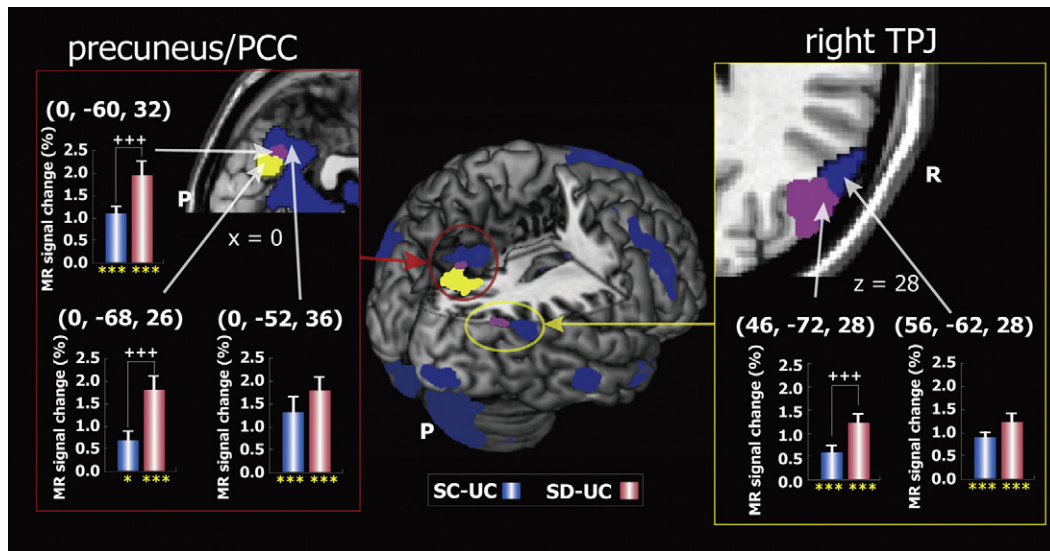


Fig. 4. Neural substrates of emotional comprehension ((SD-UC) & (SC-UC), blue), perspective-taking ((SD-SC), yellow) and the areas activated by both processes ((SD-SC) & (SD-UC) & (SC-UC), violet) projected onto a three-dimensional high-resolution MR image. “&” indicates the intersection. The magnified sagittal view ($x=0$) of the PCC (left inset), and the transaxial view ($z=28$) of the right TPJ (right inset) of an anatomically normalized magnetic-resonance image (MNI template) are shown. The bar graphs show linear contrasts of the parameter estimates of the regressors of interest, the (SC-UC) contrast (closed blue bars) and the (SD-UC) contrast (closed magenta bars), of each ROI corresponded to the percent signal change relative to the mean global activity, which was scaled to 100. *** $p < 0.001$ (paired t -test); * $p < 0.05$ (one sample t -test), *** $p < 0.001$ (one sample t -test).

states during mentalizing processes (Hynes, Baird, & Grafton, 2006), including embarrassment (Berthoz, Armony, Blair, & Dolan, 2002). Thus, emotional comprehension recruited the well-known neural substrates of mentalizing.

4.3. Neural substrates of spatial perspective-taking

The neural substrates of spatial perspective-taking that were identified by the (SD-SC) contrast included the right TPJ and the precuneus/PCC. These areas are known to be related to spatial perspective-taking during simulated action (Ruby & Decety, 2001). The TPJ is also specifically involved in reasoning about the contents of another person's mind in written stories (Saxe & Kanwisher, 2003). Saxe and Wexler (2005) reported that the right TPJ was selectively recruited during the attribution of mental states, and not for other socially relevant facts about a person; furthermore, the response in the right TPJ was modulated by the congruence or incongruence of multiple relevant facts about the mind of the target. Frith and Frith (2006) proposed that the posterior STS and the adjacent TPJ are associated with processing another person's perspective, allowing us to realize that other people can have knowledge that differs from our own and might have false beliefs about the world (e.g., “He thinks that he is safe because he cannot see the bear coming up behind him”).

