

# Neural correlates of the judgment of lying: A functional magnetic resonance imaging study

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## ABSTRACT

Lie judgment is an estimation of the speaker's intention to deceive inevitably accompanied by moral judgment. To depict their neural substrates, we conducted a functional magnetic resonance imaging study. Eighteen subjects read short stories and made judgments in three different tasks: a control gender judgment task, a moral judgment task, and a lie judgment task. Compared with the control task, both the moral and lie judgment tasks activated the left temporal lobe, the medial prefrontal cortex, the lateral orbitofrontal cortex extending to the dorsolateral prefrontal cortex, the caudate nucleus, the left temporo-parietal junction (TPJ), and the right cerebellum. Neural activations were greater in the left middle frontal gyrus, the bilateral TPJ, and the right superior temporal sulcus in the lie judgment condition than in the moral judgment condition. In addition, the left TPJ showed greater activation when a protagonist told lies for anti-social rather than pro-social purposes. These data suggest that the judgment of lies is mediated by the neural substrates of moral judgment (conventionality) and those involved in detecting the intent to deceive (intentionality), and that the left TPJ might play a key role in processing both the conventional and the intentional information involved in the judgment of lying.

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## 1. Introduction

The majority of our verbal communication with others consists of exchanges of truthful information. Often, however, we encounter others making statements that do not reflect the true state of affairs. Such untruthful statements take the form of honest mistakes, jokes, ironies, sarcasm, or outright lies, which are used for different communicative purposes. For example, jokes are meant to amuse, sarcasm to belittle, and lies to deceive. Correctly detecting untruthful statements, and deducing the likely purpose that they serve, is of significant importance to successful interpersonal communication.

A lie is defined as a statement that the speaker believes to contain false information, which is communicated in order to instill a false belief into the mind of the hearer (Chisholm and Feehan, 1977). Lying is one of the speech acts that are rule-governed intentional behaviors (Searle, 1969). The motive behind speech acts can vary, but in general they serve an interpersonal function in a social and/or cultural context. Lee (2000) described how a specific speech act can be characterized by five features: factuality, the surface or literal meaning of a statement, the deeper meaning of a statement, the intention of the speaker, and the speaker's belief. Different combinations of these features result in different forms of speech acts, such as accurate and honest statements, honest mistakes, verbal errors, metaphors, irony, and lies (Lee, 2000). In particular, the intention to deceive someone is a crucial component of lying. The unintentional utterance of an untruthful statement is a "slip of the tongue", not a lie.

A speech act contains components that are related to social conventions and intentionality (Lee, 2000). The conventionality component refers to the socially and culturally defined rules of

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conversation that are shared by communities and societies (Grice, 1980; Sweetser, 1987). These rules are hierarchically organized. At the top of the hierarchy is a general cooperative rule: a meta-maxim, which governs all communicative acts in all settings, stating that the goal of social communication is to “try to help, not to harm”. Below this meta-maxim lie two sets of conversational rules that guide verbal communication in either informal or formal settings. In an informal setting, we are expected to follow Grice’s maxim of conversation (1980). The maxim of quality expects the speaker to be truthful and to avoid falsehood, the maxim of quantity requires the speaker to provide as much information as necessary, the maxim of relation dictates that the speaker must convey relevant information, and the maxim of manner asks the speaker to avoid ambiguity and obscurity. In a polite or formal setting, maintaining and enhancing amicable social relations is of most importance. In this setting, interlocutors are expected to follow rules of politeness. Thus, at least in formal settings, adhering to convention is important, forming one basis on which a statement can be the target of the moral evaluation.

The meaning and function of a speech act is mediated and determined not only by the literal meaning of a sentence, but also by the intentional states of the speaker. Lying is a communicative act wherein there is a discrepancy between what the speaker intends the listener to believe, and what is believed by the speaker. This discrepancy is referred to as the “intent to deceive” (Chisholm and Feehan, 1977). Unlike many other forms of speech acts (e.g., an honest mistake or metaphor), lying often violates the most fundamental conventions of communication such as the general cooperative meta-maxim and the maxim of quality. Because of these violations, lying often evokes strong emotive reactions from communicational partners. Lying is therefore a morally charged and value-laden speech act (Lee, 2000).

In the field of philosophy, the nature of lying and its moral implications have long been debated (Bok, 1978). Any statement that meets the abovementioned conceptual definition is a lie, regardless of the context in which it was made or the reason for making it. According to this view, a gift-receiver who, in order to be polite, claims to like a gift that he or she really dislikes is lying, even though the purpose of the miscommunication is pro-social in nature. Theorists who hold this view also tend to believe that the process of judging whether a lie has a positive or negative moral value is independent of perceiving the statement as a fact or as a lie. Determining whether a statement is a lie involves making a conceptual judgment, whereas determining a statement’s moral valence involves making a value judgment, related to possible breaches in moral and/or social norms. By contrast, other theorists (e.g., Sweetser, 1987) believe that the judgment of whether a verbal statement is a lie is intrinsically a value judgment. It is not enough to base the judgment on whether an untruthful statement meets the abovementioned conceptual definition of a lie; whether an untruthful statement is a lie also depends on whether it serves a pro-social or anti-social purpose (i.e., whether the statement serves to help or to harm the listener). When the statement serves to help the listener, the statement (though untruthful and intended to deceive the listener) might not be a lie. Thus, according to this second view, determining whether a statement is a lie is in and of itself a value judgment.

Morality depends on a set of rules designed to regulate interpersonal behavior and to allow people to live together in harmony (Hogan, 1973). It requires the internalization of social norms (Hawley, 2003), which are standards of behavior that are based on widely shared beliefs about how individual group members should behave in a given situation (Fehr and Fischbacher, 2004). Evidence has suggested that both reasoning and affective response have important roles to play in moral processing. Moral

reasoning has historically been given prominence in theories that account for the processes of moral judgment; however, emotion is increasingly recognized as playing a key role (Greene and Haidt, 2002). Greene et al. (2001) showed that reading “personal” moral violations, which were those likely to cause serious bodily harm to a particular person, activated the medial prefrontal cortex, posterior cingulate cortex, and angular gyrus bilaterally more strongly than “impersonal” moral violations in which no serious harm was likely to occur. They attributed the activation pattern to the emotional component of the task, and concluded that affect plays an important role in personal moral judgment.

The ability to infer other people’s mental state including thoughts, feelings, and intentions, is commonly referred to as mentalizing (Frith and Frith, 2003, 2006). In predicting another individuals’ behavior through mentalizing, it is implicitly assumed that the behavior of others is determined by their desires, attitudes, and beliefs. These are not states of the world, but rather states of the mind. This is important because, in everyday life, beliefs rather than reality determine how people behave (Frith and Frith, 2003). A typical example of this is the false-belief task (Wimmer and Perner, 1983).

Previous research on the development of the concept of lying and its moral implication suggests that these two components are developed sequentially (Lee, 2000). Understanding of the concept of lying, particularly of its intentionality component, emerges as early as 3 years of age. At around 4 years of age, children reliably pass the false-belief task. Children begin to understand the moral implications of lying during the preschool years. At 6 years of age, children begin to treat the intention of the speaker as an important factor in making moral judgments. Social conventions more gradually become an important factor in children’s moral judgment of lying. Hence, the concept of a “lie” matures throughout childhood to become a social-cognitive construct that includes aspects of both intentionality and conventionality (Lee, 2000). However, it is not known how these two components interact during judgment of lying, or the neural substrates associated with these processes.