It has been suggested that activity in the right TPJ may not be selective for mentalizing, but rather is also involved in reorienting attention (Mitchell, 2008). In a quantitative meta-analysis of functional neuroimaging studies, Decety and Lamm (2007) reported

significant overlap of the neural representations of mentalizing and reorienting attention in the right TPJ. They also observed that the representation of mentalizing extended posteriorly, while activity related to the reorienting attention was located anteriorly. The weighted centre of the foci activated by mentalizing was [50, −53, 21] and that for reorienting attention was [54, −46, 23].

Compared to these areas, the focus of activation in the present study was located more posteriorly, at [46, −72, 28]. Thus, it is not likely related to attention. This is consistent with the notion that perspective-taking is an important component of empathy, which is categorized as a kind of mentalizing. Furthermore, the present study showed co-activation of the PCC, which is often observed in social cognition paradigms, but not in reorienting attention tasks (Corbetta, Patel, & Shulman, 2008). On the other hand, the (SD-SC) contrast did not show VFC activation, which, along with the right TPJ, is a component of the ventral attention network (Corbetta et al., 2008). Thus, the greater activation in the PCC and right TPJ is likely related to perspective-taking, rather than the redirection of attentional processes.

However, this does not necessarily mean that the activation is not related to the reorienting attention. Corbetta et al. (2008) argued that “internally directed processing such as introspection, self-referential thoughts, or projecting oneself into a situation” involves a “default” network (Raichle et al., 2001), whereas the dorsal attention network controls environmentally-directed processes such as perception and action. The ventral attentional network including the right TPJ may function “as a system to switch (reorient) between internally and externally directed activities” (Corbetta

Table 2

Activation in the (SD-SC) contrast within the areas of (SD-UC) + (SC-UC) (perspective-taking).

Cluster level		MNI coordinates (mm)			t -Value	FDR corrected p	Location		
p -Value	Size	x	y	z			Side	Area	BA
<0.001	461	2	−68	26	6.72	0.02	Rt	PCu	31
0.142	81	46	−72	28	5.16	0.02	Rt	TPJ	39

Rt, right. The p values were corrected for multiple comparison through the search volume defined by the activated areas by (SC-UC) + (SD-UC) that was survived the $p < 0.05$ corrected at cluster level. The areas were corresponding to those indicated by violet colour in Fig. 4. BA, Brodmann Area; PCu, precuneus; TPJ, temporo-parietal junction.

et al., 2008). They suggest that “the attention signals in the right TPJ may be important to switch between internal, bodily, or self-perspective and external, environmental, or another’s viewpoint”, a key component of mentalizing.

The precuneus is activated when inferring the knowledge and beliefs of someone who lived a long time ago (e.g., whether Christopher Columbus would have known what an object was used for; Goel, Grafman, Sadato, & Hallet, 1995) and when reading written stories (Saxe & Kanwisher, 2003; Saxe & Powell, 2006; Saxe & Wexler, 2005). In particular, the PCC activation is associated with taking a third-person perspective, as several imaging studies have demonstrated its involvement in tasks requiring “mind-reading” (Brunet et al., 2000; Fletcher & Frith, et al., 1995; Goel et al., 1995). Völlm et al. (2006) reported PCC activation when subjects empathized with cartoons. Furthermore, the PCC is important for visuo-spatial cognition (i.e., visual imagery and spatial perception) in the situation model for narrative comprehension (Ferstl & von Cramon, 2007). In a positron-emission tomography (PET) study, Ruby and Decety (2001) proposed that the precuneus has a role in perspective-taking (i.e., a third-person perspective compared to a first-person perspective) during action simulation. In the present study, these areas were activated by the (SC–UC) contrast; thus, they appear to be related to emotional comprehension, presumably as part of the situation model. The precuneus/PCC region might therefore constitute part of the network involved in emotional comprehension during spatial perspective-taking, together with the mPFC, temporal pole, TPJ, all of which are known to be involved in mentalizing.

4.4. Emotional comprehension and false-belief reasoning both involve perspective-taking

The information effect is closely related to spatial perspective-taking, because the spatial perspective is important for understanding another’s standpoint and perceptions, which are clues as to what an interlocutor knows. Thus, spatial perspective-taking might be related to false belief – that is, when the ability to reason about another’s beliefs is discordant with the facts. Developmentally, belief emerges later than other mental state concepts, such as goals, perceptions and feelings; thus, “belief” might be a distinct component of the human understanding of others’ minds (Saxe & Powell, 2006). The ability to understand false belief is considered to be a critical marker indicating a theory of mind or ToM (Baron-Cohen, Leslie, & Frith, 1985; Gallagher et al., 2000; Kobayashi, Glover, & Temple, 2007; Sabbagh, Moses, & Shiverick, 2006; Saxe & Kanwisher, 2003; Sommer et al., 2007; Wimmer & Perner, 1983; Yazdi, German, Defeyter, & Siegal, 2006), which is an important aspect of mentalizing (Frith & Frith, 2003). A number of recent developmental psychology studies have looked at children’s understanding of both true-belief and false-belief tasks (e.g., Ruffman, Garnham, Import, & Connolly, 2001; Wellman & Bartsch, 1988; Yazdi et al., 2006); these authors have concluded that children come to understand true-belief tasks earlier (i.e., at 3 years old) than they understand false-belief tasks (i.e., at 4 years old; Wellman & Bartsch, 1988). When children are aged between 4 and 6 years, they begin to understand that a person’s beliefs will determine his or her emotional reaction to a situation, which is an important landmark in the development of emotional comprehension (Pons & Harris, 2004). This developmental order suggests that false belief and emotional comprehension might share common psychological processes, such as perspective-taking.

Both true-belief and false-belief tasks require temporal–spatial orientation. In the “Sally–Anne” task (Baron-Cohen et al., 1985), children are told a story about a character (Sally) who has a false belief about the location of an object. Sally is described as having

placed the object in a box, but, while she is away, another character (Anne) moves it to a different location. The test question asks where Sally will look for the object (for a review, see Wellman, Cross, & Watson, 2001). Thus, temporal–spatial perspective-taking is a prerequisite for the successful performance of a false-belief task.

There are many neuroimaging and neuropsychological studies examining ToM using false-belief tasks with a variety of control conditions. For example, false belief scenarios employed to elicit ToM reasoning were contrasted with control conditions that required physical or mechanical inferences (Fletcher & Frith, et al., 1995; Fletcher & Happe, et al., 1995; Goel et al., 1995; Saxe & Kanwisher, 2003). Other researchers (Saxe & Powell, 2006; Saxe & Wexler, 2005) compared reading stories that described a character’s true or false beliefs, with reading stories containing other information about a character, including his or her appearance, cultural background, or even internal, subjective sensations. Kobayashi et al. (2007) compared a ToM story condition consisting of second-order false belief stories (“what they are thinking” stories) with non-ToM stories, which described physical causal situations (“what is happening” stories); this study used both verbal (story) and non-verbal (cartoon) versions of the task for both adults and children. “False” photograph tasks (Apperly, Samson, Chiavarino, Bickerton, & Humphreys, 2007) were used as control conditions for the false belief tasks in recent ERP and fMRI studies (Sabbagh et al., 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). However, there are few studies that directly compare the false-belief (false representation of the current situation) condition with the true-belief (true representation of the current situation) condition.

Using fMRI with a cartoon version of the Sally–Anne task, Sommer et al. (2007) tried to elucidate the neural substrates of false belief. By contrasting the false-belief condition with the true-belief condition, they found activation in the right TPJ. Sommer et al. (2007) interpreted this finding as representing a “perspective difference such as a person’s false belief that contrasts with the state of reality”. Although direct comparison is difficult due to differences in the tasks, their interpretation probably corresponds to the information effect of perspective-taking in the present study. Thus, emotional comprehension during narrative comprehension might share the neural substrates involved in spatial perspective-taking, such as the PCC and the TPJ, with other types of mentalizing, such as false-belief reasoning.

5. Conclusion

A situation model consists of several dimensions, such as time, space, causality and the perspective or emotional state of the protagonist (Ferstl et al., 2005; Ferstl & von Cramon, 2007; Zwaan & Radvansky, 1998). Our present study shows that, along with the mentalizing network, the PCC and the right TPJ are involved in spatial perspective-taking during narrative emotional comprehension. This finding implies that the neural representation of the situation model for narrative comprehension includes the regions involved in mentalizing.