Lying is characterized by the violation of the conventions of communication (Lee, 2000). These conventions are based on the social norms that prescribe certain actions and proscribe others (Bond et al., 1992). We therefore hypothesized that detecting the presence of a lie is intimately related to the monitoring of social norms, and hence the moral framework, in which a statement is evaluated. Gibbs (1999) described two forms of knowledge that are accessed during normal language understanding: primary pragmatic information that includes widely shared, deep, and default background knowledge, which provides an interpretation of what is said; and secondary pragmatic information that relates to what is inferred or implied within the communication. The latter depends on specific, local contextual factors that provide an interpretation of the implication of the speaker’s words. Social norms, which comprise one type of primary pragmatic information, are monitored to elucidate what is implied by the speaker’s utterance (secondary pragmatic information), and from this, an “intent to deceive” can be detected. We therefore hypothesized that recognition of a lie is simultaneous with evaluation of the deceit within a framework of accepted social norms. The same processing that monitors relevant social norms is necessary for determining the moral value of the lie; we therefore reasoned that moral judgments would share, and lie perception would share, neural correlates related to detecting conventionality.

Based on this hypothesis, we conducted an event-related functional magnetic resonance imaging (fMRI) study that included social norm judgment (M), lie detection (L), and the control of gender discrimination (C). Participants read a short scenario

describing a protagonist's behavior, which could be either morally good or bad. This was followed by one of three possible task cues: first, a control gender judgment task (C) that required the subjects to determine whether the protagonist was a boy or a girl; second, a social norm judgment task (M) in which the participants indicated whether the protagonist's action was morally good or bad; and third, a lie judgment task (L), in which participants judged the protagonist's response to be truthful or false, based on the narrative of the story.

We anticipated that the neural substrates of the conventionality component of lying comprehension would correspond to those of social norm judgment, and that the brain regions that were active in association with the intentionality components would be similar to those that have been previously linked to mentalizing (Frith and Frith, 2006). Furthermore, assuming that lie comprehension involves an interaction between processing related to perceived conventionality and intentionality, we compared the “modesty lie” in the pro-social context with the anti-social lie that follows an anti-social deed. Based on behavioral observations (Lee, 2000), we hypothesized that the neural substrates responsible for detecting an “intent to deceive” would be modulated by the pro-social or anti-social characteristics of the lie.

## 2. Subjects and methods

### 2.1. Subjects

Eighteen healthy subjects participated in this study (10 females and eight males, with a mean age of  $25.3 \pm 4.2$  years). All subjects were native Japanese speakers, college-educated, and right-handed according to the Edinburgh handedness inventory (Oldfield, 1971). None of the subjects had a history of neurological or psychiatric illness. The protocol was approved by the National Institute for Physiological Sciences, Japan, and all subjects gave their written informed consent.

### 2.2. Stimulus preparation

We prepared 28 stories, four of which were used for the pre-fMRI training, while the remaining 24 were used in the fMRI experiment. One half of the stories described a protagonist performing a good deed (good deed stories), and the other half described a protagonist performing a bad deed that transgressed social norms (bad deed stories). Each story consisted of three sentences. The first and second sentences described the behavior of the protagonist, and in the last sentence another person asked the

protagonist about his/her deed. The length of the first sentence was  $42 \pm 4.7$  characters, the second was  $45 \pm 5.3$  characters long, and the third was  $30 \pm 2.9$  characters long. The length of the sentences was matched between the good and the bad deed stories. Examples of the stories used in this experiment are listed in Table 1.

### 2.3. Experimental design and task procedure

We used an event-related design which consisted of three types of event condition: moral judgment trials (M), lie judgment trials (L), and the control gender judgment trials (C). Stimulus presentation and response collection was performed using Presentation 0.50 (Neurobehavioral Systems, Albany, CA) implemented on a personal computer (Dimension 8200; Dell Computer, Round Rock, TX). Visual stimuli were projected onto a translucent screen, which subjects viewed through a mirror attached to the head coil of the MRI scanner. In all trials, the story was initially presented visually (visual angle =  $\sim 6.6 \times 1.5^\circ$ ) in the center of the black screen sentence-by-sentence, and each sentence was shown for 5 s.

After a 12-s fixation period, a visual cue was presented for 5 s instead of a white cross-hair. For the moral judgment trials, the visual cue was either “I”, indicating “Is the protagonist's behavior morally bad?”, or “M”, indicating “Is the protagonist's behavior morally good?” Subjects were asked to push a button with their right index finger to answer “yes” to the cued question, or with their right middle finger to answer “no”.

For the lie judgment trials, the visual cue was “Y”, which meant that the protagonist answered “yes” when asked by another character in the story whether he/she had done a particular deed; “N” meant that the protagonist answered “No” to the question. Subjects were asked to judge whether the protagonist told the truth or a lie. Subjects pushed a button with their right index finger if the protagonist told the truth or with their right middle finger if the protagonist lied. The subjects' responses were deemed correct if they pushed the button with their right index finger when the protagonist made a true statement or with their right middle finger when the protagonist made a false statement.

For the gender judgment trials the visual cue was “G”, indicating “Is the protagonist a girl?”, or “B”, indicating “Is the protagonist a boy?” Subjects were asked to push a button with their right index finger to answer “yes” and with their right middle finger to answer “no”.

After a fixation period of 12 s, a red cross-hair was presented for 1 s to signal that the subjects should respond. This was followed by another fixation period for 12 s. The inter-trial interval (ITI) was 57 s. The 24 stories were presented once per session for a total of

**Table 1**  
Four kinds of stories used in the fMRI experiment.

	Cues		
	Moral	Lie (when protagonist says Yes)	Control gender (*)
Hiromi used her favorite sketchbook in an art class. She cut a piece of the sketchbook and gave it to her friend, as the friend forgot to bring on a sketchbook by mistake. The friend said to her: “Is it your favorite one?”	Good	Truth	Girl
Takashi went to a park with his mother and was playing on his favorite swing. Although he was still on the swing, he told his mother he was tired of the swing and wanted to move to the sandbox, just as a younger child came to the swing. His mother said to him: “Are you really tired of the swing?”	Good	Lie	Boy
Hiroko damaged a borrowed book by mistake. She thought that her mistake would not be noticed if she did not tell anyone, and she returned it to the library shelf as it was. A librarian said to her later: “Did you damage this book?”	Bad	Truth	Girl
Noboru's mother asked him to clean the rooms leading out of the house. However, he made his younger brother clean the rooms, as he wanted to watch television. His mother said to him later: “Did you clean the rooms?”	Bad	Lie	Boy

(\*) Hiromi and Hiroko are girl's names, and Takashi and Noboru are boy's names. The cues were counterbalanced, and the protagonists of one half of the sentences were boys and the others were girls.

three sessions for each of the three task conditions, giving a total of 72 events. The 24 trials (eight moral, eight lie, and eight gender judgment conditions) were presented in a fixed order in each fMRI session. Each session contained all three task conditions so that subjects were not able to anticipate a given task condition until a cue was presented. The order of the sessions was randomized for each subject. The instructions and all 24 stories were presented in Japanese (Fig. 1).