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Appendix A

See Table A1.

Table A1

Task materials. Translated into English from the original Japanese.

S1	S2	Cue	Answer
SC Tsutomu is at a restaurant eating a hamburger, which is his favourite dish; his mother is with him at the restaurant.	Tsutomu's mother collapsed suddenly at the restaurant and was taken to hospital.	N	Yes
SD Tsutomu is engrossed in his favourite game at a video arcade.		P	Yes
UC Rie is engrossed in her favourite game at a video arcade.		N	No
SC Tae is at home doing homework in her weakest subject, which has piled up.	The cake that Tae had ordered by mail arrived.	P	Yes
SD Tae is at school taking a class in her weakest subject.		N	Yes
UC Masao is at school taking a class in his weakest subject.		N	No
SC Ai is about to eat her lunch, which she has been looking forward to.	Ai's lunch was snatched away by a ferocious stray dog.	P	No
SD Ai is absorbed in performing forward flips on the horizontal bar, which she is good at.		P	Yes
UC Tsuyoshi is absorbed in performing forward flips on the horizontal bar, which he is good at.		P	No
SC Masao is at a bookstore looking for a popular novel for which he had eagerly waited.	The bookstore does not have the novel Masao is looking for because it is sold out.	N	Yes
SD Masao is at an amusement park riding the go carts which is his favourite ride.		N	No
UC Michi is at an amusement park riding a Ferris wheel which is her favorite ride.		P	No
SC Yumi is at the airport which is bustling with people going home for the holidays.	The flight that Yumi's father is on has landed safely.	P	Yes
SD Yumi is on a packed and stifling train.		N	Yes
UC Tsutomu is on a packed and stifling train.		P	No
SC Kumi is in her room looking at her much-loved home	Kumi's goldfish has died and is floating in the home aquarium.	P	No
SD Kumi is admiring the beautiful view from the window of her		N	No
UC Kiyoshi is admiring the beautiful view from the window of		N	No
SC Maki is having fun chatting with her friends in front of her house.	Maki's dog was hit by a truck in front of her house.	N	Yes
SD Maki is looking for some cute-looking clothes at a department store.		P	Yes
UC Akira is looking for some cool-looking clothes at a department store.		N	No
SC Kazuo is browsing a website which is very straining to his	The winning number for the prize competition that Kazuo had entered is shown on the webpage.	P	Yes
SD Kazuo is reluctantly tending to the garden which is covered in dry grass.		P	No
UC Emi is reluctantly tending to the garden which is covered in dry grass.		P	No
SC Hitoshi went to visit his best friend who he had been looking forward to seeing.	Hitoshi's best friend is no longer at the house having suddenly moved far away.	P	No
SD Hitoshi is reading a very funny comic book at home.		N	No
UC Mika is reading a very funny comic book at home.		N	No

Table A1 (Continued)

S1	S2	Cue	Answer
SC Kana is playing with her much-loved stuffed toy.	Kana's stuffed toy was pecked and ripped by a bird in her room.	P	No
SD Kana is watching her favorite comedy at the movie theater.		N	No
UC Norio is watching his favorite comedy at the movie theater.		P	No
SC Norio is about to leave for school on his prized bike which had recently been bought for him.	The bicycle that Norio uses to get to school has a flat tire.	N	Yes
SD Norio is about to leave for school on the school bus which he enjoys riding.		N	No
UC Mayu is about to leave for school on the school bus which she enjoys riding.		P	No
SC Akira is struggling to stay awake and watch television.	The athlete that Akira likes is on television.	N	No
SD It is Akira's turn to sing karaoke which he does not enjoy.		P	No
UC It is Kumi's turn to sing karaoke which she does not enjoy.		P	No
SC Ai is checking her family's mailbox in the midst of a storm, which she hates.	An invitation from Ai's best friend has arrived in her family's mailbox.	P	Yes
SD Ai is in hospital with severe flu.		P	No
UC Jiro is in hospital with severe flu.		P	No
SC Mikito has gone round to the high school for which he had taken the entrance test; he is there with his best friend.	Mikito's identification number is not listed on the bulletin board at the high school for which he had taken the entrance test.	P	No
SD Mikito is listening to his favorite music in his room.		P	Yes
UC Yuri is listening to her favorite music in her room.		P	No
SC Miki is at home relaxing in a beautiful bathtub.	The bath at Miki's house does not have hot water because of a broken tap.	N	Yes
SD Miki is bathing in a hot spring, which she loves doing, at the country inn where she is staying.		P	Yes
UC Jiro is bathing in a hot spring, which he loves doing, at the country inn where he is staying.		N	No
SC Kiyoshi has gone round to the university for which he had taken the entrance test; his rival, who he hates, is there too.	Kiyoshi's identification number is listed on the bulletin board at the entrance test.	N	No
SD Kiyoshi is swimming, something he struggles with in physical university for which he had taken education class.		P	No
UC Yuka is swimming, something she struggles with in physical education class.		N	No
SC Emi is feeding her pet rabbit, which she loves.	Emi's pet rabbit has lost its appetite.	P	No
SD Emi is on a family trip to Canada, where she had always dreamed of travelling.		N	No
UC Yasuo is on a family trip to Canada, where he had always dreamed of travelling.		N	No
SC Mikito is taking care of his dog while struggling to stay	Mikito's dog gave birth to cute puppies in the middle of the night	N	No
SD Mikito is being seen at the emergency unit of a hospital for a cold that is getting worse.		P	No

Table A1 (Continued)

S1	S2	Cue	Answer
UC Maki is being seen at the emergency unit of a hospital for a cold that is getting worse.		P	No
SC Maki is beside her aunt who is usually very strict.	Maki's aunt is buying a present for her.	N	No
SD Maki is lost, having strayed from her aunt.		N	Yes
UC Hitoshi is lost, having strayed from his aunt.		N	No
SC Tsuyoshi is reading the letters column in a badly printed newspaper.	Tsuyoshi's letter about his experience studying abroad, which he had submitted to the newspaper, has been published.	N	No
SD Tsuyoshi is reluctantly studying for a test, using a study		P	No
UC Chie is reluctantly studying for a test, using a study guide.		N	No
SC Hiroshi is in his room assembling his favorite kind of plastic model.	Hiroshi's plastic model was broken by his cat in his room.	N	Yes
SD Hiroshi is visiting the zoo, which he loves, on a field trip Organized by a neighborhood association.		N	No
UC Yumi is visiting the zoo, which she loves, on a field trip organized by a neighborhood association.		P	No
SC Yuuji has been on a raft sitting in an awkward position holding a fishing pole for long time.	Yuuji's fishing pole caught a big fish for the first time.	P	Yes
SD Yuuji is resting inside a cabin after getting seasick on a ship; he does not like traveling by boat.		N	Yes
UC Yuki is resting inside a cabin after getting seasick on a ship; she does not like traveling by boat.		N	No
SC Yasuo has gone to a very crowded bakery during his lunch break.	They still have Yasuo's favourite sandwich left at the bakery.	N	No
SD Yasuo is feeling sick and is resting in the nurse's office during his lunch break.		N	Yes
UC Kana is feeling sick and is resting in the nurse's office during her lunch break.		P	No
SC Aki is taking care of her little brother who cries constantly and requires a lot of attention.	Aki's cherished 1-year-old brother spoke for the first time.	P	Yes
SD Aki is staying in the mountains to attend a training camp organized by her very strict cram school.		P	No
UC Kenji is staying in the mountains to attend a training camp organized by his very strict cram school.		N	No