#### 2.4. MRI acquisition

A time-course series of 461 volumes was acquired using T2\*-weighted gradient-echo echo-planar imaging (EPI) sequences with a 3.0 T MR imager (Allegra, Siemens, Erlangen, Germany). Each volume consisted of 44 slices, with a slice thickness of 3.0 mm and a 0.5-mm gap, which included the entire cerebral and cerebellar cortices. Oblique scanning was used to exclude the eyeballs from the images. The time interval (TR) between two successive acquisitions of the same slice was 3000 ms, and the echo time (TE) was 30 ms. The flip angle (FA) was 85°. The field of view (FOV) was 192 mm. The in-plan matrix size was 64 × 64 pixels with a pixel dimension of 3.0 mm × 3.0 mm. Tight, but comfortable, foam padding was placed around each subject's head to minimize head movement. In addition, a T1-weighted three-dimensional magnetization-prepared rapid-acquisition gradient-echo (MPRAGE) image (TR = 2500 ms, TE = 4.38 ms, FA = 8°, FOV = 230 mm, matrix size = 256 mm × 256 mm, slice thickness = 1 mm, voxel dimension = 0.9 mm × 0.9 mm × 1.0 mm, a total of 192 transaxial images) was obtained for each subject, in order to acquire a detailed structural whole-brain image.

#### 2.5. Imaging data analysis

##### 2.5.1. Preprocessing

The first three and last two volumes of each session were discarded, and the remaining 456 volumes per session (1368 volumes per subject) were used for the analyses. The data were analyzed using statistical parametric mapping (SPM2; Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks, Sherborn, MA) (Friston et al., 1995a,b). After realignment, the parameters for affine and non-linear transformation in a template EPI image that was already fitted to a standard stereotaxic space (Montreal Neurological Institute [MNI] template; Evans et al., 1994) were estimated based on the first fMRI image using least-squares means (Friston et al., 1995a). The parameters were applied to all the fMRI images. The anatomically normalized

fMRI images were filtered using a Gaussian kernel of 8 mm (full width at half-maximum) in the x, y, and z-axes.

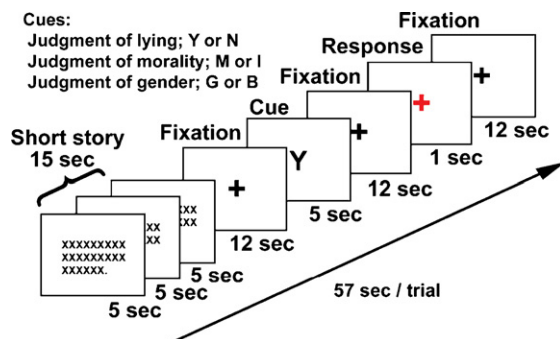
##### 2.5.2. Statistical analysis

Statistical analysis was conducted at two levels. First, individual task-related activation was evaluated. Second, to make inferences at a population level, individual data were summarized into a random effect model (Friston et al., 1999).

**2.5.2.1. Individual analysis.** The signal time course of each subject with 1368 time points was modeled with high-pass filtering (128 s), session effects, and five regressors convolved with a hemodynamic response function: a sentence period (S) with 15 s duration; moral (M), lie (L), and gender judgment periods (C) with 5 s duration; and a response (R) period with zero duration. Of these five conditions, we focused on M, L, and C. The proportion of no response (i.e., reaction time > 1 s) over all trials was relatively small:  $3.0 \pm 1.6\%$  for the lie condition,  $2.8 \pm 1.5\%$  for the moral condition, and  $3.9 \pm 1.6$  for the control condition. As our main interest was cue-related activation, rather than the response itself, fMRI image data from both correct and incorrect trials were included in the analysis.

To test hypotheses about regionally specific condition effects, the estimates for each condition were compared by means of the linear contrasts (Table 2). The resulting set of voxel values for each comparison constituted a statistical parametric map (SPM) of the  $t$  statistic (SPM{ $t$ }). The SPM{ $t$ } was transformed to normal distribution units [SPM{ $Z$ )]. The statistical threshold was set at  $P < 0.05$  corrected for multiple comparisons at the cluster level, with a threshold of  $Z > 3.09$  (Friston et al., 1996).

**2.5.2.2. Group analysis with the random effect model.** The weighted sum of the parameter estimates in the individual analyses constituted “contrast” images, which were used for the group analysis (Friston et al., 1999). The contrast images obtained by the individual analyses represent the normalized task-related changes of the MR signal for each subject. A total of 18 subjects with seven different conditions (M, L, C, M–C, L–C, M–L, and L–M) were used for the analysis. The resulting set of voxel values for each contrast constituted an SPM{ $t$ }. The SPM{ $t$ } was transformed into normal distribution units (SPM{ $Z$ }). As in the individual analysis, the statistical threshold was set at  $P < 0.05$  corrected for multiple comparisons at the cluster level, with a threshold of  $Z > 3.09$  (Friston et al., 1996). One-sample  $t$ -tests for M–C and M–L were performed within the regions that were significantly activated in M, and those for L–C, and L–M were performed within the regions activated by L. This “masking” procedure confirms that the depicted areas respond positively compared with the implicit “baseline” condition (Table 2). Finally, we evaluated the effect of the “morality” of the preceding deed on the lie detection-related activities. First, the L condition was subdivided into two categories: lies that followed a good deed (Lg) and lies that followed a bad deed (Lb). The Lg category contained those stories wherein the



**Fig. 1.** Task design. Initially, a short story was presented for 15 s, divided into three 5-s parts. After a fixation period of 12 s, a visual cue was presented for 5 s. After another 12-s fixation period, a red cross-hair was presented for 1 s to cue subjects to respond by pushing a button with their right index or middle finger. The initial fixation period then followed for 12 s. The ITI was 57 s.

**Table 2**  
Predefined contrasts.

	S	Cue			Response
		Control	Lie	Moral	
L	0	0	1	0	0
M	0	0	0	1	0
L–C	0	–1	1	0	0
M–C	0	–1	0	1	0
L–M	0	0	1	–1	0
M–L	0	0	–1	1	0

protagonist might lie about their good deed (i.e., a modesty lie or a false statement to show humility, which is highly valued by Eastern Asian cultures; Lee, 2000). The Lb category consisted of those stories in which the protagonist might lie about their bad deed in order to conceal a transgression of social norms (i.e., an anti-social lie). Differential neural activations to these two forms of lying were investigated in all the regions that were significantly activated in the (L–M) contrast.

### 3. Results

#### 3.1. Behavioral performance

The percentages of correct responses across all subjects for the judgment of L, M, and C (excluding reaction time >1 s) were  $84.9 \pm 3.0\%$ ,  $91.3 \pm 2.5\%$ , and  $90.7 \pm 2.9\%$  (mean  $\pm$  S.E.M.), respectively. Results from a repeated-measures one-way ANOVA of

**Table 3**

Task-related activation. (\*) corrected for multiple comparisons at cluster level.

Cluster level		x (mm)	y (mm)	z (mm)	Z value	Location		
P*	Size					Side	Area	BA
L–C masked with L condition								
<0.001	2525	–6	46	40	6.25	Lt	prMFC	8
<0.001	3833	–52	18	14	5.42	Lt	GFi	44
		–48	28	–10	5.24	Lt	GFi	47
		–48	18	38	5.14	Lt	DLPFC	9
		–54	4	–30	4.29	Lt	GTm	20
<0.001	1082	52	18	46	4.58	Rt	GFm	8
		60	30	16	4.19	Rt	GFi	45
		52	30	18	4.04	Rt	DLPFC	46
0.032	166	44	30	–12	3.76	Rt	GFi	47
<0.001	2424	–50	–60	46	5.47	Lt	LPi	40
		–58	–52	26	5.29	Lt	TPJ	39/40
0.045	148	–4	–78	40	3.76	Lt	PCu	7
0.007	250	50	–54	28	4.3	Rt	TPJ	39
<0.001	555	–56	–42	0	4.07	Lt	GTm	21
0.002	316	52	–30	–10	4.05	Rt	GTm	21
0.042	151	46	6	–44	4.57	Rt	GTm	20
0.044	149	–28	26	0	4.33	Lt	insula	
0.002	337	–10	8	14	4.11	Lt	NC	
		–16	4	0	3.61	Lt	GP	
<0.001	696	10	0	18	4.98	Rt	NC	
		16	0	0	4.02	Rt	GP	
		6	–18	–4	3.9	Rt	NR	
<0.001	1200	28	–82	–40	5.05	Rt	Cerebellum	
M–C masked with M condition								
<0.001	1292	–8	44	46	5.2	Lt	prMFC	8
<0.001	2014	–48	16	–34	4.99	Lt	temporal pole	38
		–50	16	16	4.9	Lt	GFi	44
		–52	26	–10	4.77	Lt	GFi	47
0.019	193	–46	6	50	3.6	Lt	PMd	6
		–36	24	44	3.52	Lt	DLPFC	8
0.008	242	–56	–42	0	4.25	Lt	GTm	21
0.019	193	32	–86	–36	3.98	Rt	Cerebellum	
0.045	149	14	8	0	3.65	Rt	NC	
L–M masked with L condition								
<0.001	749	–48	–58	40	4.59	Lt	LPi	40
		–50	–54	24	4.12	Lt	TPJ	39/40
		–38	–58	20	3.47	Lt	GTs	22
0.006	230	54	–52	28	4.37	Rt	TPJ	39
		50	–52	40	3.51	Rt	LPi	40
0.002	302	–46	26	44	4.51	Lt	DLPFC	8
0.005	242	54	–28	–12	4.42	Rt	GTm	21
M–L masked with M condition								
No suprathreshold clusters								

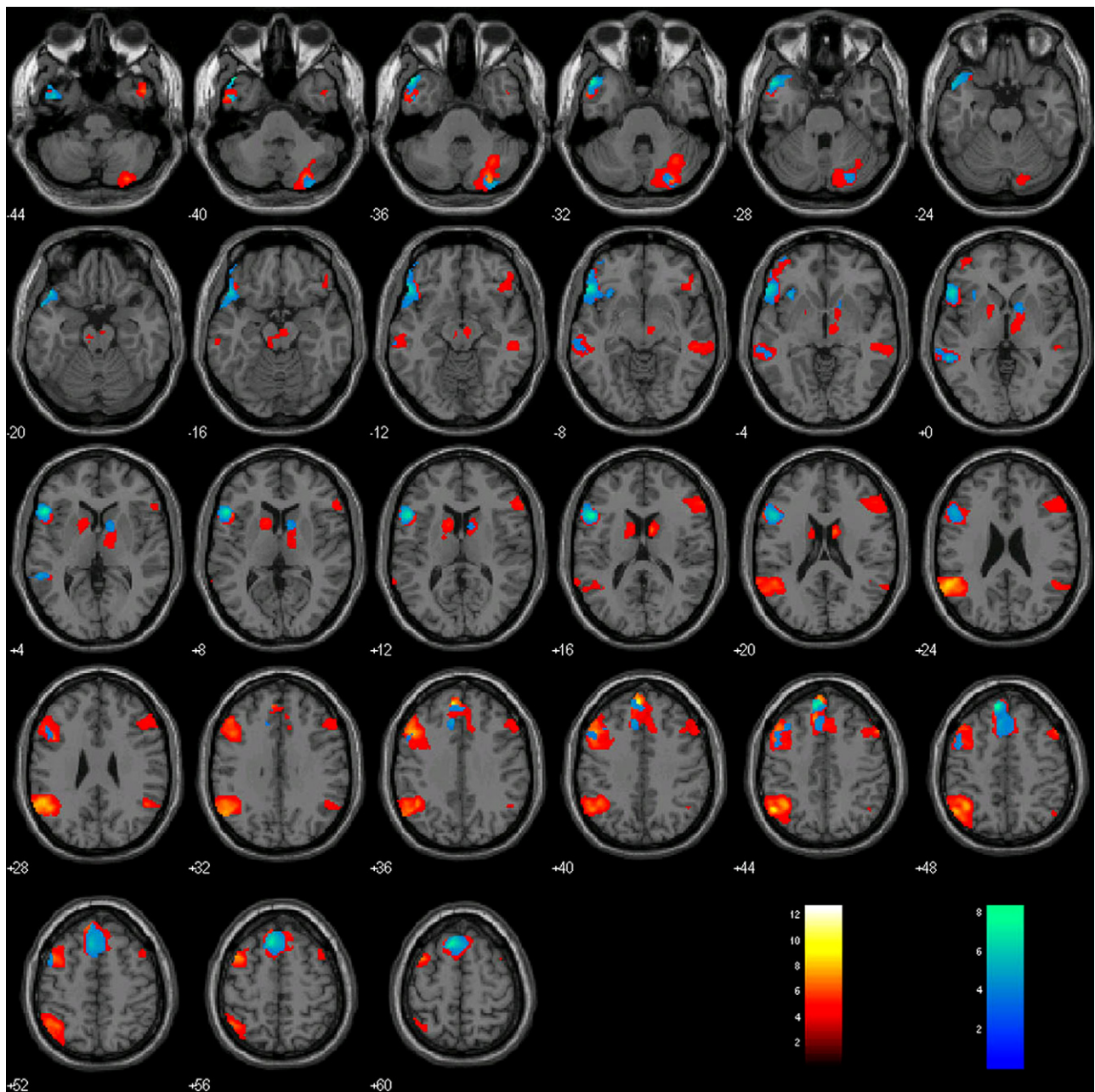
Coordinates (x, y, z) are of the voxel of local maximal significance in each brain region according to the Montreal Neurological Institute template, based on the stereotaxic coordinate system of Talairach and Tournoux (1988). DLPFC, dorsolateral prefrontal cortex; GFd, medial frontal gyrus; GFi, inferior frontal gyrus; GFm, middle frontal gyrus; GP, globus pallidus; Gsm, supramarginal gyrus; GTm, middle temporal gyrus; GTs, superior temporal gyrus; LPi, inferior parietal lobule; NC, caudate nucleus; NR, red nucleus; PCu, precuneus; PMd, dorsal premotor cortex; prMFC, posterior rostral medial frontal cortex; TPJ, temporo-parietal junction.