References

- Apperly, I. A., Samson, D., Chiavarino, C., Bickerton, W. L., & Humphreys, G. W. (2007). Testing the domain-specificity of a theory of mind deficit in brain-injured patients: Evidence for consistent performance on non-verbal, "reality-unknown" false belief and false photography tasks. *Cognition*, 103, 300–321.
- Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition*, 21, 37–46.
- Berthoz, S., Armony, J. L., Blair, R. J. R., & Dolan, R. J. (2002). An fMRI study of intentional and unintentional (embarrassing) violations of social norms. *Brain*, 125, 1696–1708.
- Blair, R. J. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Conscious Cognition*, 14, 698–718.
- Bower, G. H., & Morrow, D. G. (1990). Mental models in narrative comprehension. *Science*, 247, 44–48.
- Brunet, E., Sarfati, Y., Hardy-Bayle, M. C., & Decety, J. (2000). A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage*, 11, 157–166.
- Buchel, C., & Friston, K. J. (1997). Modulation of connectivity in visual pathways by attention: Cortical interactions evaluated with structural equation modelling and fMRI. *Cerebral Cortex*, 7, 768–778.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron*, 58, 306–324.
- de Vega, M., Leon, I., & Diaz, J. M. (1996). The representation of changing emotions in reading comprehension. *Cognition and Emotion*, 10, 303–321.
- Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology*, 44, 113–126.
- Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to meta-cognition. *The Neuroscientist*, 13, 580–593.
- Dixon, J. A., & Moore, C. F. (1990). The development of perspective-taking: Understanding differences in information and weighting. *Child Development*, 61, 1502–1513.
- Evans, A. C., Kamber, M., Collins, D. L., & MacDonald, D. (1994). An MRI-based probabilistic atlas of neuroanatomy. In S. D. Shorvon (Ed.), *Magnetic resonance scanning and epilepsy* (pp. 263–274). New York: Plenum Press.

- Ferstl, E. C., & von Cramon, D. Y. (2002). What does the frontomedian cortex contribute to language processing: Coherence or theory of mind? *Neuroimage*, 17, 1599–1612.
- Ferstl, E. C., Rinck, M., & von Cramon, D. Y. (2005). Emotional and temporal aspects of situation model processing during text comprehension: An event-related fMRI study. *Journal of Cognitive Neuroscience*, 17, 724–739.
- Ferstl, E. C., & von Cramon, D. Y. (2007). Time, space and emotion: fMRI reveals content-specific activation during text comprehension. *Neuroscience Letters*, 427, 159–164.
- Fletcher, P. C., Frith, C. D., Baker, S. C., Shallice, T., Frackowiak, R. S. J., & Dolan, R. J. (1995). The mind's eye: Precuneus activation in memory-related imagery. *Neuroimage*, 2, 195–200.
- Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., et al. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition*, 57, 109–128.
- Friston, K. J., Holmes, A., Poline, J. B., Price, C. J., & Frith, C. D. (1996). Detecting activations in PET and fMRI: Levels of inference and power. *Neuroimage*, 4, 223–235.
- Friston, K. J., Holmes, A. P., & Worsley, K. J. (1999). How many subjects constitute a study? *Neuroimage*, 10, 1–5.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Friston, K. J., Ashburner, J., Kiebel, S. J., Nichols, T. E., & Penny, W. D. (2007). *Statistical parametric mapping: The analysis of functional brain images*. London: Academic Press.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 358, 459–473.
- Frith, C. D., & Frith, U. (2006). The neural basis of mentalizing. *Neuron*, 50, 531–534.
- Gallagher, H. L., Happe, F., Brunswick, N., Fletcher, P. C., Frith, U., & Frith, C. D. (2000). Reading the mind in cartoons and stories: An fMRI study of 'theory of mind' in verbal and nonverbal tasks. *Neuropsychologia*, 38, 11–21.
- Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*, 15, 870–878.
- Gernsbacher, M. A. (1990). *Language comprehension as structure building*. Hillsdale, NJ: Erlbaum.
- Gernsbacher, M. A., Goldsmith, H. H., & Robertson, R. R. W. (1992). Do readers mentally represent characters' emotional states? *Cognition and Emotion*, 6, 89–111.
- Goel, V., Grafman, J., Sadato, N., & Hallet, M. (1995). Modeling other minds. *Neuroreport*, 6, 1741–1746.
- Happe, F., Ehlers, S., Fletcher, P., Frith, U., Johansson, M., Gillberg, C., et al. (1996). 'Theory of mind' in the brain. Evidence from a PET scan study of Asperger syndrome. *Neuroreport*, 8, 197–201.
- Hynes, C. A., Baird, A. A., & Grafton, S. T. (2006). Differential role of the orbital frontal lobe in emotional versus cognitive perspective-taking. *Neuropsychologia*, 44, 374–383.
- Kiebel, S. J., & Holmes, A. P. (2007). The general linear model. In K. J. Friston, J. Ashburner, S. J. Kiebel, T. Nichols, & W. Penny (Eds.), *Statistical parametric mapping* (pp. 101–125). Boston: Academic Press.
- Kintsch, W. (1998). *Comprehension: A paradigm for cognition*. Cambridge: Cambridge University Press.
- Kobayashi, C., Glover, G. H., & Temple, E. (2007). Children's and adults' neural bases of verbal and nonverbal 'theory of mind'. *Neuropsychologia*, 45, 1522–1532.
- Komeda, H., & Kusumi, T. (2006). The effect of a protagonist's emotional shift on situation model construction. *Memory & Cognition*, 34, 1548–1556.
- Mar, R. A. (2004). The neuropsychology of narrative: Story comprehension, story production and their interrelation. *Neuropsychologia*, 42, 1414–1434.
- Mitchell, J. P. (2008). Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cerebral Cortex*, 18, 262–271.
- Moll, J., de Oliveira-Souza, R., & Eslinger, P. J. (2003). Morals and the human brain: A working model. *Neuroreport*, 14, 299–305.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97–113.
- Pons, F., & Harris, P. L. (2004). Emotion comprehension between 3 and 11 years: Developmental periods and hierarchical organization. *European Journal of Developmental Psychology*, 1, 127–152.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 676–682.
- Rall, J., & Harris, P. L. (2000). In Cinderella's slippers? Story comprehension from the protagonist's point of view. *Developmental Psychology*, 36, 202–208.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective-taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, 4, 546–550.
- Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience*, 16, 988–999.
- Ruffman, T., Garnham, W., Import, A., & Connolly, D. (2001). Does eye gaze indicate implicit knowledge of false belief? Charting transitions in knowledge. *Journal of Experimental Child Psychology*, 80, 201–224.
- Sabbagh, M. A., Moses, L. J., & Shiverick, S. (2006). Executive functioning and preschoolers' understanding of false beliefs, false photographs, and false signs. *Child Development*, 77, 1034–1049.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people: The role of the temporo-parietal junction in "theory of mind". *Neuroimage*, 19, 1835–1842.
- Saxe, R., & Powell, L. J. (2006). It's the thought that counts: Specific brain regions for one component of theory of mind. *Association for Psychological Science*, 17, 692–699.
- Saxe, R., & Wexler, A. (2005). Making sense of another mind: The role of the right temporo-parietal junction. *Neuropsychologia*, 43, 1391–1399.
- Sommer, M., Dohnel, K., Sodian, B., Meinhardt, J., Thoermer, C., & Hajak, G. (2007). Neural correlates of true and false belief reasoning. *Neuroimage*, 35, 1378–1384.
- van Dijk, T. A., & Kintsch, W. (1983). *Strategies in discourse comprehension*. New York: Academic Press.
- Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., et al. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage*, 14, 170–181.
- Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., et al. (2006). Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. *Neuroimage*, 29, 90–98.
- Wellman, H. M., & Bartsch, K. (1988). Young children's reasoning about beliefs. *Cognition*, 30, 239–277.
- Wellman, H. M., Cross, D., & Watson, J. (2001). Meta-analysis of theory-of-mind development: The truth about false belief. *Child Development*, 72, 655–684.
- Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13, 103–128.
- Yazdi, A. A., German, T. P., Defeyter, M. A., & Siegal, M. (2006). Competence and performance in belief-desire reasoning across two cultures: The truth, the whole truth and nothing but the truth about false belief? *Cognition*, 100, 343–368.
- Zwaan, R. A. (1999). Five dimensions of narrative comprehension: The event-indexing model. In S. R. Goldman, A. C. Graesser, & P. van den Broek (Eds.), *Narrative comprehension, causality and coherence: Essays in honor of Tom Trabasso* (pp. 93–110). Mahwah, NJ: Erlbaum.
- Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychology Bulletin*, 123, 162–185.