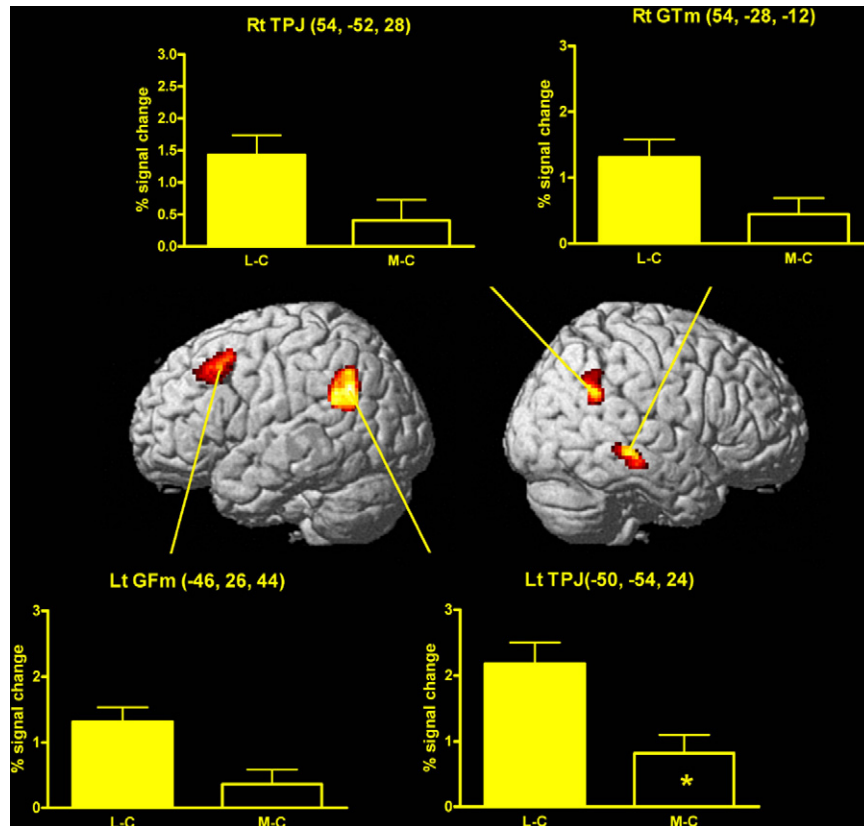
accuracy revealed that there were significant differences across the task conditions ( $F(2,34) = 8.82$ ,  $P < 0.01$ ). *Post hoc* pair-wise comparisons with a Bonferroni correction revealed that the accuracy in the lie condition was significantly lower than those in the moral condition ( $P < 0.01$ ) and the control condition ( $P < 0.01$ ), whereas there was no significant difference between C and M ( $P > 0.9$ ). Subjects did not differ in the accuracy of their responses to the anti-social and pro-social lie judgment trials ( $86.0 \pm 5.0\%$  for Lg and  $81.2 \pm 3.2\%$  for Lb;  $P = 0.27$ , paired *t*-test). There were no significant differences in reaction times (excluding both reaction time  $> 1$  s and incorrect trials) across the tasks ( $604 \pm 28$  ms for L,  $603 \pm 31$  ms for M, and  $606 \pm 27$  ms for C, mean  $\pm$  S.E.M.;  $F(2,34) = 0.054$ ,  $P = 0.948$ ).

### 3.2. Task-related activation patterns

Comparison of the lie judgment task with the control condition (L–C; Table 3 and Fig. 2) revealed that L significantly activated the following areas relative to the control: the bilateral inferior frontal gyri (GFi) extending to the dorsolateral prefrontal cortex (DLPFC), the temporal pole, the TPJ, the globus pallidus, and the caudate nucleus; the left posterior rostral medial frontal cortex (prMFC, defined by Amodio and Frith, 2006), the insula, the inferior parietal lobule (LPI), and the precuneus (PCu); and the right red nucleus and the cerebellum. Comparison of the morality judgment condition with the control condition (M–C) revealed activations

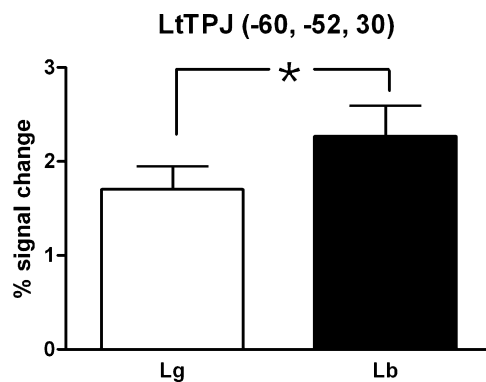


**Fig. 2.** Brain regions active during the judgment of L compared with the C task (red), and during the judgment of M compared with the C task (blue). Activated foci are shown as pseudocolor SPM{Z} statistics superimposed on a high-resolution anatomical MRI in 27 contiguous transaxial slices with a 4-mm interval, extending from the MNI coordinates  $z = -44$  (top left) to  $z = +60$  (bottom). The statistical threshold was set at  $Z > 3.09$  and  $P < 0.05$ , corrected for multiple comparisons at the cluster level. The left side of the brain corresponds to the left side of the image.



**Fig. 3.** SPM of the average neural activity within the group during the judgment of lying compared with the activity during the judgment of morality, within the significantly activated areas during the judgment of lying. The statistical threshold for all maps was set to an uncorrected  $P < 0.001$  at the voxel level and to  $P < 0.05$  with a correction for multiple comparisons at the cluster level. The activities were superimposed on surface-rendered high-resolution MRI images unrelated to the subjects of the present study. The upper left and right panels and the bottom left and right panels indicate the average percentage signal change from the control condition for the judgment of lying (L-C) and the judgment of morality (M-C) in the right LPI (54, -52, 28) corresponding to the TPJ and GTm (54, -28, -12), and the left GFm (-46, 26, 44) and LPI corresponding to the TPJ (-50, -54, 24), respectively. The percentage signal change was calculated individually at the peak voxel for each cluster. These data represent the mean  $\pm$  S.E.M. of 18 subjects. (\*) Significant activation ( $t = 3.0$ ,  $P = 0.008$ , one-sample  $t$ -test).

in the following areas: the left GFi extending to the DLPFC, the temporal pole (Brodmann Area [BA] 38), the GTm (BA21), the prMFC (BA 8/9), the LPI, and the dorsal premotor cortex (PMd); and the right DLPFC, the caudate nucleus, and the cerebellum (Table 3 and Fig. 2). These areas were commonly activated by both contrasts (L-C) and (M-C), because the activations observed in response to the morality judgment task all lay within the regions activated in the lie judgment task (Fig. 2).



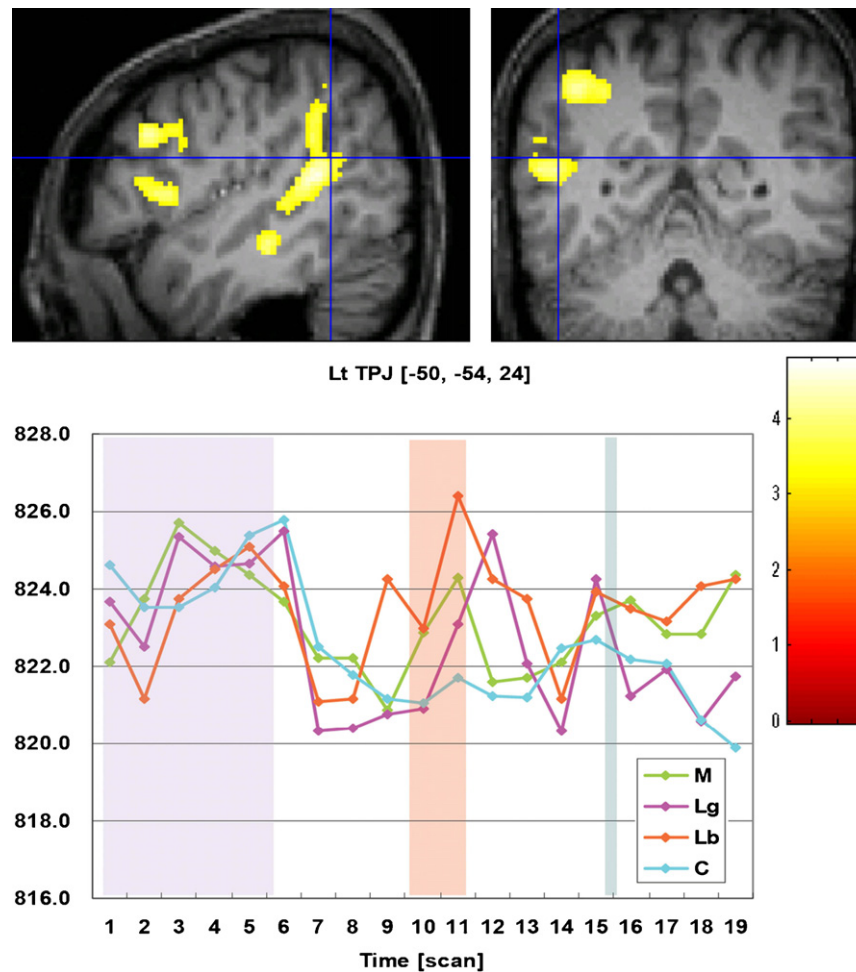
**Fig. 4.** Context effect of the lie detection-related blood-oxygen-level dependent (BOLD) responses in the left TPJ. Lg is the judgment based on lying about one's good deed (a modesty lie), and Lb is that based on lying to conceal a transgression of social norms (an anti-social lie).

Compared with moral judgments, lie judgments were associated with more prominent activation in the bilateral LPI extending to the TPJ and the GTs, the left DLPFC, and the right GTm close to the superior temporal sulcus (STS; Table 3 and Fig. 3). The left TPJ showed activation during both the L-M and the M-C contrasts. This implies that the left TPJ is involved in detecting both intentionality (as shown by L-M) and conventionality (as shown by M-C). Furthermore, the left TPJ (-60, -52, 30) showed more prominent activation during the judgment of anti-social lies than during the judgment of modesty lies ( $P = 0.039$ , two-tailed paired  $t$ -test; Fig. 4), suggesting that an interaction between these two processes might occur here. Typical individual data are shown in Fig. 5.

#### 4. Discussion

##### 4.1. Cognitive components and tasks

The present study examined the behavioral and neural correlates of judgments of lying in a narrative context. A major finding was that the conventionality component shared the neural substrates with moral judgments, and the intentionality component was lying specific, both recruiting the mentalizing network. These findings suggest that a valuation based on social norms is a cognitive function common to both lying comprehension and moral judgment, and inferring that “intent to deceive” is lying comprehension-specific. For example: *Hiroko damaged a borrowed*



**Fig. 5.** Individual analysis of the lying judgment in contrast to moral judgment (L–M;  $P < 0.001$  uncorrected) superimposed on the high-resolution MRI of the subject (YM), of the sagittal and coronal sections that cross at  $(-50, -54, 24)$  (top). The time course of the averaged MR signal (arbitrary unit) plotted against the peri-stimulus time (scan). Purple shading indicates the presentation of the short story, orange shading indicates cue presentation, and gray shading indicates the response period. In the temporo-parietal junction at  $(-50, -54, 24)$  the response to the bad lie cue (Lb) was more prominent than that to the good lie cue (Lg;  $Z = 2.41$ ,  $P = 0.008$ ).

book by mistake. She thought that her mistake would not be noticed if she did not tell anyone, and she returned it to the library shelf as it was. A librarian said to her later: “Did you damage this book?” This scenario provides the information that Hiroko damaged a borrowed book, and that she thought that her mistake would not be noticed if she did not tell anyone. In the M condition, the cue prompts the moral judgment of what has been done by the protagonist, which might require reference to a social norm. In the L condition, if the protagonist replies with a “No”, it is indicated that the speaker (Hiroko) intends the listener (a librarian) to believe something that the speaker knows to be false. The M condition contains no information about whether the speaker tries to deceive the librarian or not (no reply is made) and therefore the areas activated by the L–M contrast should include the neural representation of inferring “intent to deceive”. As there was no moral judgment-specific activation (by means of the M–L contrast), the common cognitive process is moral judgment. This is consistent with the idea that the judgment of whether a verbal statement is a lie is intrinsically a value judgment (e.g., Sweetser, 1987).

It should be noted that the lie-judgment task used in the present study differs greatly from many real-life situations, where often one must perceive intent to deceive in the absence of any direct evidence. Interpersonal deception is composed of multiple

mental operations (Sip et al., 2007). One must infer whether a person is telling a truth from indirect information, by assessing the individual’s personality and background, as well as his/her manner (e.g., facial expressions and tone of voice). Liars might manage the impression they create to generate a reputation for being trustworthy, allowing for greater success in deceptive actions. However, the main purpose of the present study was to prove the hypothesis that the judgment of lies is mediated by the neural substrates of moral judgment and those involved in detecting the intent to deceive. Thus, explicit information for inferring the intent to deceive was provided.

#### 4.2. Behavioral performance

There was no difference in accuracy between subjects’ responses to the gender judgment trials and the moral judgment trials, whereas the response accuracy was significantly lower during the lie judgment task. This difference was probably due to the additional processing required in making decisions in the lie judgment task (i.e., judgment of intention to deceive). In both the gender judgment and moral judgment tasks, subjects could perform the task using only the existing information in the story (i.e., basing their judgments on the obviously male/female name or the explicitly described behavior of the protagonist). In the lie



judgment trials, subjects needed to base their judgments on the behavior of the protagonist in the context of their personal definition of lying. It should be noted, however, that the overall accuracy was high for both the lie and moral judgment trials. Also, the subjects did not differ in their responses to the lie judgment trials in the context of anti-social and pro-social deeds.

#### 4.3. Neural correlates of moral judgments

##### 4.3.1. Lack of moral judgment-specific activation

Compared with the control trials, the moral decision task activated the left temporal pole, the middle temporal gyrus, the medial prefrontal cortex, the left lateral orbitofrontal cortex extending to the dorsolateral prefrontal cortex, the caudate nucleus, and the right cerebellum. These neural correlates associated with making moral judgments all lay within the regions activated by lying judgments. In no region were the activations in response to the moral judgment task greater than those in response to the lie judgment tasks. This suggests that judgments about lies and morality share common underlying neural processes, consistent with our hypothesis that both tasks share information processing related to the monitoring of social norms. The lack of moral judgment-specific activation is consistent with the idea that the judgment of whether a verbal statement is a lie is intrinsically a value judgment (e.g., Sweetser, 1987). The judgment of whether an untruthful statement is a lie automatically involves the determination of whether the statement meets certain social norms (i.e., the conventionality component).

##### 4.3.2. Activation common to lie judgment and moral judgment

The temporal pole is a potential site for multi-sensory convergence, and also has limbic inputs (Moran et al., 1987). The left temporal pole is also associated with linguistic processes (Bottini et al., 1994; Fletcher et al., 1995; Maguire et al., 1999; Vandenberghe et al., 1996, 2002) and with autobiographical memory retrieval (Fink et al., 1996; Maguire and Mummery, 1999; Maguire et al., 2000). Based on these findings, Frith and Frith (2003) speculated that the left temporal pole is concerned with generating, on the basis of past experience, a wider semantic and emotional context or script (Schank and Abelson, 1977) for the material currently being processed. Scripts are built up through experience, and record the particular goals and activities that take place in a specific setting at a certain time. Scripts provide a useful framework within which reasoning for moral decisions can be applied. Considering the left middle temporal gyrus/STS area is engaged in semantic integration at the sentence level (Noppeney et al., 2005; Vandenberghe et al., 2002), the left temporal areas might partly represent social norms.

The posterior rostral medial frontal cortex (prMFC, Amodio and Frith, 2006; Steele and Lawrie, 2004) has been associated with cognitive tasks. The prMFC is known to be activated by inductive reasoning rather than deductive reasoning (Goel et al., 1997) ((−16, 32, 36) in Talairach coordinates). Induction is typically viewed as a form of hypothesis generation and testing that requires searching a large database and determining which pieces of information are relevant, and how they are to be mapped onto the present situation. Goel et al. (1997) suggested that the prMFC activation might be associated with inductive reasoning involving generalization and abstraction over world knowledge. In line with this view, the prMFC is activated by different kinds of tasks, such as linguistic coherence judgment (Ferstl and von Cramon, 2002) (−6, 26, 35), and pragmatic comprehension (Uchiyama et al., 2006) (−6, 44, 42). The prMFC activation in the present study is probably related to the inductive reasoning involved in recognizing the moral value of the action of the protagonist within the framework of social norms.

The left GFi was activated during the moral judgment trials relative to the gender discrimination task. The left GFi, particularly BA 47, might serve as a semantic executive system (Dapretto and Bookheimer, 1999; Gabrieli et al., 1996; Kapur et al., 1994; Wagner et al., 1997), which consists of semantic retrieval, selection, and evaluation. In the M condition, the semantic processing of the story sentences might be evaluated in the context of social norms. By contrast, in the C condition, gender discrimination can be conducted without such evaluation. Hence, the more prominent activation during the M condition than during the C condition might represent semantic evaluation with reference to social norms.

##### 4.3.3. Neural correlates specific to judgments of lying

In the present study, the lie judgment trials were cued by a signal that indicated the response of the protagonist. As the moral judgment task was cued by a different signal, which did not contain information about the protagonist's response, lie judgment-related processing did not occur during the moral judgment condition. Therefore, we expected that the L–M comparison would reveal the neural substrates involved in processing information specific to lying (i.e., determining whether or not the protagonist intended to deceive). Detecting this intention to deceive activated the bilateral TPJ, the right GTm close to the STS, and the left DLPFC. Given the lower response accuracy in the lie judgment task than in the moral judgment task, it is possible that stronger brain activation associated with the lie judgment task could be due to the relative task difficulty. However, the only region commonly activated by the M task and the L–M contrast was the left TPJ, supporting the hypothesis that activity in the GFm and the right GTm marks neural processing distinct from lie detection as compared with moral judgment. Furthermore, the common TPJ activation is unlikely to be explained by differences in task difficulty, given that the left TPJ showed greater activation when a protagonist told lies for anti-social rather than pro-social purposes, while the accuracy of their responses to the anti-social and pro-social lie judgment trials were similar. Rather, the TPJ seems to have a special role in certain aspects of perspective-taking and reasoning in these tasks.

The TPJ is one of the association areas where various kinds of information converge (Matsushashi et al., 2004) and are processed to create a central representation of one's own body (Blanke, 2004), or a shifting perspective of the self (Corradi-Dell'Acqua et al., 2008). This area might be related to taking another person's spatial perspective, because abnormal activity in this region is associated with “out of body” experiences, in which patients see their own bodies from a third-person perspective (Blanke, 2004). This area is also related to evaluating another person's mental perspective and predicting what they might know (i.e., mentalizing; Frith and Frith, 2003; Frith and Frith, 2006). It has been reported that the TPJ is associated with the specific (representational) contents of mental states, such as beliefs (Saxe and Kanwisher, 2003; Saxe and Powell, 2006; Saxe and Wexler, 2005). Damage to the left TPJ causes selective deficits in judging the contents of others' beliefs (Samson et al., 2004). This area is also thought to be involved in intention detection (Frith and Frith, 1999; Winston et al., 2002). The TPJ might play a broad role in social, and even moral, cognition (Greene and Haidt, 2002; Moll et al., 2003). Consistent with these findings, in the present study, the left TPJ was also activated by the M–C comparison. This suggests that the left TPJ might represent both the intentionality and conventionality components of lie judgments. In addition, previous behavioral studies showed that there is an interaction between moral judgment and the concept of lying: modesty or pro-social lies were evaluated to be “less of a lie” than anti-social lies (Lee, 2000; Lee and Ross, 1997). In agreement with this finding, the left TPJ showed a context effect: its lie detection-related activity was more prominent for anti-social lies than for

modesty lies, while there was no difference in accuracy in the two tasks. This finding emphasized the importance of the left TPJ in lie comprehension.

The posterior STS that is included in the TPJ is known to be related to predicting intentions from movement (Grezes et al., 2004; Pelphrey et al., 2003; Saxe et al., 2004). The right posterior STS is activated during explicit judgments about trustworthiness based on viewing faces, and intention detection is a critical component of such a judgment (Winston et al., 2002). Activation of the DLPFC might represent an executive function used to combine predictions based on social norms with inferences about the intent to deceive. Thus, the left TPJ and these fronto-temporal areas might constitute a network involved in the detection of the intent to deceive.

## 5. Conclusion

In summary, a lie judgment consists of both conventionality and intentionality components. Regarding the former, the neural substrates of lie judgments include those involved in impersonal moral judgments, consistent with the notion that a lie judgment is intrinsically a value judgment. Regarding the latter, the intention to deceive is associated with activation of the left dorsolateral prefrontal cortex, the right GTm, and the bilateral TPJ. In the left TPJ, the lie judgment-related activation was more prominent for anti-social lies than for pro-social lies. Thus, the left TPJ might play a key role in the processing of both the conventionality and intentionality components of lie judgments.

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## References

- Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. *Nat. Rev. Neurosci.* 7, 268–277.
- Blanke, O., 2004. Out of body experiences and their neural basis. *BMJ* 329, 1414–1415.
- Bok, S., 1978. *Lying: Moral Choice in Public and Private Life*. Vintage, New York.
- Bond, C.F., Omar, A., Pitre, U., Lashley, B.R., Skaggs, L.M., Kirk, C.T., 1992. Fishy-looking liars: deception judgment from expectancy violation. *J. Pers. Soc. Psychol.* 63, 969–977.
- Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., Frackowiak, R.S., Frith, C.D., 1994. The role of the right hemisphere in the interpretation of figurative aspects of language. A positron emission tomography activation study. *Brain* 117 (Pt 6), 1241–1253.
- Chisholm, R.M., Feehan, T.D., 1977. The intent to deceive. *J. Philos.* 75, 143–159.
- Corradi-Dell'Acqua, C., Ueno, K., Ogawa, A., Cheng, K., Rumiat, R.I., Iriki, A., 2008. Effects of shifting perspective of the self: an fMRI study. *Neuroimage* 40, 1902–1911.
- Dapretto, M., Bookheimer, S.Y., 1999. Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron* 24, 427–432.
- Evans, A.C., Kamber, M., Collins, D.L., MacDonald, D., 1994. An MRI-based probabilistic atlas of neuroanatomy. In: Shorvon, S.D. (Ed.), *Magnetic Resonance Scanning and Epilepsy*. Plenum Press, New York, pp. 263–274.
- Fehr, E., Fischbacher, U., 2004. Social norms and human cooperation. *Trends Cogn. Sci.* 8, 185–190.
- 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.
- Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.D., 1996. Cerebral representation of one's own past: neural networks involved in autobiographical memory. *J. Neurosci.* 16, 4275–4282.
- Fletcher, P.C., Frith, C.D., Baker, S.C., Shallice, T., Frackowiak, R.S., Dolan, R.J., 1995. The mind's eye—precuneus activation in memory-related imagery. *Neuroimage* 2, 195–200.
- Friston, K.J., Ashburner, J., Frith, C.D., Heather, J.D., Frackowiak, R.S.J., 1995a. Spatial registration and normalization of images. *Hum. Brain Mapp.* 2, 165–189.
- Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.B., Frith, C.D., Frackowiak, R.S.J., 1995b. Statistical parametric maps in functional imaging: a general linear approach. *Hum. Brain Mapp.* 2, 189–210.
- 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.
- Frith, C.D., Frith, U., 1999. Interacting minds—a biological basis. *Science* 286, 1692–1695.
- Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. *Philos. Trans. R. Soc. Lond., Ser. B, Biol. Sci.* 358, 459–473.
- Frith, C.D., Frith, U., 2006. How we predict what other people are going to do. *Brain Res.* 1079, 36–46.
- Gabrieli, J.D.E., Desmond, J.E., Demb, J.B., Wagner, A.D., 1996. Functional magnetic resonance imaging of semantic memory processes in the frontal lobes. *Psychol. Sci.* 7, 278–283.
- Gibbs, R.W.J., 1999. Interpreting what speakers say and implicate. *Brain Lang.* 68, 466–485.
- Goel, V., Gold, B., Kapur, S., Houle, S., 1997. The seats of reason? An imaging study of deductive and inductive reasoning. *Neuroreport* 8, 1305–1310.
- Greene, J.D., Haidt, J., 2002. How (and where) does moral judgment work? *Trends Cogn. Sci.* 6, 517–523.
- Greene, J.D., Sommerville, R.B., Nystrom, L.E., Darley, J.M., Cohen, J.D., 2001. An fMRI investigation of emotional engagement in moral judgment. *Science* 293, 2105–2108.
- Grice, H.P., 1980. *Studies in the Way of Words*. Harvard University Press, Cambridge, MA.
- Hawley, P.H., 2003. Strategies of control, aggression, and morality in preschoolers: an evolutionary perspective. *J. Exp. Child Psychol.* 85, 213–235.
- Hogan, R., 1973. Moral conduct and moral character: a psychological perspective. *Psychol. Bull.* 79, 217–232.
- Kapur, S., Rose, R., Liddle, P.F., Zipursky, R.B., Brown, G.M., Stuss, D., Houle, S., Tulving, E., 1994. The role of the left prefrontal cortex in verbal processing: semantic processing or willed action. *Neuroreport* 5, 2193–2196.
- Lee, K., 2000. Lying as doing deceptive things with words: a speech act theoretical perspective. In: Astington, J.W. (Ed.), *Minds in the Making: Essays in Honor of David R. Olson*. Blackwell, Oxford, pp. 177–196.
- Lee, K., Ross, H., 1997. The concept of lying in adolescents and young adults: testing Sweetser's folkloristic model. *Merrill-Palmer Q.* 43, 255–270.
- Maguire, E.A., Mummery, C.J., 1999. Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus* 9, 54–61.
- Maguire, E.A., Frith, C.D., Morris, R.G., 1999. The functional neuroanatomy of comprehension and memory: the importance of prior knowledge. *Brain* 122 (Pt 10), 1839–1850.
- Maguire, E.A., Mummery, C.J., Buchel, C., 2000. Patterns of hippocampal–cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus* 10, 475–482.
- Matsushashi, M., Ikeda, A., Ohara, S., Matsumoto, R., Yamamoto, J., Takayama, M., Satow, T., Begum, T., Usui, K., Nagamine, T., Mikuni, N., Takahashi, J., Miyamoto, S., Fukuyama, H., Shibasaki, H., 2004. Multisensory convergence at human temporo-parietal junction—epicortical recording of evoked responses. *Clin. Neurophysiol.* 115, 1145–1160.
- Moll, J., de Oliveira-Souza, R., Eslinger, P.J., 2003. Morals and the human brain: a working model. *Neuroreport* 14, 299–305.
- Moran, M.A., Mufson, E.J., Mesulam, M.M., 1987. Neural inputs into the temporopolar cortex of the rhesus monkey. *J. Comp. Neurol.* 256, 88–103.
- Noppeney, U., Price, C.J., Duncan, J.S., Koepp, M.J., 2005. Reading skills after left anterior temporal lobe resection: an fMRI study. *Brain* 128, 1377–1385.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Pelphrey, K.A., Singer, J.D., Allison, T., McCarthy, G., 2003. Brain activation evoked by perception of gaze shifts: the influence of context. *Neuropsychologia* 41, 156–170.
- Samson, D., Apperly, I.A., Chiavarino, C., Humphreys, G.W., 2004. Left temporoparietal junction is necessary for representing someone else's belief. *Nat. Neurosci.* 7, 499–500.
- 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. *Psychol. Sci.* 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.
- Saxe, R., Xiao, D.K., Kovacs, G., Perrett, D.I., Kanwisher, N., 2004. A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia* 42, 1435–1446.
- Schank, R.C., Abelson, R.P., 1977. *Scripts, Plans, Goals and Understanding*. Erlbaum, Hillsdale.
- Searle, J.R., 1969. *Speech Acts: An Essay in the Philosophy of Language*. Cambridge University Press, Cambridge.
- Sip, K.E., Poeppel, A., McGregor, W., Frith, C.D., 2007. Detecting deception: the scope and limit. *Trends Cogn. Sci.* 12, 48–53.
- Steele, J.D., Lawrie, S.M., 2004. Segregation of cognitive and emotional function in the prefrontal cortex: a stereotactic meta-analysis. *Neuroimage* 21, 868–875.
- Sweetser, E.E., 1987. The definition of lie: an examination of the folk models underlying a semantic prototype. In: Holland, D. (Ed.), *Cultural Models in Language and Thought*. Cambridge University Press, New York, pp. 43–66.

- Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, New York.
- Uchiyama, H., Seki, A., Kageyama, H., Saito, D.N., Koeda, T., Ohno, K., Sadato, N., 2006. Neural substrates of sarcasm: a functional magnetic-resonance imaging study. *Brain Res.* 1124, 100–110.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., Frackowiak, R.S., 1996. Functional anatomy of a common semantic system for words and pictures. *Nature* 383, 254–256.
- Vandenberghe, R., Nobre, A.C., Price, C.J., 2002. The response of left temporal cortex to sentences. *J. Cogn. Neurosci.* 14, 550–560.
- Wagner, A.D., Desmond, J.E., Demb, J.B., Glover, G.H., Gabrieli, J.D.E., 1997. Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. *J. Cogn. Neurosci.* 9, 714–726.
- Wimmer, H., Perner, J., 1983. Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition* 13 (1), 103–128.
- Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nat. Neurosci.* 5, 277–283.